

# The intrinsic growth rate as a predictor of population viability under climate warming

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## Summary

1. Lately, there has been interest in using the intrinsic growth rate ( $r_m$ ) to predict the effects of climate warming on ectotherm population viability. However, because  $r_m$  is calculated using the Euler-Lotka equation, its reliability in predicting population persistence depends on whether ectotherm populations can achieve a stable age/stage distribution in thermally variable environments. Here, we investigate this issue using a mathematical framework that incorporates mechanistic descriptions of temperature effects on vital rates into a stage-structured population model that realistically captures the temperature-induced variability in developmental delays that characterize ectotherm life cycles.

2. We find that populations experiencing seasonal temperature variation converge to a stage distribution whose intra-annual pattern remains invariant across years. As a result, the mean annual per capita growth rate also remains constant between years. The key insight is the mechanism that allows populations converge to a stationary stage distribution. Temperature effects on the biochemical processes (e.g. enzyme kinetics, hormonal regulation) that underlie life-history traits (reproduction, development and mortality) exhibit well-defined thermodynamical properties (e.g. changes in entropy and enthalpy) that lead to predictable outcomes (e.g. reduction in reaction rates or hormonal action at temperature extremes). As a result, life-history traits exhibit a systematic and predictable response to seasonal temperature variation. This in turn leads to temporally predictable temperature responses of the stage distribution and the per capita growth rate.

3. When climate warming causes an increase in the mean annual temperature and/or the amplitude of seasonal fluctuations, the population model predicts the mean annual per capita growth rate to decline to zero within 100 years when warming is slow relative to the developmental period of the organism (0.03 – 0.05 °C per year) and to become negative, causing population extinction, well before 100 years when warming is fast (e.g. 0.1 °C per year). The Euler-Lotka equation predicts a slower decrease in  $r_m$  when warming is slow and a longer persistence time when warming is fast, with the deviation between the two metrics increasing with increasing developmental period. These results suggest that predictions of ectotherm population viability based on  $r_m$  may be valid only for species with short developmental delays, and even then, only over short time-scales and under slow warming regimes.

**Key-words:** climate warming, development, fecundity, fitness, mortality, stable age/stage distribution, temperature variation

## Introduction

Climate warming is predicted to cause large-scale species extinctions (Walther *et al.* 2002; Root *et al.* 2003; Parmesan 2006; Sinervo, Fausto & Miles 2010). Identifying

which species are most at risk of extinction is therefore a high research priority. The challenge is in developing a metric for estimating population viability that is both empirically measurable and sufficiently general to have broad applicability.

The intrinsic growth rate ( $r_m$ ) is a useful metric for quantifying population persistence because populations cannot recover from low densities unless  $r_m$  is positive.

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Recent studies have used empirical data on the temperature dependence of  $r_m$  to investigate the effects of climate warming on ectotherms (Deutsch *et al.* 2008; Tewksbury, Huey & Deutsch 2008; Huey *et al.* 2009). These studies calculate temperature-induced changes in  $r_m$  based on the changes in diurnal and seasonal temperature regimes experienced by species inhabiting different latitudes. They use these calculations to predict that tropical ectotherms are more at risk of extinction due to climate warming than temperate ectotherms.

Studies that use  $r_m$  to predict population viability use initial values calculated using the Euler-Lotka equation for age-structured population dynamics (Lotka 1907; Lotka & Sharpe 1911), the data for which come from experiments conducted under constant temperatures [e.g. Dreyer & Baumgartner (1996); Medeiros *et al.* (2000, 2003); Morgan, Walters & Aegerter (2001); Dannon *et al.* (2010)]. The Euler-Lotka equation is derived under the assumption of a stable age/stage distribution in a constant environment (Lotka 1907; Lotka & Sharpe 1911; Charlesworth 1980; Roff 1992). Therefore, predictions about how  $r_m$  changes due to climate warming are valid only if species can achieve stable age/stage distributions in the face of perturbations to their thermal environment.

Most ectotherms inhabit environments with diurnal and/or seasonal variation in temperature. Hence, a necessary prerequisite for using  $r_m$  to estimate population viability is to determine whether ectotherm populations can achieve a stable age/stage distribution under the typical regimes of temperature variation they experience in nature. If populations do converge to a stable age/stage distribution under typical temperature variation, we can proceed to investigate how perturbations to the typical thermal environment (e.g. warming) influence age/stage structure. For instance, if warming occurs sufficiently rapid or is sufficiently dynamic (i.e. the process of warming changes over time) that populations cannot achieve a stationary age/stage distribution under the warming regime, we cannot use  $r_m$  to predict the effects of warming. However, the ways in which warming disrupts the age/stage distribution may still be informative. If warming occurs relatively slowly so that populations have sufficient time to adjust to the new temperature regime and achieve a stationary age/stage distribution, we may be able to use  $r_m$  to predict population viability.

Here, we investigate this question using a model that combines mechanistic descriptions of temperature effects on birth, maturation and mortality rates with stage-structured population dynamics. We identify the conditions under which a stationary stage distribution could be achieved under typical (e.g. seasonal) temperature variation and investigate how different scenarios of climate warming (e.g. an increase in the mean annual temperature and/or an increase in the amplitude of temperature fluctuations) influence the stage distribution. We compare  $r_m$  calculated from the Euler-Lotka equation to the per capita growth rate calculated from the population model to

determine the margin of error associated with using  $r_m$  to predict population viability under climate warming.

## Background

Transition matrices of all age-structured populations have the same special form [i.e. the top row gives the fecundity of individuals in each age class, and all other rows contain exactly one element, the age-specific survivorship; (Otto & Day 2007)], which allows us to write its characteristic polynomial as:

$$\sum_{x=1}^n e^{-r_m x} l_x b_x = 1 \quad \text{eqn 1}$$

where  $n$  is the number of age classes,  $l_x$  is the probability that an individual survives to age class  $x$ ,  $b_x$  is the fecundity of an individual in age class  $x$  and  $r_m$  is the intrinsic rate of increase (i.e. per capita change in the population per unit time). Equation (1), typically referred to as the Euler-Lotka equation (Lotka 1907; Lotka & Sharpe 1911), gives the expected lifetime reproductive success of a newborn individual in a population growing at the rate  $r_m$  that has achieved a stable age distribution, that is, the proportion of the population in each age class remains constant over time.

When the number of age classes is large, we can write Equation (1) in its integral form:

$$\int_{\alpha}^{\infty} e^{-r_m x} l_x b_x dx = 1 \quad \text{eqn 2}$$

where  $\alpha$  is the age at sexual maturity.

The Euler-Lotka equation allows us to calculate the intrinsic growth rate ( $r_m$ ) of any population for which cohort life table data are available. It is a useful metric because it allows us to compare different populations of the same species experiencing different environments to determine which environment is more favourable to the species. It is particularly important in determining the ability of a species to recover from low densities, because density-dependent factors such as resource limitation and natural enemies are less important at low densities than the intrinsic ability of the species to achieve a net increase in birth and developmental rates relative to death rates. If environmental conditions are such that  $r_m$  cannot be positive when the species is rare, one would not expect the population to be viable in that environment.

A distinctive attribute of  $r_m$  compared with other measures of population viability is that it incorporates not only survival and reproduction, but also development, and hence the effects of environmental factors on the entire life cycle. Thus, it is a particularly useful metric for assessing the viability of many ectothermic taxa (e.g. invertebrates, fish, amphibians) that have complex life cycles.

Mounting evidence for climate warming has made it necessary to find a metric for predicting population

viability that can apply broadly across ectothermic taxa. Recent studies (Deutsch *et al.* 2008; Tewksbury, Huey & Deutsch 2008; Huey *et al.* 2009) have used  $r_m$  calculated using the Euler-Lotka equation to predict times to extinction under climate warming. However, given that the Euler-Lotka equation is derived under the assumption of a constant environment in which all age classes/life stages grow at the same (exponential) rate and achieve a stable age/stage distribution (Charlesworth 1980; Roff 1992; Stearns 1992; Charnov 1993), the question arises as to whether  $r_m$  is an appropriate measure for estimating population viability in variable environments. This makes it important to investigate the degree to which populations deviate from a stable age/stage distributions in thermally variable environments, and hence the margin of error associated with using  $r_m$  to estimate population viability. If this error is relatively small, we have greater confidence in our predictions of which species are more at risk of extinction due to climate warming.

