PAPER • OPEN ACCESS

Population dynamics in the face of climate change: Analysis of a cubic thermal performance curve in ectotherms

View the article online for updates and enhancements.

IOP ebooks™

Bringing you innovative digital publishing with leading voices to create your essential collection of books in STEM research.

Start exploring the collection - download the first chapter of every title for free.

Population dynamics in the face of climate change: Analysis of a cubic thermal performance curve in ectotherms

V Saldaña-Núñez[1], F Córdova-Lepe[1], and F N Moreno-Gómez[1]
[1] Universidad Católica del Maule, Talca, Chile

E-mail: victor.saldana.1038@alu.ucm.cl

Abstract. The objective of this study is to perform an analysis on the effect of the increase in temperature under the context of climate change on the dynamics of a population of ectothermic organisms, which are highly susceptible to these changes, as their body temperatures depend crucially on the environmental temperature. In our modelling approach, population abundance is governed by a logistic growth, where the intrinsic growth rate is affected by the change in temperature. The relationship between environmental temperature and the intrinsic rate of increase will be represented by a thermal performance curve type. In order to facilitate analytical simplicity but also novelty, a cubic expression is proposed to represent the thermal performance curve, the intensity of intraspecific competition is considered to remain constant and the tendency of temperature increase follows a linear expression. Finally, consequences on the trends of population abundance curves are assessed.

1. Introduction
Currently, climate change is one of the most worrisome issues for society, where the increase in the average environmental temperature has received special attention. The increments in the environmental temperature are generating adverse consequences on the life on Earth, its effects include alterations at different levels of life organization, ranging from individuals to ecosystems [1-3]. At a population level, for understanding the changes in abundance in response to temperature fluctuations, is needed to determine which are the conditions that may allow for the persistence of populations in variable environments [4].

By using mathematical model, this study analyses the consequences of the increase in temperature in the abundance of an ectothermic population. These organisms are highly susceptible to changes in temperature because their body temperature depends heavily on the temperature of the environment in which they inhabit. As the temperature has an important effect on different aspects that determine population dynamics, i.e. birth and death rates, it is expected that the population size is highly sensitive to the warming of the environment. A good depiction of the effects of changes in temperature in ectothermic organisms are the thermal performance curves (TPC), which represent the performance of the organism in relation to its body temperature [5].

In this modelling approach, the population grows under a logistic law, but the intrinsic rate of increase will vary according to a thermal effect determined by the TPC properties. In order to facilitate analytical simplicity but also novelty, a cubic polynomial functional model is proposed. Note that, the cubic order in some cases is skewed to the left, a common property of thermal performance curves. Regarding the temperature, it is assumed a linear increment.

XIV Applied Mathematics Meeting and XI Statistics Meeting

IOP Conf. Series: Journal of Physics: Conf. Series **1329** (2019) 012007

IOP Publishing

doi:10.1088/1742-6596/1329/1/012007

In section 2, we will consider the population dynamics and its main determinants (thermal performance curve and temperature increment). In the next section (section 3), the cubic model that will represent the growth rate will be presented, studying the characteristics reaffirming its relationship with the TPC and denoting its possible technical advantages over other curves presented by the theory. Some important comments about the form of the population growth curve are made in section 4. In section 5, we will evaluate the sensitivity of our population considering the effects on the initial characteristics, the speed in temperature change and the range of thermal tolerance through simulations. Finally, in section 6, some general conclusions are presented.

2. Determinant elements of population dynamics

2.1. Thermal performance curve

In thermal ecology, a TPC is a descriptor of how the change in body temperature of an ectotherm influences its performance [5,6]. These curves indicate that at extreme body temperatures (high and low), the performance of an organism is highly impaired, including the lethal consequences. These extremes are called "critical temperatures" (τ_{min} and τ_{max}) [7]. Between these extremes, performance reaches a maximum value r_{op}, at an optimum temperature τ_{op} [5], see Figure 1.

