SUPPLEMENT 1

Section S1: Table of variables and parameters

Table S1. Summary of variables and parameters. Note that some variables and parameters are presented in the equations given in additional supplement sections.

Symbol	Name	units	Type	Eq.
A	Ratio	ºC	constant	5
D_{min}	Minimum biological time	Clock time	constant	4
δ	Fluctuation shape constant	None	constant	S5
E_1	Minimum tolerance range	ºC	constant	S9
E_2	Maximum tolerance range	ºC	constant	S9
ε_1	Constant	ºC	constant	6
ε_2	Constant	Clock time^{-1}	constant	6
f_{csm}	Maximum signal level	None	constant	S6
fr	Fraction of phenotypic change	ºC^{-1}	Variable	8
f_{rm}	Maximum rate of change	ºC^{-1}	constant	8
f_{sp1}	Phenotype state 1	None	constant	9
f_{sp2}	Phenotype state 2	None	constant	9
$F_{C\rightarrow S}$	Function: cue to signal	None	variable	7
$F_{S\rightarrow P}$	Function: signal to phenotype	None	variable	9
k_m	Rate constant	ºC^{-1}	constant	S3
k_μ	Rate constant	ºC^{-1} Clock time^{-1}	constant	3
k_r	Half saturation temperature	ºC	constant	8
k_s	Signal shape constant	ºC^{-1}	constant	7
k_t	Rate constant	Clock time^{-1}	constant	S3
k_τ	Rate constant	ºC Clock time	constant	4
L_{max}	Minimum biological time^{-1}	Clock time^{-1}	variable	5
m	Magnitude in extrinsic frame	ºC	variable	1
$\boldsymbol{M}$	Matrix of partial derivatives	several	variable	2
M_0	Optimal temperature	ºC	constant	6
M_{crit}	Critical temperature	ºC	constant	6
μ	Magnitude in intrinsic frame	none	variable	1
R,r	Invariant Response	Mass	variable	1
S	Stenothermic function	ºC^{-1}	variable	3
S_0	Minimum sensitivity	ºC^{-1}	constant	3
t	Clock time scale	Clock time	variable	1
t^*	Extrinsic observation time	Clock time	variable	1
τ	Intrinsic time scale	None	variable	1
τ^*	Biological observation time	None	variable	1
x	Time	Clock time	variable	7
x_u	Threshold time	Clock time	constant	S7
y	Temperature	ºC	variable	7
y_u	Threshold temperature	ºC	constant	7
z	Sensitivity	ºC	constant	6

Section S2: Additional properties of space of fluctuations and the reference frame

The *mt*-projection shows following properties: (1) All fluctuations are projected the upper half plane, i.e., as points located in the part of the plane where *t* is positive (fluctuations with negative period do not exist). For simplicity, I will assume that $m>0$ because experiments usually focus on either high or low temperature with respect to a thermal optimum, for which *m* can be conveniently rescaled to be positive. Hence, the properties mentioned below do no change if *m* is also considered to be negative. However, (2) *m* cannot be zero because there is no fluctuation of any type that can be represented exactly as $m=0$. Hence, the vertical line at $m=0$ constitutes a so-called "open boundary": points describing fluctuations can be located infinitely near the boundary but not on it. (3) There is no fluctuation characterised by $t=0$; therefore, the horizontal line at $t=0$ is also an open boundary, which can be approximated by very small fluctuations. (4) Treatments of constant temperature can be viewed as a fluctuation where the period tends to infinity. Therefore, a given constant condition (characterised by a value of *m*), is projected in the plane as a point belonging to a so-called "line at infinity" (Fig. 5a), i.e. an horizonal line that can be never reached. (5) The values of *m* and *t* of the extrinsic frame define a rectangular grid, as a map with cartesian coordinates (Fig. 5a).