### Mathematical framework

We develop a stage-structured model of density-independent population dynamics that incorporates variable developmental delays resulting from temperature effects on the maturation rate. We use this model to investigate whether ectotherm populations can attain a stationary stage distribution under (i) typical regimes of seasonal temperature variation and (ii) perturbations to the thermal environment caused by climate warming. [Stationary here means that the statistical parameters, mean and standard deviation, of the process do not change with time Kot (2001).] Gurney, Nisbet & Lawton (1983) and Nisbet & Gurney (1983); Nisbet (1997) were the first to rigorously develop stage-structured population models with variable developmental delays. Our new contribution is to develop a framework that incorporates mechanistic descriptions (derived from first principles of thermodynamics; see below) of life-history trait responses to temperature into stage-structured models that realistically capture the developmental delays that characterize ectotherm life histories.

We begin with the simplest possible representation of the ectotherm life cycle: a two-stage model of juveniles and adults:

$$\begin{aligned}\frac{dJ(t)}{dt} &= b(T(t))A(t) - M_J(t) - d_J(T(t))J(t) \\ \frac{dA(t)}{dt} &= M_J(t) - d_A(T(t))A(t) \\ M_J(t) &= b(T(t - \tau(t)))A(t - \tau(t))S(t) \frac{m_J(T(t))}{m_J(T(t - \tau(t)))} \\ \frac{dS(t)}{dt} &= S(t) \left[ \frac{m_J(T(t))d_J(T(t - \tau(t)))}{m_J(T(t - \tau(t)))} - d_J(T(t)) \right] \\ \frac{d\tau(t)}{dt} &= 1 - \frac{m_J(T(t))}{m_J(T(t - \tau(t)))}\end{aligned}\quad \text{eqn 3}$$

where  $b(T(t))$ ,  $d_J(T(t))$  and  $d_A(T(t))$  are, respectively, the per capita birth rate, juvenile mortality rate and the adult mortality rate. These rates are both temperature- and time dependent to allow for seasonal or other forms of temperature variation that affects population dynamics. The quantity  $M_J(t)$  is the per capita maturation rate, which is given by the recruitment rate into the juvenile stage  $\tau(t)$  time units ago multiplied by the fraction of juveniles that survive to complete development ( $S(t)$ ) (Nisbet & Gurney 1983; Nisbet 1997; Murdoch, Briggs & Nisbet 2003). The function  $m_J(T(t))$  depicts variation in the juvenile maturation rate with time due to its dependence on the environmental temperature ( $m_J = \frac{1}{\tau}$  in a constant environment).

### TEMPERATURE DEPENDENCE OF VITAL RATES

The organismal-level temperature responses of reproduction, development and mortality are determined by temperature effects on the underlying biochemical processes (e.g. reaction kinetics, hormonal regulation; Johnson & Lewin (1946); Sharpe & DeMichele (1977); Schoolfield, Sharpe & Magnuson (1981); Nijhout (1994); Van der Have & de Jong (1996); Van der Have (2002); Ratkowsky, Olley & Ross (2005); Kingsolver (2009); Kingsolver *et al.* (2011)). Temperature affects these processes in a predictable manner. For instance, temperature effects on biochemical rate processes (e.g. reaction kinetics and enzyme inactivation) give rise to temperature responses at the organismal level that are monotonic or left-skewed. Per capita mortality rate of all ectotherms increases monotonically with increasing temperature (see references in Gillooly *et al.* (2002)) and is well described by the Boltzmann–Arrhenius function for reaction kinetics (Van der Have & de Jong 1996; Gillooly *et al.* 2002; Savage *et al.* 2004):

$$d(T) = d_{T_R} e^{A_d \left( \frac{1}{T_R} - \frac{1}{T} \right)} \quad \text{eqn 4}$$

where  $d(T)$  is the mortality rate at temperature  $T$  (in K),  $d_{T_R}$  is the mortality rate at a reference temperature (in K, typically between 293–303 K, the commonest being 297–298 K; Sharpe & DeMichele (1977); Schoolfield, Sharpe & Magnuson (1981)) and  $A_d$  is the Arrhenius constant, which quantifies the temperature sensitivity of mortality, that is, how fast it increases with increasing temperature.

Ectotherm developmental rates exhibit a left-skewed temperature response (Sharpe & DeMichele 1977; Schoolfield, Sharpe & Magnuson 1981; Van der Have & de Jong 1996; Van der Have 2002; Kingsolver 2009; Kingsolver *et al.* 2011) that results from the reduction in reaction rates at low and high temperature extremes due to enzyme inactivation. This response is well described by a thermodynamic rate process model (Sharpe & DeMichele 1977; Schoolfield, Sharpe & Magnuson 1981; Ratkowsky, Olley & Ross 2005):

$$m(T) = \frac{\frac{m_{T_R} T}{T_R} e^{\frac{A_m}{T_R} \left( \frac{1}{T} - \frac{1}{T_R} \right)}}{1 + e^{\frac{A_L}{T_{L/2}} \left( \frac{1}{T} - \frac{1}{T_{L/2}} \right)} + e^{\frac{A_H}{T_{H/2}} \left( \frac{1}{T} - \frac{1}{T_{H/2}} \right)}} \quad \text{eqn 5}$$

where  $m_{T_R}$  is the maturation rate at the reference temperature  $T_R$  at which the enzyme is 100% active,  $A_m$  (enthalpy of activation divided by the universal gas constant  $R$ ) quantifies temperature sensitivity,  $T_{L/2}$  and  $T_{H/2}$  are, respectively, the low and high temperatures at which the enzyme is 50% active, and  $A_L$  and  $A_H$  are the enthalpy changes associated with low and high temperature enzyme inactivation divided by  $R$  (Johnson & Lewin 1946; Schoolfield, Sharpe & Magnuson 1981; Sharpe & DeMichele 1977; Van der Have & de Jong 1996; Van der Have 2002; Ratkowsky, Olley & Ross 2005). The numerator gives the exponential increase in the maturation rate within the temperature range that the enzyme is active, and the denominator gives the reduction in the maturation at low and high temperature extremes due to the enzyme inactivation. If the typical temperature range experienced by a species is above the low temperature threshold and below the high temperature threshold for enzyme inactivation, as appears to be the case with a large number of ectotherm species (Trudgill, Honek & van Straalen 2005; Bowler & Terblanche 2008; Dixon *et al.* 2009), maturation rate will increase monotonically with temperature and can be described by the Boltzmann–Arrhenius function (Equation (4)).

Temperature effects on biochemical regulatory processes [e.g. neural and hormonal regulation; Hochachka & Somero (2002); Long & Fee (2008); Nijhout (1994)] involve negative feedback/ rate processes on the left and right hand sides push the system towards an intermediate optimum. These effects result in a unimodal and symmetrical temperature response at the organismal level that is well described by a Gaussian function:

$$b(T) = b_{T_{\text{opt}}} e^{-\frac{(T - T_{\text{opt}})^2}{2s_b^2}} \quad \text{eqn 6}$$

where  $T_{\text{opt}}$  is the temperature (in  $K$ ) at which the trait value is maximized ( $b_{T_{\text{opt}}}$ ) and  $s_b$  gives the temperature range over which negative feedback processes can push the system towards the optimum. Most reproductive traits (e.g. mating frequency, fecundity) exhibit this type of temperature response (e.g. Dreyer & Baumgartner (1996); Carriere & Boivin (1997); Morgan, Walters & Aegerter (2001); Jandricic *et al.* (2010); Hou & Weng (2010); Dannon *et al.* (2010); Dell, Pawar & Savage (2011); Amarasekare & Savage (2012), P. Amarasekare, unpublished data).

Data from a large number of studies from invertebrates to reptiles (see references in Huey & Berrigan (2001); Gillooly *et al.* (2002); Savage *et al.* (2004); Frazier, Huey & Berrigan (2006); Kingsolver (2009); Dell, Pawar & Savage (2011); Kingsolver *et al.* (2011); Amarasekare &

Savage (2012)) show that temperature responses of mortality, development and reproduction follow the monotonic, left-skewed and symmetrical unimodal patterns predicted by theory (Johnson & Lewin 1946; Sharpe & DeMichele 1977; Schoolfield, Sharpe & Magnuson 1981; Van der Have & de Jong 1996; Van der Have 2002; Ratkowsky, Olley & Ross 2005).