The fundamental parameters that define the form of these curves are the top of the TPC or modal point (τ_{op}, r_{op}) and the temperatures that define the tolerance range is $R = \tau_{max} - \tau_{min}$. In general, they are considered non-linear, unimodal and asymmetrical functions, which from low to high temperatures their images gradually grow to an optimum performance and then decrease abruptly. In the case of ectothermic organisms, the optimum performance within in the tolerance range is shifted to the right (skewed to the left). Example from experimental data, obtained for the thermal biology of a solitary lizard and for the performance of jump in frogs *Clamitans*, it is possible to find them in the works of Huey [8,9]. In the latter case, the TPC obtained was modelled after the product of exponential functions [10]. A quadratic polynomial has also been proposed.

As stated by Estay *et al*. [11] a temperature rate population growth curve will be used as an extension to TPC, which are generally associated with whole performance organismic traits.
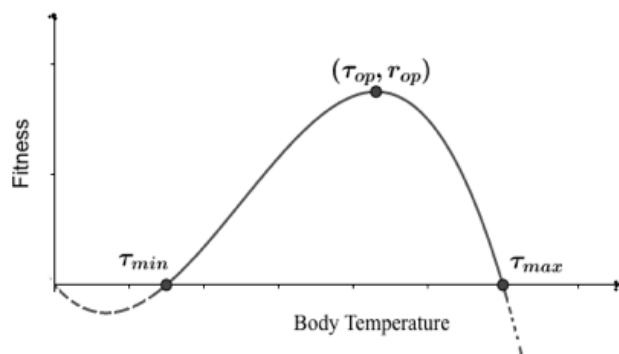
Figure 1. Thermal performance curve for a hypothetical ectotherm, with key descriptive parameters τ_{min}, τ_{max}, tolerance range, performance amplitude, optimum temperature τ_{op} and optimum rate r_{op}.

2.2. Evolution of temperature

The mean temperature of the ecological systems is changing, it is expected to consider an upward trend that we will assume is linear. This is the function $\tau: [0,\infty) \longrightarrow [0,\infty)$, which is defined by Equation (1).

$$\tau(\rho, t) = \tau_i + \frac{1}{\rho}\{\tau_{max} - \tau_{min}\} = \tau_i + \frac{R}{\rho}, \text{ with } t \geq 0, \tag{1}$$

where τ_I is the starting temperature and ρ is the time needed to route the tolerance thermal range R.

2.3. Population abundance curve

Considering a (r,k)-logistic law with an intrinsic rate of thermo-dependent growth $r[\tau(\rho,t)]$ and carrying capacity $k[\tau(\rho,t)]=r[\tau(\rho,t)]/\lambda$, where λ indicates intensity in intraspecific competition. In this way, denoting biomass t- time function by $N(t)$, the differential law that model's growth is given by Equation (2).

$$N'(t)= r[\tau]N\left\{1-\frac{N(t)}{k[\tau]}\right\}, \text{ i.e. } N'(t)= r[\tau]N\left\{1-\lambda\frac{N(t)}{r[\tau]}\right\}. \tag{2}$$

Note that using the integrating factor $E(0,t)=\exp(\int_0^t r[\tau(s)]ds)$, its explicit solution, for an initial condition N_0 at instant $t = 0$, is the Equation (3).

$$N(t)=\frac{N_0 E(0,t)}{1+\lambda N_0 \int_0^t E(0,s)ds}, \ t \geq 0. \tag{3}$$

3. Cubic adjustment of thermal performance curves

The consulted literature offers several possibilities to represent the TPC in functional terms. There are cases from simplified by a quadratic expression (parabolas) to more sophisticated expressions by exponential functions (Gaussian, Weibull, and modified Gaussian) [12].