The μτ -projection has the following properties: (1) All fluctuations of $m>0$ are projected within triangle characterised by two open boundaries: the first open boundary is at $\tau_{open}= \mu/(k_\tau k_\mu)$ (see below). Additional open boundaries are given by the lines at $\tau=0$ and $\mu=0$ because they correspond to cases where $t=0$ or $m=0$. In practice, the space occupied by the fluctuations manipulated in a real experiment will be less than the octant and will depend on the maximum time scale and amplitude manipulated in the experiment. Hence, there is a practical limit (black curve in Fig. 5c) which will approach the open boundary as the time scale of the fluctuation increases. Such area is expanded with large values of S_0 and D_{min} or small values of k_μ and k_τ. (3) When $S_0 = D_{min} = 0$, the 2D space (Fig. 5c) collapses into a 1D space, because equations 3 and 4 result in that μ and τ are multiples from each other.

Calculation of τ_{open}: First, I obtain the upper (closed) boundary (black points in Fig. 5c), with equation:

$$\tau_{closed} = \mu t_{max}/[\mu D_{min} + k_\tau(S_0 + k_\mu t_{max})] \text{ (Eq. S2)}$$

where t_{max} is the maximum value of *t* used in a real-world experiment. This is not a theoretical limit; it will be set by constraints in the maximum amount of time allowed in a given experiment. Thus, t_{max} does not have any particular meaning from the theoretical point of view. Equation S2 is obtained as follows. The close boundary is calculated as a function of the intrinsic coordinates from:

$$\mu = m(S_0 + k_\mu t)$$

noting that the equation for τ can be re-written as

$$\tau\ (mD_{min} + k_\tau) = tm$$

By expanding the equation of μ and by substitution I obtain:

$$\mu = mS_0 + k_\mu tm = mS_0 + k_\mu \tau\ (mD_{min} + k_\tau)$$

In addition, the equation of τ can be further rewritten as:

$$\tau\, k_\tau = m(t - \tau D_{min}) => m = \tau\, k_\tau/(t - \tau D_{min})$$

By plugging *m* into the equation of μ we obtain:

$$\mu = \frac{S_0 \tau\, k_\tau}{(t - \tau D_{min})} + k_\mu \tau \left[\frac{D_{min} \tau\, k_\tau}{(t - \tau D_{min})} + k_\tau\right]$$

$$\mu = \frac{S_0 \tau\, k_\tau}{(t - \tau D_{min})} + k_\mu \tau \left[\frac{D_{min} \tau\, k_\tau}{(t - \tau D_{min})} + \frac{k_\tau (t - \tau D_{min})}{(t - \tau D_{min})}\right]$$

$$\mu = \frac{S_0 \tau\, k_\tau}{(t - \tau D_{min})} + k_\mu \tau \left[\frac{D_{min} \tau\, k_\tau + k_\tau t - k_\tau \tau D_{min}}{(t - \tau D_{min})}\right]$$

$$\mu = \frac{S_0 \tau\, k_\tau}{(t - \tau D_{min})} + k_\mu \tau \left[\frac{k_\tau t}{t - \tau D_{min}}\right]$$

$$\mu(t - \tau D_{min}) = S_0 \tau\, k_\tau + k_\mu \tau\; k_\tau t \implies \mu t - \mu \tau D_{min} = \tau\left(S_0\, k_\tau + k_\mu\; k_\tau t\right)$$

$$\mu t = \tau\left(S_0\, k_\tau + k_\mu\; k_\tau t + \mu\, D_{min}\right)$$

$$\boxed{\tau = \mu t/[\mu D_{min} + k_\tau(S_0 + k_\mu t)]} \checkmark$$

The limit is obtained by noting that its inverse can be written as:

$$1/\tau_{closed} = \left(\frac{D_{min}}{t_{max}}\right) + \left(\frac{k_\tau S_0}{\mu\, t_{max}}\right) + \left(\frac{k_\tau k_\mu}{\mu}\right)$$

$$\boxed{\lim_{tmax \to \infty} 1/\tau_{closed} = \left(\frac{k_\tau k_\mu}{\mu}\right)} \checkmark$$

Therefore, we obtain an open boundary $\tau_{open} = \mu/(k_\tau k_\mu)$.