#### STAGE-STRUCTURED POPULATION DYNAMICS IN A CONSTANT THERMAL ENVIRONMENT

When the environmental temperature is constant, a population experiencing density-independent population dynamics [Equation (3)] will attain a long-run per capita growth rate that depends on the environmental temperature:

$$r(T) = -d_A(T) + \frac{1}{\tau(T)} W\left(b(T)\tau(T)e^{(d_A(T) - d_J(T))\tau(T)}\right) \quad \text{eqn 7}$$

and a ratio of juveniles and adults that also depends on the environmental temperature:

$$\frac{J}{A}(T) = \frac{b(T)(1 - e^{-(r(T) + d_J(T))\tau(T)})}{r(T) + d_A(T)}. \quad \text{eqn 8}$$

Here,  $W$  is the principal (positive) branch of the Lambert  $W$  function or the product logarithm (Corless *et al.* 1996) and the functions

$$b(T), \tau(T) = \frac{1}{m(T)}, d_X(T) (X = J, A)$$

depict the temperature responses of reproduction [Equation (6)], development [Equation (5)] and mortality [Equation (4)] as defined above.

The key point is that we can predict the long-run growth rate and the stable stage distribution achieved under a given temperature for any species for which data on the temperature responses of life-history traits are available.

#### STAGE-STRUCTURED POPULATION DYNAMICS IN SEASONALLY VARYING ENVIRONMENTS

When population growth is density independent and there are no feedback processes (e.g. density dependence) that cause population cycles, seasonal temperature variation is the only source that causes periodicity in population dynamics. Hence, life-history trait responses to seasonal temperature variation are likely to lead to a per capita growth rate and a stage distribution that vary seasonally with a period of one year. If this seasonal pattern converges to a stationary distribution, one would expect the mean annual growth rate and  $\frac{J}{A}$  to remain constant across years.

We incorporate seasonal temperature variation into the model [Equation (3)] in the following way. Let  $T = s(t)$  where  $T$  is the temperature in  $K$ ,  $t$  is time in days and  $s(t)$  depicts seasonal temperature variation. Then,



$$s(t) = M_T - A_T \cos\left(\frac{2\pi t}{\text{year}}\right) \quad \text{eqn 9}$$

where  $M_T$  is the mean annual temperature,  $A_T$  is the amplitude of seasonal temperature fluctuations and year = 365. The cosine function ensures that the daily temperature fluctuates around the mean temperature with an amplitude given by  $A_T$  and a period of one year. Seasonal variation affects life-history traits in the following manner. Because  $T = s(t)$ ,  $k(T) = k(s(t))$  where  $k$  is the trait of interest (e.g.  $k = b, m_J, d_J, d_A$ ). In this way, when the temperature changes over time, the value of the trait changes accordingly. For instance, seasonal variation in temperature causes corresponding seasonal changes in the life-history traits (Fig. 2a,b,c). These changes in turn affect juvenile and adult abundances, the per capita growth rate and the juvenile-to-adult ratio.

To test whether the juvenile-to-adult ratio converges to a stationary distribution, we numerically integrated the population model (Equation (3)) for 100 years. In order to examine the intra-annual variation in the growth rate, we calculated the daily per capita growth rate of the adult population as  $\ln\left(\frac{A(t)}{A(t-1)}\right)$  where  $t$  is measured in days.

In our analyses, we used parameter values for life-history traits that are realistic for insect species. Since temperature responses are conserved across taxa, thermodynamical constraints dictate that temperature sensitivity parameters such as Arrhenius constants take only a narrow range of values. Indeed, the theory on metabolic scaling (Gillooly *et al.* 2001, 2002; Brown *et al.* 2004; Savage *et al.* 2004) suggests that values of these temperature sensitivity parameters should be largely invariant across taxa. We used parameter values for seasonal temperature variation that represent Mediterranean or temperate environments. We did so because greater seasonal fluctuations in these environments allow for a greater portion of the temperature response functions to be expressed, thus allowing us to obtain a more complete understanding of how seasonal variation influences population dynamics. We use a time-scale of 100 years both because it provides a basis for comparison with previous studies that have used the Euler-Lotka framework to predict climate warming effects on population viability [e.g. Deutsch *et al.* (2008)] and because it provides sufficient time for a given species, particularly longer-lived ones, to attain a stationary age/stage distribution. Although we have not used parameter values specific to any particular species or seasonal environment, the model we have developed is general and can be parameterized with data for any ectotherm species inhabiting any habitat type or latitude.

#### STAGE-STRUCTURED POPULATION DYNAMICS UNDER CLIMATE WARMING

Climate warming is expected to manifest as an increase in the mean annual temperature and the amplitude of seasonal fluctuations (IPCC 2007). We incorporate climate

warming as a linear increase in the mean and amplitude, that is,  $M_T(t) = M_S + \gamma t$  and  $A_T(t) = A_S + \gamma t$  where  $M_S$  and  $A_S$  are the mean annual temperature and amplitude of fluctuations under typical seasonal variation. The parameter  $\gamma$  is the rate at which the mean and amplitude increase over time, that is,  $\gamma = \frac{1}{n \text{ year}}$  is the per-day increase in the temperature where  $n$  is the number of years it takes for a 1 °C increase in temperature. Now,  $T = W(t)$  where

$$W(t) = M_T(t) - A_T(t) \cos\left(\frac{2\pi t}{\text{year}}\right). \quad \text{eqn 10}$$

Effects of warming on life-history traits are likely to become compounded over time. One would expect that there to be a characteristic time-scale over which the cumulative warming effect is sufficiently small that the stage distribution remains approximately constant. One would also expect that this time-scale to depend on the developmental period of the organism. Species with short developmental periods relative to the time-scale of warming (e.g. the time it takes for 1 °C increase in the mean annual temperature or amplitude of seasonal fluctuations) are likely to exhibit longer time periods during which the stage distribution remains constant.

With these expectations in mind, we consider three scenarios of climate warming: 0.03 °C per year, 0.05 °C per year and 0.1 °C per year (3 °C, 5 °C and 10 °C increase in 100 years). For each scenario, we quantify the intra- and inter-annual variation in the stage distribution and the per capita growth rate over a time period of 100 years.

To determine the time-scale over which the stage distribution remains invariant, we calculated the % deviation of the mean annual juvenile-to-adult ratio ( $\frac{J}{A}$ ) from that observed under typical seasonal variation, that is,  $\frac{(\frac{J}{A})_{w_i} - (\frac{J}{A})_{s_i}}{(\frac{J}{A})_{s_i}}$ , where  $(\frac{J}{A})_{s_i}$  is the mean annual  $\frac{J}{A}$  in year  $i$  under typical seasonal variation and  $(\frac{J}{A})_{w_i}$  is the mean annual  $\frac{J}{A}$  in year  $i$  under a given warming regime.

We also investigated the effect of the developmental period on the warming response. Since the developmental delay is itself a function of temperature, we considered a range of delays ( $\tau_{T_R} = \frac{1}{m_{T_R}}$ ; Equation (5)) at 24 °C: 30, 60, 120, 180 and 365 days.

It should be noted that the warming regime depicted by Equation (10) is meant to be illustrative rather than to depict an actual climate change scenario. One could in principle incorporate any regime of climate warming into any pattern of ambient seasonal variation. We use a linear increase in temperature because it is the simplest scenario to envision. The model could easily be adapted to investigate nonlinear forms of climate warming.