To express the curve $r[\tau]$, or adjust in the case of data, we choose an approximation using a cubic polynomial. It has certain advantages in the analytical case and is determined by only three parameters. Although its insufficiency is found in that in parameters set $\{\tau_{min}, \tau_{op}, \tau_{max}, r_{op}\}$ only three of them are independent, that is, the fourth is determined by the rest. Nevertheless, it has a higher level of realism (one degree of freedom more) compared with the quadratic one. So that, we consider the Equation (4).

$$r[\tau]= r_{op}\frac{\tau(\tau- \tau_{min})(\tau_{max}- \tau)}{\tau_{op}(\tau_{op}- \tau_{min})(\tau_{max}- \tau_{op})}, \ \tau \in J=[\tau_{min}, \tau_{max}]. \tag{4}$$

3.1. Optimal temperature

Remark 1: Considering τ_{min}, τ_{max} ($0< \tau_{min}< \tau_{max}$) and r_{op} as the free parameters. The temperature τ_{op} such that $r[\tau_{op}]=r_{op}$, is given by Equation (5).

$$\tau_{op}=\frac{2}{3}\left[\bar{\tau}+\frac{1}{2}\sqrt{4\bar{\tau}^2-3\tau_g^2}\right] \in J, \tag{5}$$

where $\bar{\tau}=(\tau_{min}+\tau_{max})/2$ and $\tau_g=\sqrt{\tau_{min}\tau_{max}}$.

Proof: The critical points of the cubic polynomial $r[\tau]$ are the τ such that $r'[\tau]=0$. They are given by $\tau_{\pm}=\left[2\bar{\tau}\pm\{4\bar{\tau}^2-3\tau_g^2\}^{1/2}\right]/3$. Since $\tau_+ \in J$, we have $\tau_{op}= \tau_+$, this is, Equation (5). This value corresponds to a maximum point for $r[\cdot]$, since we have $r''[\tau_+] < 0$.

From $\tau_{min}- \tau_{max}<0$, amplifying by $3\tau_{max}$, we get $3\tau_{min}\tau_{max}<3\tau_{max}^2$. When adding τ_{max}^2 and reordering it, we get $2\tau_{min}\tau_{max}+\tau_{max}^2<4\tau_{max}^2-\tau_{min}\tau_{max}$. Adding τ_{min}^2 and forming a square on the left side, you get $(\tau_{min}+\tau_{max})^2<4\tau_{max}^2-\tau_{min}\tau_{max}+\tau_{min}^2$. Now, subtracting $3\tau_{min}\tau_{max}$ and factoring to the right side, when applying root $\sqrt{(\tau_{min} + \tau_{max})^2 - 3\tau_{min}\tau_{max}} < 2\tau_{max} - \tau_{min}$. Then $(\tau_{min} + \tau_{max}) + \sqrt{(\tau_{min} + \tau_{max})^2 - 3\tau_{min}\tau_{max}} < 3\tau_{max}$. So, clearly $\tau_{op} < \tau_{max}$. Analogously, proving that $\tau_{min}< \tau_{op}$, is enough to begin from the affirmation $\tau_{min}< \tau_{max}$. Now amplifying by $3\tau_{min}$ and adding $-6\tau_{min}\tau_{max}$ on

both sides we have $9\tau_{min}^2-6\tau_{min}\tau_{max}-6\tau_{min}^2<-3\tau_{min}\tau_{max}$. So, adding $4\bar{\tau}^2$ we get $\left(3\tau_{min}^2-2\bar{\tau}^2\right)^2<4\bar{\tau}^2-3\tau_g^2$. Now, extracting square root and clearing, we finally obtain $\tau_{min}<\tau_{op}$.

3.2. Inflection point

Remark 2: The temperature τ_c at the curvature of r $[\cdot]$ changes ($r''[\tau_c]=0$) is $\tau_c=(2/3)\bar{\tau}$. The value r_c of the cubic TPC in this temperature is given by Equation (6):

$$r_c=\frac{2}{27}\frac{\bar{\tau}(\tau_{max}-2\tau_{min})(2\tau_{max}-\tau_{min})}{\tau_{op}(\tau_{op}-\tau_{min})(\tau_{max}-\tau_{op})}r_{op}=\frac{2}{27}\frac{\bar{\tau}(R-\tau_{min})(\tau_{max}+R)}{\tau_{op}(\tau_{op}-\tau_{min})(\tau_{max}-\tau_{op})}r_{op} \qquad (6)$$

Proof: Notice that $r''[\tau_c]=r_{op}(4\bar{\tau}-6\tau_c)/\{\tau_{op}(\tau_{op}-\tau_{min})(\tau_{max}-\tau_{op})\}$. So $r''[\tau_c]=0$ if $\tau_c=2\bar{\tau}/3$. Moreover, $r''[\tau]>0$ (respect <) if $\tau<\tau_{op}$ (resp. >). Directly, we have $r_c=r[\tau_c]$.