Above such boundary, fluctuations would be characterised by negative amplitude (m<0) and period (t<0) as measured in clock time. Fluctuations of positive *t* but negative amplitude are projected to different quadrants of Figure 5b.

Section S3: Case 1, modelling body mass as the response R

I consider a simple response:

$$R = e^{f(t,m)\cdot t^*} \text{(Eq. S3a)}$$

$$f(m,t) = -(k_m m + k_t t) \text{ (Eq. S3b)}$$

The function *f(m,t)* is a rate of decrease driven by the magnitude and time scale of a thermal fluctuation (k_m and k_t are constants). Because we observe the response at a single time ($t^*= 1$) the function reduces to an exponential decay function of *t* and *m*, with the sensitivity to each fluctuation component described by the respective constants (Fig. 6a). In the biological frame, the functions of equations 3 and 4 distort the shape of the response (Fig. 6b): in the example, the response function varies mostly with the biological time scale of the fluctuation (τ) but very little with the biologically normalised magnitude (μ).

One can have an analytical expression of *r* by setting *t* and *m* as a function of μ and τ. For *m*, I first write μ and τ as follows:

$$\mu = m(S_0 + k_\mu t)\ ,\ \tau\ (mD_{min} + k_\tau) = tm$$

Then, I expand the equation of μ and substitute *tm* to obtain *m*:

$$\mu = mS_0 + k_\mu tm\ ,\ \mu = mS_0 + k_\mu \tau\ (mD_{min} + k_\tau)$$

$$\boxed{m = (\mu - k_\mu k_\tau \tau)/(S_0 + k_\mu D_{min}\tau)} \checkmark$$

For *t*, I substitute *m* in the equation for μ

$$\mu = (\mu - k_\mu k_\tau \tau)(S_0 + k_\mu t)/(S_0 + k_\mu D_{min}\tau)$$

The terms are manipulated to obtain *t*.

$$\mu\frac{(S_0+k_\mu D_{min}\tau)}{(\mu-k_\mu k_\tau \tau)} = (S_0 + k_\mu t) \Rightarrow \mu\frac{(S_0+k_\mu D_{min}\tau)}{(\mu-k_\mu k_\tau \tau)} - S_0 = k_\mu t \Rightarrow \frac{\mu(S_0+k_\mu D_{min}\tau)-S_0(\mu-k_\mu k_\tau \tau)}{(\mu-k_\mu k_\tau \tau)} = k_\mu t$$

$$\Rightarrow \frac{\mu S_0+\mu k_\mu D_{min}\tau-S_0\mu+S_0 k_\mu k_\tau \tau}{(\mu-k_\mu k_\tau \tau)} = k_\mu t \Rightarrow \frac{\mu k_\mu D_{min}\tau+S_0 k_\mu k_\tau \tau}{(\mu-k_\mu k_\tau \tau)} = k_\mu t$$

$$\boxed{t = \tau\frac{(\mu D_{min}+S_0 k_\tau)}{(\mu-k_\mu k_\tau \tau)}} \checkmark$$

I then express the response in terms of μ and τ *and* set $t^*=1$:

$$r(\tau,\mu) = exp\left\{-k_m\left(\frac{\mu-a\tau}{S_0+b\tau}\right) - k_t\tau\left(\frac{\mu+aD_{min}}{\mu-a\tau}\right)\right\} \text{(Eq. S4)},$$

where $a= k_\mu k_\tau$, $b=k_\mu D_{min}$, $c=S_0 k_\tau$

Section S4: Similarities between cases 1 and 2

Cases 1 and 2 share a number of common features, which should also be shared with other cases as long as the functions *L* and *S* are respectively defined as inverse of *D* and *E*. First, they leave empty spaces reflecting the existence of areas where fluctuations are not allowed to exist as point vectors. In the above two cases, the mapping functions contain a hyperbolic relationship. This is better appreciated by expressing the tolerances (E_1,E_2, for cases 1 and 2 respectively) and developmental times (D_1,D_2) as:

$$E_1 = c_1/(1 + c_2 t)\ ,\ E_2 = \log\ (c_3/t^z)$$

$$D_1 = c_4 + c_5/m\ ,\ D_2 = \exp(c_6 + c_7/m\ )$$

where c_i (i=1,…7) are constants. Notice that by applying the transformations, $E'_2=exp(E_2)$ and $D'_2=log(D_2)$ we recover inverse power functions (the hyperbolic function for E'_2 would be a special case with z=1); one could then express the intrinsic frame in terms of the coordinate system with $\mu' = m/E'_2$ *and* $\tau' = t/D'_2$.

In addition, in Case 1, as *E(t)* tends to zero, μ tends to infinity, but τ acquires values depending on *m*; hence, the horizonal line represented by $t=exp(E_{max}/z)$ is projected into the intrinsic frame as a vertical line at infinity, which in practice lies outside the area where the response is quantified.

Section S5: Modelling plasticity

Briefly, the mapping of the cue to signal is modelled as a sigmodal function (see e.g. Nijhout & Reed 1916) incorporating threshold phenomena in response to the value of the cue (e.g. Fowler 2008, Condon et al 2010). The second function maps the signal to the phenotype through a linear conditional function where the rate of phenotypic change increases with temperature. The third function maps the phenotype to the tolerance using a linear equation. Modelling the alternative of discrete forms of plasticity (documented in Buoro et al. 2009, Reid & Acker 2022) would require a sigmoidal or step function at this stage.

An important point in this model is that one must consider processes occurring during the fluctuation. Therefore, in addition to the consideration of the fluctuations as magnitudes and time scales, I will define an additional time variable (=x). Here, notice that time is introduced as an additional variable, which is not the same as the time scale of the fluctuation (t) nor the observation time (t^*); both t and t^* are specific values of x which ranges from the initiation of the experiment to the moment when observations are made.

I modelled the fluctuation as a square wave (Figs. S1, S2), so that temperature increases faster towards the maximum value, given by the magnitude *(=m*). In consequence, the differences in the rate of temperature increase among waves of different time scales is minimized as compared to using a sine or cosine function. The fluctuation is modelled as a solitary wave using the equation:

$$y(x) = \frac{m}{arcan(\delta)} \cdot \arctan\left[\delta \cdot \sin\left(\frac{2\pi x}{2t}\right)\right] \text{(Eq. S5)}$$

The parameter δ determines how flat the wave will become and t is the time scale of the fluctuation, here defined as half the wave period (=$2t$).

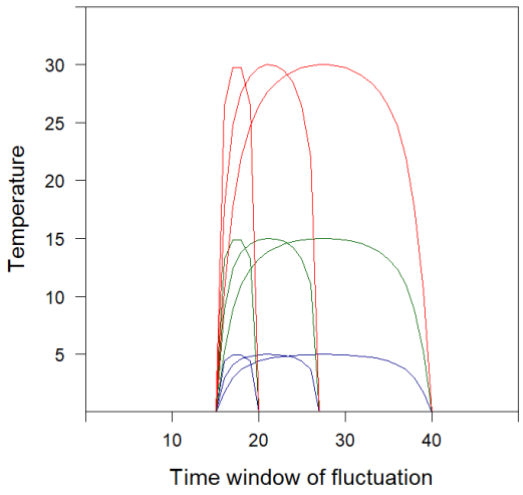


Figure S1. A subset of the modelled fluctuations, combining three magnitudes (m= 5, 15 and 15 °C) and time scales (5,15 and 25 days). All fluctuations were modelled from equation S5, with δ=4.