#### COMPARISON BETWEEN GROWTH RATES CALCULATED FROM THE EULER-LOTKA EQUATION AND THE STAGE-STRUCTURED POPULATION MODEL

If populations do not attain a stationary stage distribution under climate warming,  $r_m$  calculated from the

Euler-Lotka equation may not provide an accurate estimate of population persistence under warming. It is therefore important to determine the extent to which predictions based on  $r_m$  deviate from predictions based on the per capita growth rate calculated from the stage-structured population model. In previous work, we (Amarasekare & Savage 2012) derived a mechanistic description of the temperature response of  $r_m$  based on the temperature responses of reproduction, development and mortality:

$$r_m(T) = -d(T) + \frac{1}{\alpha(T)} W\left(m_{\alpha_{\text{peak}}}(T)\alpha(T)e^{(d(T)-\bar{d}(T))\alpha(T)}\right). \quad \text{eqn 11}$$

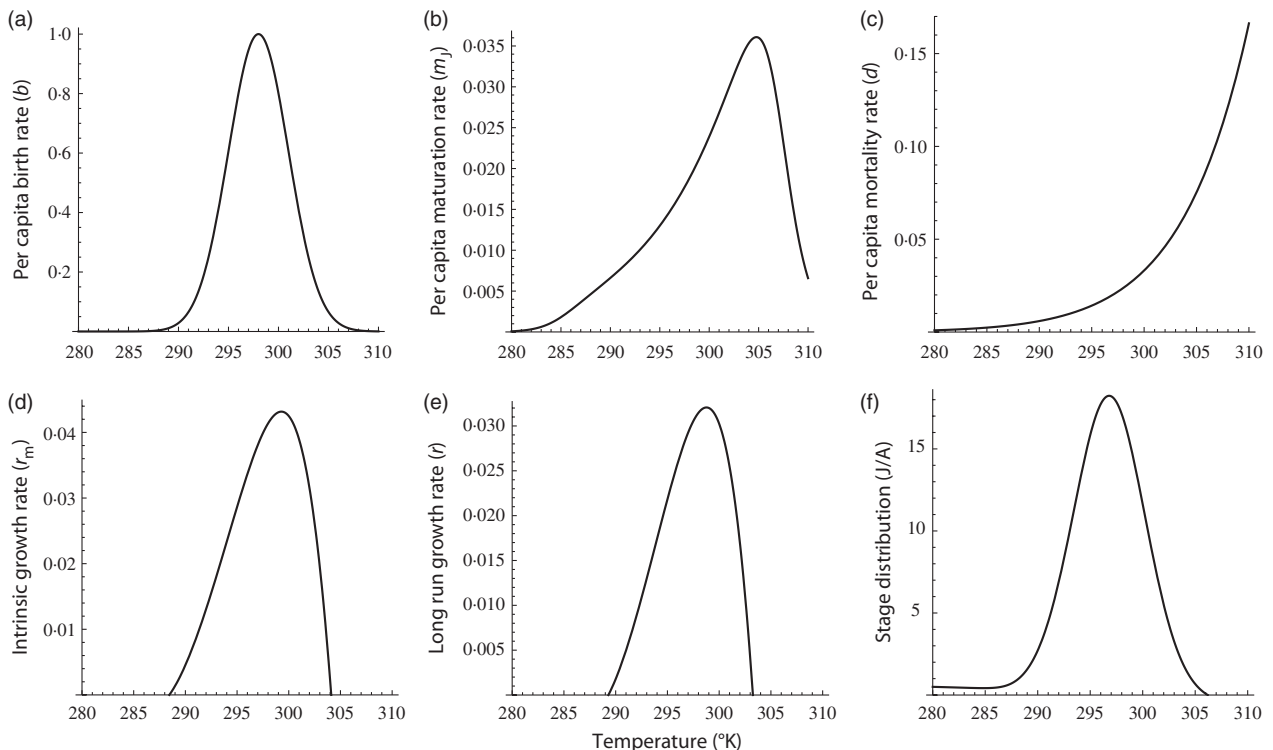
The functions  $m_{\alpha_{\text{peak}}}(T)$ ,  $\bar{d}(T)$ ,  $d(T)$  and  $\alpha(T)$  are, respectively, the empirically measured temperature response functions for maximum per capita fecundity, average mortality during the juvenile stage, adult mortality and the age at maturity. The temperature response of average fecundity provides a reasonable approximation for the temperature response for maximum fecundity when data on the latter are unavailable [see Amarasekare & Savage (2012) for details].

We simulated Equation (11) under the three warming scenarios described above for a period of 100 years and calculated the mean annual  $r_m$  for each year. We calculated the % deviation of mean annual  $r_m$  from the mean annual growth rate from the population model (Equation (3)), i.e.,  $\frac{\bar{r}(t) - \bar{r}_m(t)}{\bar{r}(t)}$ , where  $\bar{r}(t)_i$  is the mean annual per capita growth rate in year  $i$  and  $\bar{r}_m(t)_i$  is the mean annual  $r_m$  in year  $i$ .

## Results

### PER CAPITA GROWTH RATE AND THE STAGE DISTRIBUTION UNDER CONSTANT TEMPERATURES

Figure 1 depicts the temperature responses of the long-run per capita growth rate ( $r(T)$ ) and the stable stage distribution  $\frac{1}{A}(T)$  calculated from Equations (7) and (8) when the environmental temperature is constant. The long-run growth rate shows the characteristic left-skewed pattern exhibited by the temperature response of  $r_m$  calculated from the Euler-Lotka equation (Huey & Berrigan (2001); Frazier, Huey & Berrigan (2006); Deutsch *et al.* (2008); Kingsolver (2009); Amarasekare & Savage (2012)).



**Fig. 1.** Temperature responses of life-history traits and per capita growth rates in a constant thermal environment. The top row depicts the temperature responses of birth, maturation and mortality rates. The bottom row depicts the intrinsic growth rate  $r_m(T)$  calculated using the Euler-Lotka equation (Equation (11, panel (d)) and the long-run per capita growth rate  $r(T)$  [Equation (17, panel (e))] and the stage distribution  $\frac{1}{A}(T)$  [Equation (8), panel (f)] calculated from the stage-structured population model. Parameter values are as follows:  $b_{T_{\text{opt}}} = 1.0$ ,  $T_{\text{opt}_b} = 298\text{K}$ ,  $s_b = 3.0$  for the birth rate,  $T_R = 297\text{K}$ ,  $m_{J_{T_R}} = \frac{1}{60}$  ( $\tau = 60$  days at  $297\text{K}$ ),  $A_m = 10500$  for the maturation rate,  $d_{J_{T_R}} = 0.02$ ,  $A_{d_j} = 12000$  for the juvenile mortality rate and  $d_{A_{T_R}} = 0.02$ ,  $A_d = 15000$  for the adult mortality rate. Note that the Boltzmann–Arrhenius function [Equation (4)] was used to describe the temperature response of development rather than the left-skewed temperature function [Equation (5)] because it allowed us to obtain analytical results for the per capita growth rate and the stable stage distribution.