3.3. Average thermal performance

On the thermal range, $J=[\tau_{min},\tau_{max}]$, the performance curve average $(1/R)\int_J r[\tau]d\tau$, is denoted by $\bar{r}$, takes a value, which is obtained by direct integration, factorizations and reductions, this is the Equation (7).

$$\bar{r}=\frac{r_{op}}{\tau_{op}R\left(\tau_{op}-\tau_{min}\right)\left(\tau_{max}-\tau_{op}\right)}\int_J\left[\tau^2(\tau_{min}+\tau_{max})-\tau\tau_{min}\tau_{max}-\tau^3\right]d\tau=$$
$$\frac{r_{op}\left(\tau_{max}-\tau_{min}\right)^2(\tau_{min}+\tau_{max})}{12\tau_{op}\left(\tau_{op}-\tau_{min}\right)\left(\tau_{max}-\tau_{op}\right)}=\frac{r_{op}R^2\bar{\tau}}{6\tau_{op}(\tau_{op}-\tau_{min})(\tau_{max}-\tau_{op})}. \qquad (7)$$

Remark 3: The lowest temperature value, $\tau_*\in J$ where $r[\tau_*]=\bar{r}$, is given by Equation (8):

$$\tau_*=\frac{2}{3}\left\{\bar{\tau}-\sqrt{4\bar{\tau}^2-3\tau_g^2}\cos\left(\phi-\frac{2}{3}\pi\right)\right\} \text{ , with } \phi=\frac{1}{3}\arccos\left\{\frac{\bar{\tau}^3}{(4\bar{\tau}^2-3\tau_g^2)^{3/2}}\right\}. \qquad (8)$$

Proof: We obtained τ_* using the Vieta's method. In fact, $r[\tau_*]=\bar{r}$, implies $\tau_*(\tau_*-\tau_{min})(\tau_{max}-\tau_*)=(\tau_{max}-\tau_{min})^2(\tau_{max}+\tau_{min})/12=R^2\bar{\tau}/6$, which is reduced to $\tau_*^3-2\bar{\tau}\tau_*^2+\tau_g^2\tau_*+R^2\bar{\tau}/6=0$. By Descartes's Rule has the most two positive roots and also one negative root.

The Vieta's formula for x^3+ax^2+bx+c with real roots is $x_k=-2\sqrt{Q}\cos\left(\phi-\frac{2k\pi}{3}\right)-a/3$, k $\in$ { 0 $\pm$ 1}, where $\phi=\left(\frac{1}{3}\right)arc\,cos(S/\sqrt{Q^3})$, with S=$(2a^3-9ab+27c)/54$ and Q=$(a^2-3b)/9$. In our case Q=$(4\bar{\tau}^2-3\tau_g^2)/9>0$ and S=$(\bar{\tau}/3)^3>0$. So that, $0<\phi<\pi/6$. Then, $\cos\left(\phi+\frac{2\pi}{3}\right)<\cos\left(\phi-\frac{2\pi}{3}\right)<\cos(\phi)$. So, we obtain Equation (8), which is the least positive root.

3.4. Skewed left

Remark 4: The function $r[\tau]$, defined for $\tau>0$, satisfies inequality "mean < median< mode", this is $\tau_{min}<\tau_*<\tau_{op}<\tau_{max}$, proper to the skewed left distributions.

Proof: Indeed, notice that by Equation (5) and Equation (7), we have $\tau_{op}-\bar{\tau}=\left(\sqrt{4\bar{\tau}^2-3\tau_g^2}-\bar{\tau}\right)/3>0$ and

$\bar{\tau}-\tau_*=\left(\bar{\tau}+\sqrt{4\bar{\tau}^2-3\tau_g^2}\cos\left(\phi+\frac{2\pi}{3}\right)\right)/3>0$. So, rest use $\tau_g<\bar{\tau}$.