From cue to signal: I model the first step as a sigmoid function mapping the environmental cue (e.g. temperature) to an internal signal that initiates the formation of the phenotype. Such threshold is related to mechanisms accounting for high "false alarm costs" of responding to the cue (Getty 1996, Laubach et al. 2018), e.g. when changing from winter to summer phenotype at the wrong time compromises survival. The first function, $F_{c\rightarrow s}$, maps the cue to the signal as:

$$F_{c\rightarrow s} = \frac{f_{csm}}{1+e^{k_s(y_u-y)}} \text{ (Eq. S6)}$$

In equation S6, $y=y(x)$ is the value of the environmental cue (i.e. temperature), which varies through time and y_u is the threshold value of the environmental cue triggering a response, i.e. the mechanism driving the formation of the phenotype. The constant f_{csm} is the maximum value of the response and k_S is a rate constant indicating how sharp is the triggering of the response. In the example (Fig. 8), the environmental cue is the same as the environmental fluctuation (=temperature).

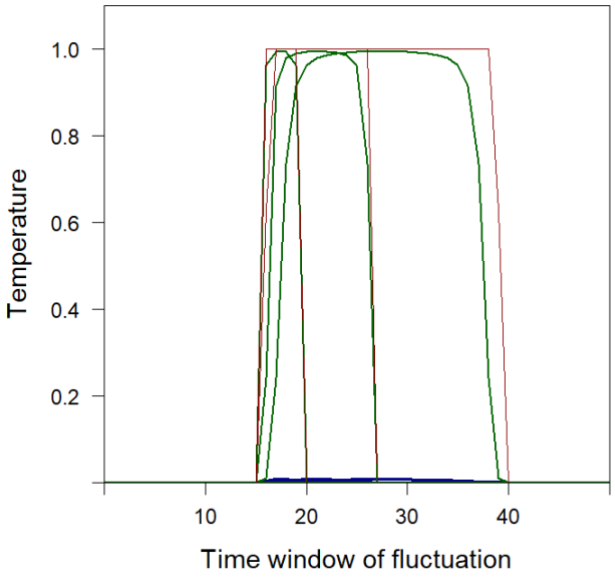


Figure S2. A subset of the modelled signal for combinations of three magnitudes (5,15 and 15 °C) and time scales (5,15 and 25 days). The signal is triggered when the cue (=temperature) reaches a threshold ($y_u=10°C$) and the function uses $Ks=1$. Note that no signal is shown in the case of fluctuations of magnitude =5°C because such fluctuations are under the threshold.

The second function $F_{s\rightarrow p}$ maps the signal to the phenotype, and indirectly determines the dynamics of the conversion of the phenotype over time from its current form (f_{sp1}) to the new form (f_{sp2}). I use the following conditions:

(1) At times $x< x_u$, when the temperature is lower than the threshold temperature (y_u) triggering the signal:

$$F_{S\rightarrow P} = f_{sp1} \text{ (S7a)}$$

(2) Beyond the above defined thresholds, the phenotype changes until the time when $F_{S\to P} = f_{sp2}$. Within those limits we have:

$$F_{S\to P} = f_{sp1} + \sum_x f_{r(x)} \text{(S7b)}$$

(3) At a given time $F_{S\to P}$ reaches a maximum f_{sp2} after which the phenotype remains at that constant value (implying that the formation of the phenotype is driven by a regulatory process). At subsequent times:

$$F_{S\to P} = f_{sp2} \text{ (S7c)}$$

In equation (S7b), $F_{s\to p}$, increases through time a sum of fractions, f_r that depend on temperature:

$$f_r = \frac{f_{rm} \cdot y}{k_r + y} \text{ (S8)}$$

where f_{rm} is the asymptotic maximum and k_r is a half saturation constant. Those fractions are rates of increase and the inverse give the time scale of the formation of the phenotype. Equation (S7) captures the realistic situation where the rate of phenotypic change increases with temperature but reaches a maximum f_{rm} reflecting a physiological constraint.