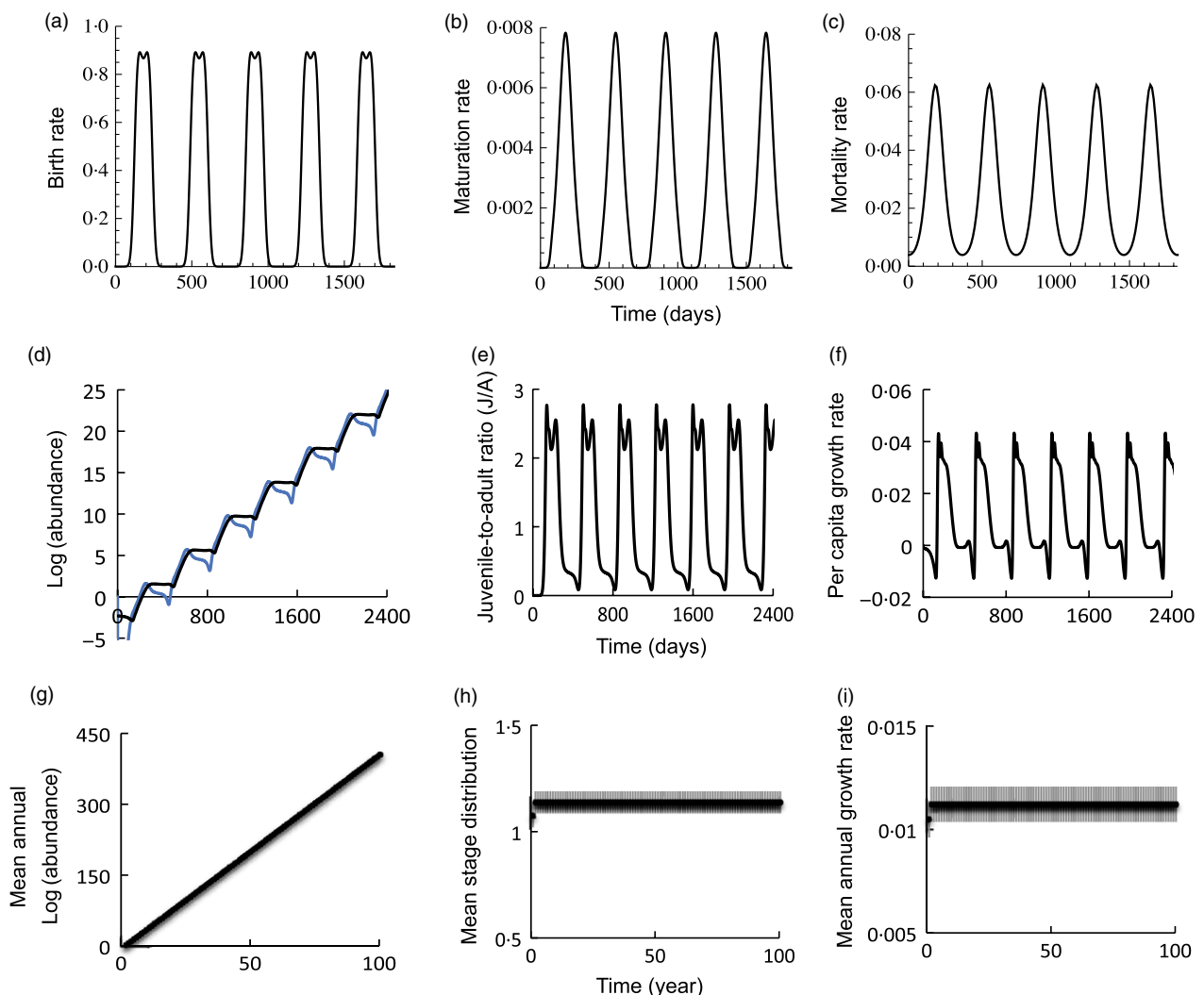
This is to be expected given that both models have their origins in the McKendrick–von Foerster equation for age-structured population dynamics (Gurney, Nisbet & Lawton 1983; Kot 2001).

#### PER CAPITA GROWTH RATE AND THE STAGE DISTRIBUTION IN SEASONALLY VARYING ENVIRONMENTS

When there is seasonal variation in the environmental temperature,  $\frac{J}{A}$  achieves a stationary distribution relatively rapidly (within one year for a species with a developmental period of 60 days), as does the daily per capita growth rate (Fig. 2). As a consequence, the mean annual per cap-

ita growth rate and  $\frac{J}{A}$  remain constant across years (Fig. 2i and j). The rate of convergence to a stationary stage distribution depends on the relative magnitudes of birth, maturation and death rates. Convergence is faster if juvenile and adult mortality rates are low relative to birth and maturation rates.

Because population growth is exponential, it is the relative rather than absolute values of birth and death rates that influence population dynamics. The greater is the difference between birth and death rates, the higher the per capita growth rate and hence the increase in abundance (Appendix S1, Fig. S1.1, Supporting information). The key parameter for population viability is the maturation rate. Even when the birth rate exceeds the death rate, the



**Fig. 2.** Effects of seasonal temperature variation on life-history traits, abundance, stage distribution and the per capita growth rate. The top row depicts seasonal variation in birth [panel (a)], maturation [panel (b)] and mortality [panel (c)] rates. The middle row depicts seasonal variation in juvenile and adult abundance [panel (d)], juvenile-to-adult ratio [ $\frac{J}{A}$ ; panel (e)] and the daily per capita growth rate [panel (f)]. The bottom row depicts the mean annual abundance of juveniles (blue) and adults [black; panel (g)], mean annual  $\frac{J}{A}$  [panel (h)] and the mean annual per capita growth rate [panel (i)]. Note that the error bars (SE) around each point depict the magnitude of intra-annual (seasonal) variation in each year. Numerical simulations that yielded these results used the left-skewed temperature function for development (Equation (5) with  $T_{L/2} = 285^\circ\text{K}$ ,  $A_L = -50\,000$ ,  $T_{H/2} = 307^\circ\text{K}$ ,  $A_H = 75\,000$ ). Other parameter values are as in Fig. 1.

per capita growth rate and hence abundance can be low if the developmental delay is sufficiently large that recruitment of new adults is low relative to losses due to mortality. If the maturation rate is sufficiently low (or equivalently, the developmental delay is sufficiently long) that the recruitment of new adults into the population falls below losses due to mortality, the population may go extinct (Fig. S1.2, Supporting information).

#### THE MECHANISMS BY WHICH A STATIONARY STAGE DISTRIBUTION IS ACHIEVED UNDER SEASONAL TEMPERATURE VARIATION

The above results raise the question of how a population can achieve a stationary stage distribution when the environmental temperature varies seasonally. The answer can be arrived via the following line of reasoning.

1. When population growth is density dependent, the mean annual stage structure and per capita growth rate will be constant across years, provided two conditions are met: First, a species should experience a predictably varying thermal environment (e.g. seasonal variation) such that the properties that characterize environmental variability (e.g. mean annual temperature and the amplitude of seasonal fluctuations) remain invariant across years. Second, the species' life-history traits should exhibit a predictable response to temperature variation, the qualitative nature of which (e.g. monotonic, unimodal) does not change over time.
2. Temperature responses of life-history traits that are observed at the phenotypic level constitute reaction norms [the range of phenotypes exhibited by a given genotype in response to environmental variation; Roff (1992)] that result from temperature effects on the underlying biochemical processes (e.g. reaction kinetics, hormonal regulation). Because the mechanisms by which temperature affects these biochemical processes follow basic rules of thermodynamics, the observed reaction norms exhibit predictable qualitative patterns (e.g. monotonic, unimodal) that are conserved within and between taxa. If the nature of temperature variation remains constant over time, there will be no selection pressure for reaction norms to evolve to a different form, and the same portion of the reaction norm (i.e. the range of trait values expressed within the temperature range experienced by the species) will continue to be expressed. For instance, in a typical seasonal environment where the mean annual temperature and the amplitude of seasonal fluctuations remain constant over time, birth, maturation and mortality rates will exhibit intra-annual patterns that are repeated across years (Fig. 2a, b, c).
3. When population growth is exponential, there is no inherent periodicity in the population dynamics. The only source of periodicity is seasonal variation. As a

result, vital rates will vary over time with a period of one year (Fig. 2a, b, c). Provided the nature of seasonal variation (mean and amplitude) remains constant over time, the pattern of intra-annual variation in vital rates will be invariant over time. As a result, juvenile-to-adult ratio ( $\frac{J}{A}$ ) and the per capita growth rate, when averaged over the year, will remain constant over time (Fig. 2h and i).