3.5. Performance breadth

The thermal performance amplitude, that we will denote by A_r, corresponds to a range of temperatures in which the organism develops (ectotherm), in such a range of temperatures, the performance of this is higher than a given performance level [13].

This amplitude is defined by the importance and consideration of the performance that is studied. For example, in Sinclair *et al.* [14], this amplitude is considered at the height of $r_{op}/2$. In our case, we will consider it at the level of r_c, this is the point in which the curvature of the performance curve changes.

Remark 5: If A_r (a positive value) is defined by $r_c = r[\tau_c] = r[\tau_c + A_r]$, see Equation (9).

$$A_r = \sqrt{3\left(4\bar{\tau}^2 - 3\tau_g^2\right)}/3 = (3\tau_{op} - 2\bar{\tau})/\sqrt{3} \qquad (9)$$

Proof: Let us denote that $z = \tau_c + A_r$, then $r[\tau_c] = r[z]$, implies that $p(z) = z(z - \tau_{min})(\tau_{max} - z) - \tau_c(\tau_c - \tau_{min})(\tau_{max} - \tau_c) = 0$. As $p(z)$ is divided by $z - \tau_c$, $p(z) = (z - \tau_c)\left[2\bar{\tau}(z + \tau_c) - (z^2 + z\tau_c + \tau_c^2) - \tau_g^2\right]$. It remains to solve $z^2 - (2\bar{\tau} - \tau_c)z - (2\bar{\tau}\tau_c - \tau_c^2 - \tau_g^2) = 0$. considering $\tau_c = 2/3\bar{\tau}$, we obtain $z = \left[2\bar{\tau} + \sqrt{3\left(4\bar{\tau}^2 - 3\tau_g^2\right)}\right]/3 > 0$. Since $A_r = z - \tau_c$, Equation (9) follows.

4. Analysis of population growth

With (r,k) constant, the population grows toward the asymptotic level k. Now, the population grows or it decreases according to: (a) $\lambda N(t) < r[\tau(\rho, t)]$ or (b) $\lambda N(t) > r[\tau(\rho, t)]$ is satisfied at time $t > 0$. It is expected that when the temperature is closer to τ_{min} or τ_{max}, $N(\cdot)$ decreases, because $r[\rho, \tau(\cdot)]$ is small and inequality (b) is more feasible. Broadly speaking, this explains the flared shape of the abundance curve shown by all the figures associated with the next section.

5. Analysis of sensitivity to parameters and initial conditions

In this section, an analysis of the abundance curve will be performed depending on the parameters. Specifically, we vary only one parameter and show the effect of climate change on the dynamics of the population, fixing all other parameters. The next tables have graphs associated (Figure 2(a)-Figure 2(h)) in which vertical lines permit represent the instants when the critical temperatures τ_{min} and τ_{max}, are reached.

5.1. Sensitivity to initial conditions

Notice that by derivation respect N_0 of Equation (3), we have $\partial_{N_0}N(t, N_0) > 0$. So, initial conditions $N_1(0)$ and $N_2(0)$ such that $N_1(0) < N_2(0)$, then $N_1(t) < N_2(t)$ at all future times $t > 0$.

Now, let us run some numerical simulations, for this, we consider the parameters of Table 1, where the first three elements determine the TPC $r[\cdot]$, the next two the temperature curve $\tau(\cdot)$, the other three are the temperatures that show the skewed left of the TPC and finally three initial conditions.

Table 1. Parameters and initial conditions.

τ_{min}	τ_{max}	r_{op}	τ_i	ρ	τ_*	$\bar{\tau}$	τ_{op}	$N_1(0)$	$N_2(0)$	$N_3(0)$
18.0	36.0	0.4	19.0	100.0	22.8	27.0	28.4	2000	4000	6000