The third function maps the phenotype to the tolerance. For simplicity, I use a linear function such that tolerance range from its previous value (E_1) up to a maximum value (E_2).

$$E = E_1 + (E_2 - E_1) \cdot F_{S\to P} \text{ (S9)}$$

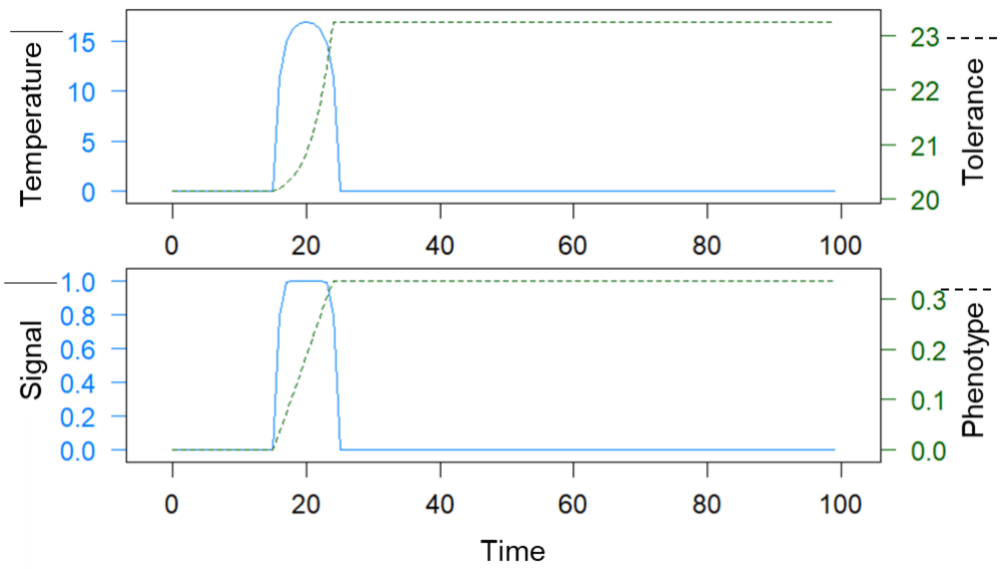


Figure S3. Summary of responses with example for *m = 20* and *t = 20*. Upper panel: changes in temperature and resulted change in the tolerance range. Lower panel: Intermediate steps: changes in the signal (following the cue of temperature) triggering the change in the phenotype. The signal follows eq. (S5) with maximum $f_{scm}=1$, $k_S=1$ and threshold temperature $y_U=10°C$. The phenotype was modelled from Eq. (S6) and Eq. (7.) In Eq. (6), the minimum and maximum values are $f_{sp1}=0$, $f_{sp2}=1$; x_U is the time which $F_{C\to S}$ reaches the threshold value $F_U= 1/6$, which

induces the change in the phenotype. In Eq. (7), driving the temperature dependence of the rate of phenotypic change, the maximum rate is f_{rm}=0.05 and the half saturation constant $k=5$. The tolerance was modelled from Eq. (8) with lower and upper thresholds $E_1=20$ and $E_2=40$.

Equations (S6) to (S9) are used to calculate the tolerance range and μ for each combinations of t and m (example in Fig S4).