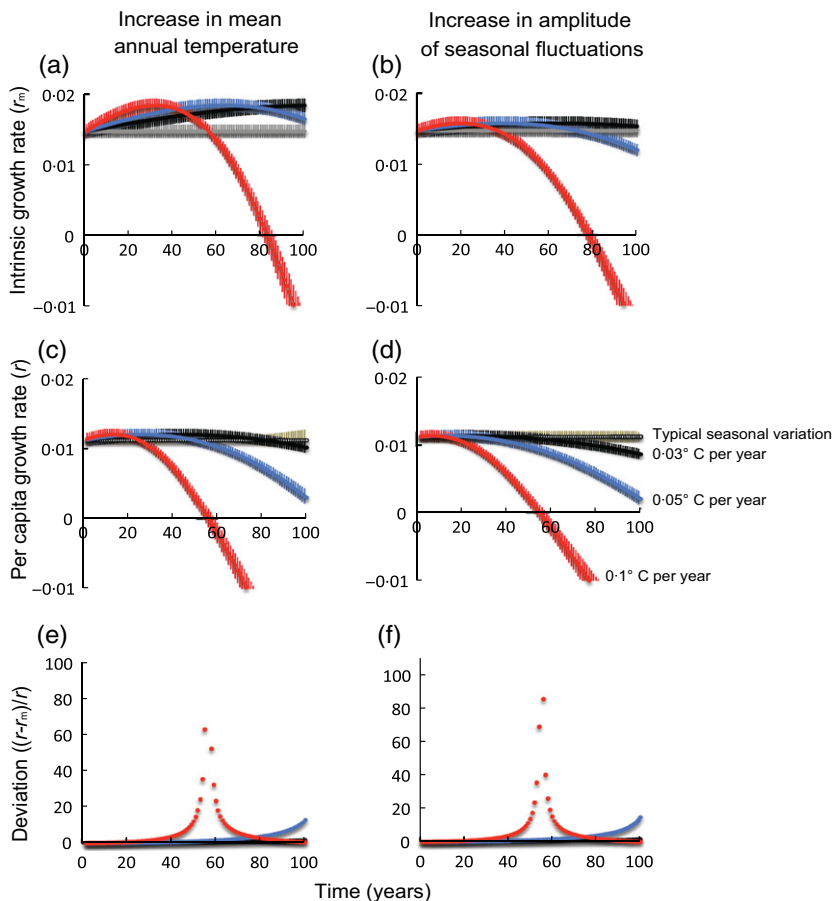
There is strong theoretical and empirical evidence that the mechanisms by which temperature affects the biochemical processes underlying life-history traits are conserved across ectothermic taxa (Sharpe & DeMichele 1977; Schoolfield, Sharpe & Magnuson 1981; Van der Have & de Jong 1996; Van der Have 2002; Ratkowsky, Olley & Ross 2005; Kingsolver 2009; Kingsolver *et al.* 2011). Indeed, the qualitative nature of the temperature responses of reproduction, development and mortality is similar across species of widely different taxonomic origins (Huey & Berrigan 2001; Gillooly *et al.* 2002; Savage *et al.* 2004; Dell, Pawar & Savage 2011; Amarasekare & Savage 2012). Hence, the above argument should apply to any ectotherm species inhabiting a predictably varying thermal environment with constant periodicity.

It follows that if there are perturbations such as climate warming that cause the pattern of seasonal variation to change over time (i.e. due to an increase in the mean annual temperature and/or amplitude of seasonal fluctuations), life-history traits' response to temperature should also change over time. In this case, mean annual  $\frac{J}{A}$  and the per capita growth rate will no longer be constant over time.

#### COMPARISON BETWEEN THE INTRINSIC GROWTH RATE FROM THE EULER-LOTKA EQUATION AND THE PER CAPITA GROWTH RATE FROM THE POPULATION MODEL

Under typical seasonal variation, both measures of the growth rate remain constant over time, for the reasons described above. When warming is slow relative to the developmental period (0.03 °C per year), Euler-Lotka equation predicts an increase in  $r_m$  above that observed under typical seasonal variation, while the population model predicts a slow decline of the per capita growth rate (Fig. 3). When warming is intermediate (0.05 °C per year), the Euler-Lotka equation predicts a much slower decline in the growth rate than the population model. When warming is fast relative to the developmental period (0.1 °C per year), both measures predict extinction within 100 years, but the intrinsic growth rate remains positive over a much longer period than the per capita growth rate (Fig. 3). Thus, the Euler-Lotka equation overestimates both the initial increase in population growth when warming is slow and the time to extinction when warming is rapid. This is likely due to the fact that the Euler-Lotka framework considers the stage distribution





**Fig. 3.** Comparison between the mean annual intrinsic growth rate ( $r_m$ ) calculated from the Euler-Lotka equation [Equation (11)] and the mean annual per capita growth rate calculated from the stage-structured population model [Equation (3)] when warming involves an increase in the mean annual temperature [panels (a), (c) (e)] and the amplitude of seasonal fluctuations [panels (b), (d), (f)]. In each panel, grey, black, blue and red curves correspond, respectively, to typical seasonal variation, 0.03°, 0.05° and 0.1 °C increase in temperature per year. Error bars (SE) around each point depict the magnitude of intra-annual (seasonal) variation in each year. Panels (e) and (f) depict the % deviation between the mean annual intrinsic growth rate and the per capita growth rate. Note that when warming is fast relative to the developmental period, the deviation is highest at the point in time when the population model predicts extinction (negative mean growth rate) and the Euler-Lotka equation predicts persistence (positive mean  $r_m$ ). Parameter values are as in Figs 1 and 2.

to be constant over time, while the population model accommodates interannual variation in the stage distribution. To better understand the nature of this deviation and to quantify it, we use the population model to examine how warming affects the stage distribution and the growth rate.

#### GROWTH RATE AND THE STAGE DISTRIBUTION UNDER CLIMATE WARMING

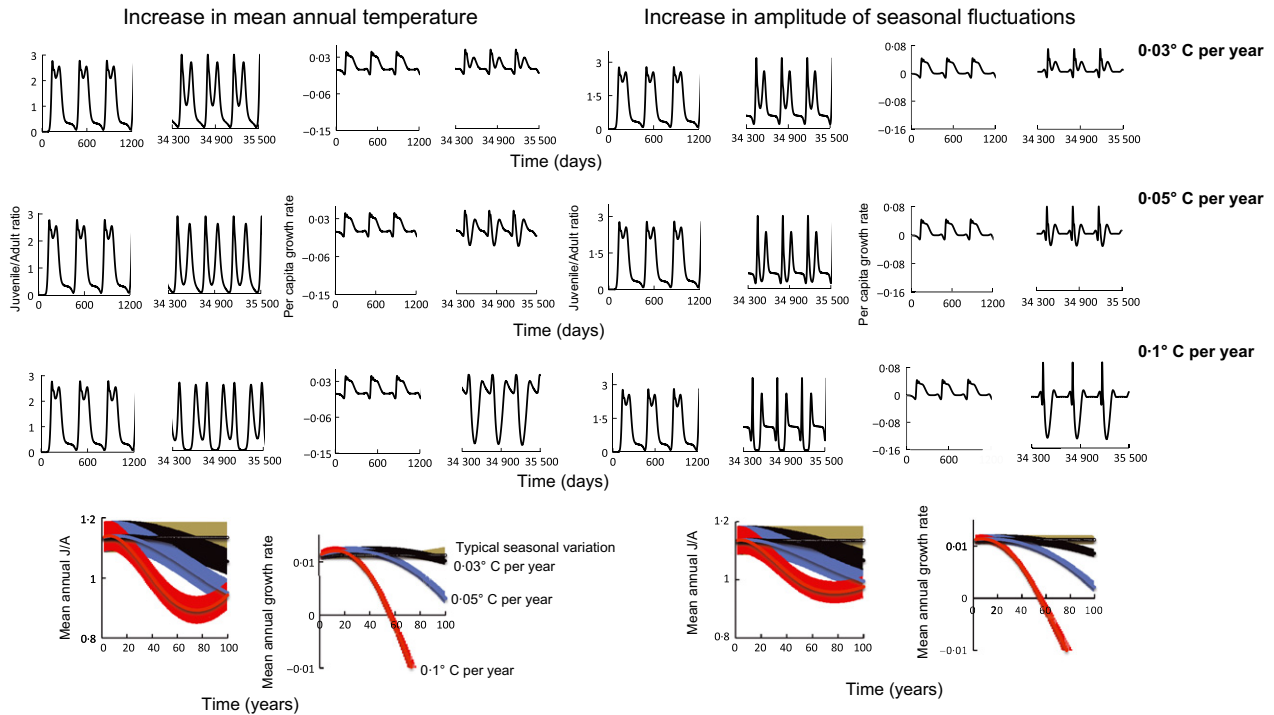
##### General results

When the environmental temperature increases over time, mean annual  $\frac{J}{A}$  remains constant initially, but starts to decline as warming proceeds. The mean annual per capita growth rate increases slightly during the period that  $\frac{J}{A}$  remains constant but declines thereafter. These patterns emerge both when warming involves an increase in the mean annual temperature and an increase in the amplitude of seasonal fluctuations (Fig. 4). The reason why mean annual  $\frac{J}{A}$  declines over time is because the responses of life-history traits to warming causes a reduction in juvenile recruitment. Under ambient seasonal variation,  $\frac{J}{A}$  remains high except during winter because reproduction and development are limited mostly by low temperature extremes (Fig. 2). As warming proceeds,  $\frac{J}{A}$  starts to

decline during summer because high temperatures reduce both adult reproduction and juvenile development (recall that both these traits exhibit unimodal temperature responses with lower performance at both low and high temperatures). If summer temperatures become sufficiently high that reproduction and development cease altogether, juvenile recruitment will approach zero. The reduction in juvenile recruitment due to warming in turn causes a reduction in the per capita growth rate of the adult population (Fig. 4).