Notice that, Figure 2(a) shows that at any time the abundances keep the order of the initial conditions. This shows that in a scenario of increasing global temperature opportunistic species that should disappear (with constant temperature) have an opportunity to survive for a while if the initial abundance is sufficient. Furthermore, if the temperature is stabilized in the future, it can be installed definitively. In addition, we can observe that the temperature and optimal performance has not been affected by the initial conditions variabilities.
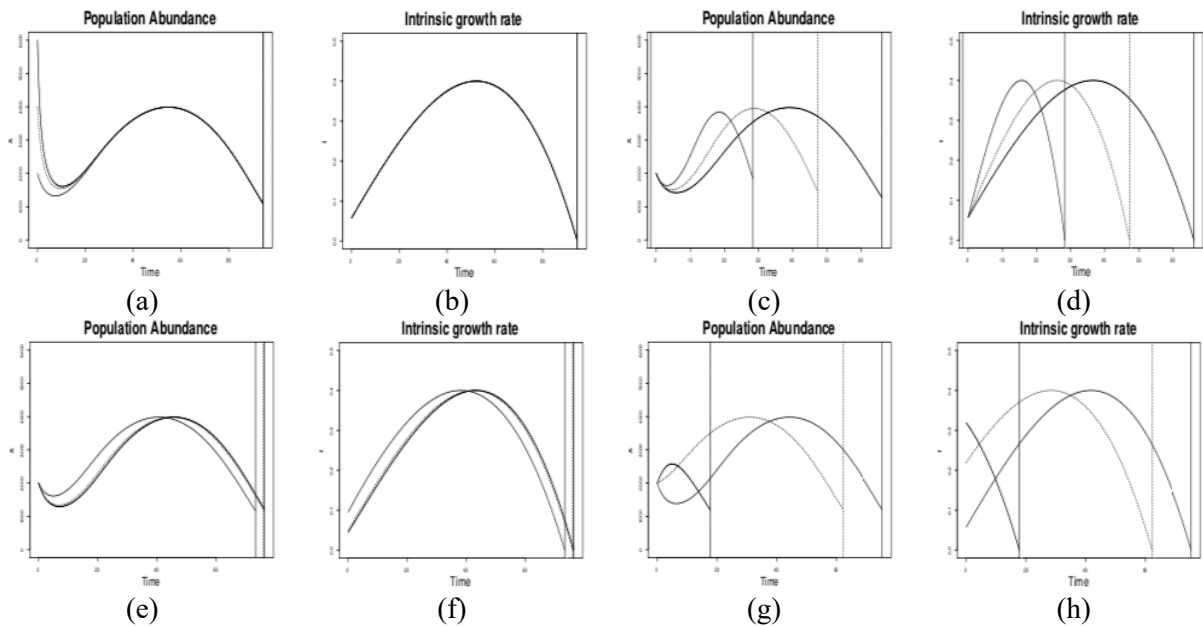
Figure 2. It is considered in: (a) $N_1(0)$ (solid curve), $N_2(0)$ (segmented curve), $N_3(0)$ (dotted curve). (c) ρ_1 (solid curve), ρ_2 (segmented curve), ρ_3 (dotted curve). (e) τ_{max1} (solid curve), τ_{max2} (segmented curve), τ_{max3} (point curve). (g) τ_{i1} (solid curve), τ_{i2} (segmented curve), τ_{i3} (dotted curve). In (b), (d), (f) and (h) the graph of the function $r[\tau(\cdot)]$ is represented with respect to time, related to (a), (c), (e) and (g) respectively.

5.2. Sensitivity to parameter ρ
In Table 2, the first three inputs determined r[ ], the next four determined different tendencies in temperature, the others are temperatures showing the skewed left of the TPC.

Table 2. Parameter variable ρ.

τ_{min}	τ_{max}	r_{op}	τ_i	ρ_1	ρ_2	ρ_3	τ_*	$\bar{\tau}$	τ_{op}	$N(0)$
18.0	36.0	0.4	19.0	30.0	50.0	70.0	22.9	27.0	28.4	2000

Considering the parameters presented, we can see in Figure 2(c) that the shapes of the curves are similar in the cases proposed, but we also corroborate what was expected, that by increasing the time required to travel ρ the abrupt decline of the population occurs over a longer time, this is related to the fact that when witnessing this situation, the intensity of the increase in temperature is lower.

5.3. Sensitivity to the range of thermal tolerance
As can be seen in Table 3, the parameters for our next study of sensitivity to change the range of thermal tolerance R (actually only varied τ_{max}), the first five data's are associated with the TPC (r[ ], for differents τ_{max}), and the following two data's determine the trend in temperature τ. The nine data's below show the temperatures that confirm the skewed left of the TPC curve and finally the initial abundance of the study. Remember that R is the length of the thermal range (τ_{max}-τ_{min}). Notice that R is present in the definition $\tau(t,R)=\tau_i+(R/\rho)t$, $t\geq0$ and $R\geq0$.

In Figure 2(e), it is observed that the population abundance is greater for smaller τ_{max}, before reaching its maximum abundance, but after this optimum value the situation is inverted, that is, there is greater abundance in populations that posse greater τ_{max}, and so tends to its extinction later.

Table 3. Range variable of thermal tolerance.

j	τ_{min}	τ_{maxj}	r_{op}	τ_i	ρ	τ_{*j}	$\bar{\tau}_j$	τ_{opj}	$N(0)$
1	18	30	0.4	19	80	21.06	24	24.7	2000
2		38				23.47	28	29.6	
3		40				24.10	29	30.9	

5.4. Sensitivity to initial temperature

Table 4 presents the parameters to study the sensitivity to the initial study temperature, where the division of columns follows the same order as the previous ones.

Table 4. Temperature initial variable.

τ_{min}	τ_{max}	r_{op}	τ_{i1}	τ_{i2}	τ_{i3}	ρ	τ_*	$\bar{\tau}$	τ_{op}	$N(0)$
18.0	36.0	0.4	19.0	22.0	32.0	80.0	22.9	27.0	28.4	2000

Figure 2(g) shows the abundance curves for different initial temperatures, which in an exploratory survey we can say that for τ_i closer to τ_{min}, the shape of the curve is described in previous sections, reaching its maximum over a long time, otherwise if they are closer to τ_{max}, the maximum abundance is reached in a very short time and being much lower than the other cases and its extinction is more likely to occur and early.

6. Conclusions

As it is known from a series of studies, climate change is affecting different expressions of life, including population dynamics. When performing a sensitivity analysis of the parameters of our proposed models to represent the ectothermic organism population dynamics and also when analyzing the rate of growth following a TPC, allowed us to assess how a population becomes extinct as a result of increases in the linear temperature. The objective of this study was to demonstrate the aforementioned and to evaluate, under the analysis of parameter sensitivity and how the extinction time was affected. Our proposal of a cubic TPC allowed us to analytically corroborate some of the consequences of the increase in temperature in the abundance of populations, because the algebraic expression of this allows us a more accessible management than those proposed in the literature.

Acknowledgments

References
[1]   Lima M 2006 *Investigación y Ciencia* **358** 46
[2]   McCarty J 2001 *Conservation Biology* **15** 320
[3]   Useros J L 2013 *An. Real Acad. Med. Cir. Valladolid* **50** 71
[4]   Amarasekare P and Coutinho R M 2014 *Am. Nat.* **184** E50
[5]   Huey R, Kearney M, Krockenberger A, Holtum J, Jess M and Williams S 2012 *Phil. Trans. R. Soc. B.* **367** 1665
[6]   Schulte P, Healy T, Frangue N 2011 *Integr. Comp. Biol.* **51** 691
[7]   Wesley W, King F and Denny M 2015 *J. Exp. Biol.* **218** 1956
[8]   Huey R B and Webster T P 1975 *Ecology* **56** 445
[9]   Huey R B and Stevenson R D 1979 *Integr. Comp. Biol.* **19** 357
[10]   Thornton K W and Lessem A S 1978 *Trans. Am. Fish. Soc.* **107** 284
[11]   Estay S, Lima M and Bozinovic F 2014 *Oikos* **123** 131
[12]   Anguilleta M J 2006 *J. Therm. Biol.* **31** 541
[13]   Huey R and Kingsolver J 1989 *Trends Ecol. Evol.* **4** 131
[14]   Sinclair B, Marshall K, Sewell M, Levesque D, Willett C, Slotsbo S, Dong Y, Harley C, Marshall D, Helmuth B and Huey R 2016 *Ecol. Lett.* **19** 1372