##### Effects of warming rate

The rate of warming has a strong effect on both the length of time during which mean annual  $\frac{J}{A}$  remains constant and the magnitude of the decline in the mean annual per capita growth rate (Table 1). When warming involves a 0.03 °C increase in the mean temperature per year, the decline in the mean annual growth rate is relatively small (Table 1). As the rate of warming increases, the decline in the mean growth rate also increases (Table 1). When warming involves 0.1 °C increase per year, the growth rate declines rapidly and becomes negative within 60 years (Table 1, Fig. 4). This is because juvenile recruitment is effectively zero during the hottest months of the summer during which juvenile and adult mortality is high.



**Fig. 4.** Effects of climate warming manifested as an increase in the (i) mean annual temperature and (ii) amplitude of seasonal temperature fluctuations on the stage distribution and the per capita growth rate. The first three rows depict the effects of the three warming regimes ( $0.03^{\circ}\text{C}$  per year,  $0.05^{\circ}\text{C}$  per year and  $0.1^{\circ}\text{C}$  per year) on the stage distribution and the per capita growth rate. The last row depicts the mean annual  $\frac{J}{A}$  mean annual per capita growth rate under the three warming regimes. In these four panels, the color scheme is as in Fig. 3 and error bars (SE) around each point depict the magnitude of intra-annual (seasonal) variation in each year. Parameter values are as in Figs 1 and 2.

**Table 1.** Effects of climate warming on the stage distribution and the per capita growth rate

Warming rate	Type of warming	Change in Juvenile -to-Adult ratio ( $\frac{J}{A}$ ) <sup>a</sup>	Per capita growth rate <sup>a</sup>
$0.03^{\circ}\text{C year}^{-1}$	Mean	-2.3%	-7.94%
	Amplitude	-1.7%	-10.35%
$0.05^{\circ}\text{C year}^{-1}$	Mean	-3.6%	-51.47%
	Amplitude	-2.4%	-58.5%
$0.10^{\circ}\text{C year}^{-1}$	Mean	-7.1%	-84.1%
	Amplitude	-4.6%	-92.4%

<sup>a</sup> Changes in  $\frac{J}{A}$  and the per capita growth rate are calculated for last 15 year period before the growth rate becomes negative.

Importantly, the decline in the growth rate is greater when warming involves an increase in the amplitude of seasonal fluctuations rather than an increase in the mean annual temperature (Table 1; Fig. 4). This is because an increase in the mean temperature causes a greater increase in winter temperatures than an increase in fluctuations and hence a smaller decline in the winter growth rate. When warming involves an increase in seasonal fluctuations, the cumulative effect of reduction in mean  $\frac{J}{A}$  during both winter and summer causes the per capita growth rate to become negative during summer and to approach zero during winter. As a result, the decline in the mean growth rate is greater than when warming involves an increase in the mean temperature (Table 1, Fig. 4).

The key point to appreciate is that under warming, populations can converge to a stationary stage distribution in the short term, but the seasonal pattern of the distribution changes as warming proceeds. However, warming-induced variation in  $\frac{J}{A}$  and the per capita growth rate occur in a predictable manner that is informative about how warming affects population dynamics. For instance, warming causes a qualitative change in  $\frac{J}{A}$  from a seasonal pattern with a large decline in the winter and a much smaller decline in the summer (Fig. 2) to one with large declines in both winter and summer (Fig. 4). The net result is an increase in both the amplitude and frequency of fluctuations in  $\frac{J}{A}$ . Because the reduction in juvenile recruitment due to warming in turn reduces the per

capita growth rate of the adult population, the seasonal pattern of the per capita growth rate also undergoes a qualitative change. When warming is slow relative to the generation time, the growth rate exhibits greater intra-annual variation as warming proceeds, but remains positive over the year. When warming is fast relative to the generation time, the growth rate approaches zero during periods of low temperature extremes and becomes negative during periods of high temperature extremes. The net result is an increase in the amplitude and frequency of fluctuations in the per capita growth rate (Fig. 4).

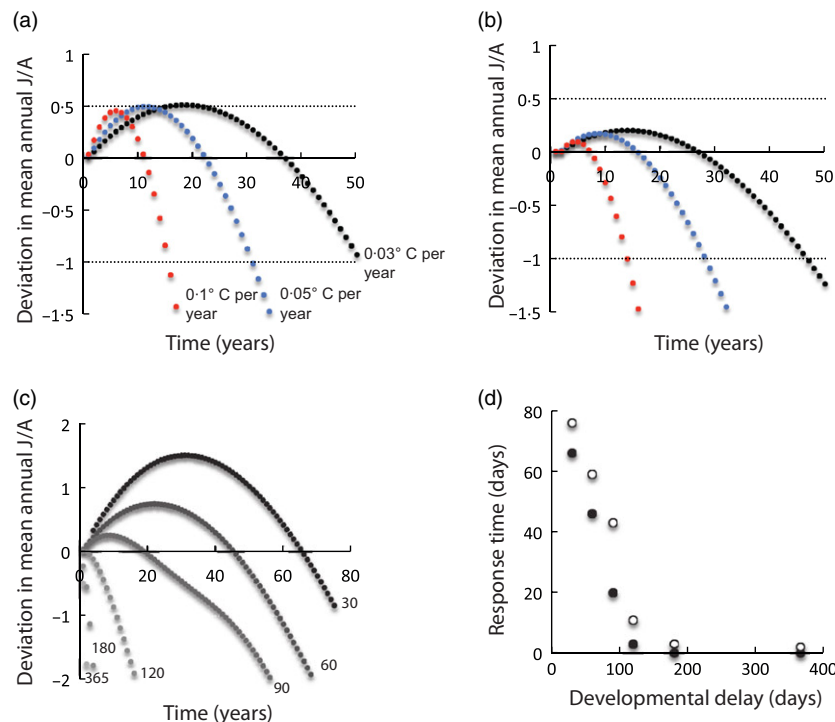
#### Time-scale of response to warming

One can quantify the response to warming in terms of the deviation of mean annual  $\frac{J}{A}$  from that observed under typical seasonal variation. This deviation is initially slightly positive (<0.5%) but becomes increasingly negative as warming effects on life-history traits become compounded (Fig. 5a and b). The time at which the deviation changes from positive to negative can be considered as the characteristic response time of the organism. A less conservative measure of the response length is the time it takes for a 1% decline in the mean annual  $\frac{J}{A}$ , which is about 5–12

years longer when warming is slow (0.03–0.05 °C per year) and 15–20 years longer when warming is faster (0.1 °C per year). (The response time is longer when warming involves an increase in fluctuations rather than the mean.) Either of these measures could be considered as the time-scale on which predictions based on  $r_m$  are valid.

#### Effects of developmental period

The developmental period has a strong effect on the characteristic response time (Fig. 5c and d). When it is short (30–60 days) relative to the time-scale of warming (0.03 °C per year), both the response time (46–66 years based on the parameters used) and the time it takes for a 1% decline in the mean annual  $\frac{J}{A}$  (59–76 years) are relatively long. Organisms with short developmental delays are also able to take advantage of the initial warming period, as evidenced by the greater initial increase in the mean annual  $\frac{J}{A}$  (Fig. 5c). However, both measures of the response time decline rapidly with increasing developmental delay. In organisms with long developmental delays relative to the time-scale of warming (9–12 months), both  $\frac{J}{A}$  and the per capita growth rate start to deviate from the



**Fig. 5.** Effects of warming on the mean annual juvenile-to-adult ratio ( $\frac{J}{A}$ ). Panels in the top row depict the deviation in the mean annual  $\frac{J}{A}$  from that observed under typical seasonal variation when warming involves an increase in the mean temperature [panel (a)] and the amplitude of seasonal fluctuations [panel (b)]. In each panel the black, blue and red curves correspond respectively, to 0.03°, 0.05° and 0.1 °C increase in temperature per year. The time it takes for the mean annual  $\frac{J}{A}$  to change from positive to negative is the characteristic response time of the organism. The dashed line at –1 denotes the boundary for a 1% decline in  $\frac{J}{A}$ . In the bottom row, panel (c) depicts the effects of developmental period on the characteristic response time, with the number next to each curve denoting the developmental delay in days. Panel (d) depicts the characteristic response time (filled circles) and the time it takes for a 1% decline in the mean annual  $\frac{J}{A}$  (open circles) as a function of the developmental delay at 24 °C. Parameter values are as follows:  $b_{T_{opt}} = 0.8$ ,  $d_{J_{TR}} = d_{A_{TR}} = 0.02$ . Other parameter values are as in Figs 1 and 2.

seasonal expectation within a year. Thus, even when the warming rate is slow, predictions based on  $r_m$  are valid only for organisms with short developmental delays.

## Discussion

Mounting evidence for climate warming makes it important that we be able to identify species that are at high risk of extinction due to warming. Recent studies have used the intrinsic growth rate calculated from the Euler-Lotka equation ( $r_m$ ) as a metric for estimating population viability. The Euler-Lotka equation assumes a stable age/stage distribution in a constant environment, which is violated when the environmental temperature changes over time. In order to use  $r_m$  to estimate population viability under warming, we need to first establish that ectotherm populations can achieve a stationary age/stage distribution in thermally variable environments.

Here, we investigate this issue using a population model with temperature-dependent vital rates. This is, to our knowledge, the first time that mechanistically derived temperature responses of life-history traits (reproduction, development, mortality) have been incorporated into a population model that realistically captures the variability in time delays induced by temperature effects on development. We report two key findings. First, when there is seasonal variation in temperature, the stage distribution varies within the year but this intra-annual variation occurs in a predictable manner that remains constant between years. As a consequence, the per capita growth rate averaged over the year also remains constant between years.

This finding poses a key question: what mechanisms enable populations to converge to a stable stage distribution in the face of seasonal variation in temperature? The answer lies in the fact that life-history traits exhibit systematic and predictable responses to temperature variation, which, unless the environmental temperature varies in a completely unpredictable manner, will lead to predictable changes in vital rates and hence, population dynamics. The reason why life-history traits exhibit predictable responses to temperature is because temperature effects on the underlying biochemical processes (e.g. reaction kinetics, hormonal regulation) follow basic rules of thermodynamics (e.g. changes in entropy and enthalpy; Johnson & Lewin (1946); Sharpe & DeMichele (1977); Schoolfield, Sharpe & Magnuson (1981); Van der Have & de Jong (1996); Ratkowsky, Olley & Ross (2005)). These thermodynamical properties define the lower and upper temperature thresholds below and above which reproduction and development cease. Beyond these thresholds, high mortality ensures that population growth is negative. As long as fluctuations in the environmental temperature occur within the thresholds set by the temperature tolerance of reproduction and development, the population will be viable and achieve a stationary stage distribution. The key implication is that  $r_m$  calculated from the Euler-

Lotka equation does provide a valid representation of population growth under typical regimes of seasonal temperature variation.

This suggestion immediately leads to the question of whether  $r_m$  provides a realistic representation of population growth under perturbations to the typical thermal environment such as climate warming. We find that a stationary stage distribution can be achieved under climate warming, but only on relatively short (e.g. decadal) time-scales. Effects of warming on reproduction, development and mortality become compounded over time, causing a qualitative change in the stage distribution. Importantly, the time-scale over which this change occurs is the time-scale over which predictions based on  $r_m$  are valid. Temperature-induced changes in the stage distribution are informative about the error associated with using  $r_m$  to predict times to extinction. As warming proceeds, the amplitude and frequency of intra-annual fluctuations in the juvenile-to-adult ratio increase. The population model that accommodates these fluctuations predicts the mean annual per capita growth rate to decline and approach zero within 100 years when warming is slow relative to the developmental period of the organism (0.03–0.05°C per year) and to become negative, causing population extinction, well before 100 years when warming is fast (e.g. 0.1°C per year). The Euler-Lotka equation, which does not take intra-annual variation into account, predicts a slower decline in the intrinsic growth rate when warming is slow and a longer persistence time when warming is fast.

The degree of error associated with using  $r_m$  to predict times to extinction depends on both the rate of warming and the developmental period of the organism. Species with short developmental delays relative to warming rate are likely to exhibit longer time periods during which the mean annual  $\frac{1}{A}$  remains constant between years. For such species,  $r_m$  may be used to predict effects of climate warming on short time-scales (50–60 years) provided the rate of warming is slow (< 0.05°C per year). For ectotherms with long developmental delays,  $r_m$  is unlikely to be a reliable predictor of warming effects, even on a decadal time-scale.

Recent studies that have used  $r_m$  to predict extinction risk due to climate warming (Deutsch *et al.* 2008) find that tropical ectotherms, mainly insects, are more at risk of extinction due to climate warming than temperate ectotherms. Given that temperate ectotherms tend to have longer developmental delays than their tropical counterparts,  $r_m$  may underestimate their risk of extinction under climate warming. Whether tropical ectotherms remain more susceptible to climate warming than temperate ectotherms once the difference in their developmental delays is taken into account is an important question that needs to be addressed.

The appeal of using the intrinsic growth rate to estimate population viability lies the fact that it provides a common, an easily quantifiable, metric that applies across



diverse ectotherm taxa and obviates the need for constructing explicit age-/stage-structured models of population dynamics for each species of interest, which is infeasible in most cases. A possible alternative to  $r_m$  that more accurately reflects the outcomes of population models is to use the temperature responses of life-history traits to compute the lower and upper temperature thresholds below and above which reproduction and development cease. These thresholds provide an estimate of the thermal limits below and above which a population cannot recover from low densities. Since the temperature responses of reproduction and development are driven by biochemical processes whose thermodynamical properties are well characterized and known to be conserved across ectothermic taxa (Johnson & Lewin 1946; Sharpe & DeMichele 1977; Schoolfield, Sharpe & Magnuson 1981; Nijhout 1994; Van der Have & de Jong 1996; Huey & Berrigan 2001; Van der Have 2002; Frazier, Huey & Berrigan 2006; Kingsolver 2009; Sunday, Bates & Dulvy 2010; Kingsolver *et al.* 2011), they will yield predictions about thermal limits to viability that do not depend on assumptions about stationary age/stage distributions and the predictability of the thermal environment. Developing a mathematical framework based on the temperature responses of life-history traits to estimate population viability is an important research priority.

There are several important directions in which our work could be extended. First, we have focused on closed populations whose dynamics are driven solely by birth, maturation and mortality in the absence of density-dependent factors. This is a necessary first step because it provides a baseline against which more complex models with additional biological features can be compared. One such feature is spatial dynamics. Investigating the effects of dispersal on stage-structured population dynamics when temperature also affects the dispersal rate is an important future direction. A second important factor is density-dependent population dynamics arising from resource limitation and/or natural enemy action. Density dependence is unlikely to be strong at extreme temperatures because abundances are likely low due to low rates of reproduction and development relative to mortality. However, it is likely to be quite strong at intermediate temperatures that are optimal for reproduction and development. The mechanisms by which temperature affects density-dependent feedback processes such as competition and frequency-dependent predation will determine the increase in the per capita growth rate during these periods relative to the decrease in the growth rate during temperature extremes. If warming increases the strength of density-dependent feedback, it will reduce the increase in the growth rate during favourable temperatures, causing the mean annual growth rate to be lower than that predicted based on models of density-independent population growth. Elucidating how temperature affects density-dependent population dynamics is therefore critical in obtaining a full understanding of how temperature variation, warming in particular, influences population viability.

Finally, the framework we have developed focuses on how temperature variation influences ecological dynamics. It does not take into account the ability of organisms to adapt to changes in the thermal regime. Provided there is sufficient genetic variation in the reaction norms for fecundity, development and survivorship, there may be selection for phenotypes better able to withstand warmer temperature regimes. If thermal responses of life-history traits can evolve over the time-scale of climate warming which, again is more likely for organisms with faster generation times, times to extinction may be longer than that predicted based on ecological dynamics alone. Investigating how temperature responses of life-history traits evolve in the face of perturbations such as climate warming is a key research priority.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Effect of developmental delay on population dynamics under typical seasonal variation.