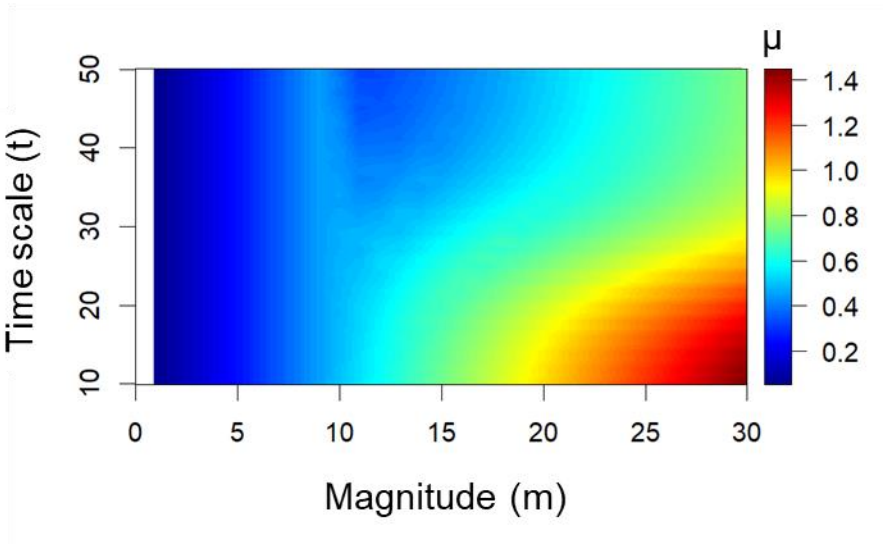


Figure S4. Heat map of μ based on equations and parameters given in the legend of Fig S3

There are three important points to notice. First, equations (S6-S9) model an irreversible mechanism because the state of the phenotype will not be updated by the cue after the fluctuation (hence, it does not return to the initial state). I did not model reversible plasticity because of the practical reason that the observations, made here after the fluctuation took place will not record the change in the tolerance range (the effects of the reversible plasticity on tolerance must be studied adding observations during the fluctuation). Although the current experimental set up does not detect transient phenomena (i.e. occurring during the fluctuation), it will detect the consequences on the response (e.g. body size). A possible scenario is that body size does not change with the time scale of the fluctuation because of the buffering effect of the plasticity. Alternatively, if the (reversible) plastic response cannot be sustained over long times (and hence the tolerance range drops while the fluctuation is taking place), then the time scale of the fluctuation will affect the response.

Second, the model used here is valid for a continuous change in the tolerance range. The continuous function mapping the phenotype to the tolerance implies that the phenotype is functional at any time, although the limitations given by equation (S7) implies that the optimal phenotype is lagging behind the thermal change during the fluctuation. Discrete changes should be modelled through an equation driving the formation of the phenotype, rather than its change, although such equation could have the same form as Eq. (S6). One could then consider a sigmoid or step function for Eq. (S8) which describes the functionality of the phenotype.

Third, it is important to identify the time lags considered in the above model. (1) The time between the moment when the observer judges that the fluctuation starts (=x_0) and the moment when organism perceives it (=x_u), i.e. when the cue is transformed into a signal; in statistical

terms, x_u is a latent (= unobserved) variable, but its effects are observed in Fig. S4 as a change in the values of μ. (2) Because the rate of change in the phenotype follows an asymptotic pattern, it will lag behind the thermal change during the fluctuation; although this is not detected in the tolerance range (i.e. it is a transient effect) it will have consequences for the response. There is a third time lag (not considered here) between the moment when the phenotype starts to be formed and the moment when it becomes functional. Such time lag would require a different model for the function mapping the phenotype to the tolerance. Time lags of this type are likely to occur in plastic responses associated to body morphology in crustaceans, as the consequence of their growth through moulting events. In such case, structures are usually formed previous to the moult but remain underneath the exoskeleton and become functional only after moulting.

Section S6: Worked example

6.1 Introduction

6.1.1. Experimental setup

The example is a simulation of an experiment where individuals of an ectothermic species were reared from hatching to metamorphosis (or maturation depending on choice), being exposed to thermal fluctuations (i.e. as a wave) of different clock time scale (= t from 10 to 50 days) and magnitude (from 1 to 10 thermal units). The experiment follows a gradient design using individual rearing (i.e. one individual per glass container. Over the text, I will comment on how to do calculations if more than one replicate is used. This experiments represents an example for the case of rearing decapod crustacean larvae from hatching to metamorphosis. The experiments would use 90 glasses; water change and re-feeding would take place every 1-2 days depending on the organism (methods in Torres et al. 2021). The experiment would be carried out using 10 water baths (or a water table: see Leiva et al. 2022 as example) keeping the temperature constant and then moving replicate units from a room, set at the baseline temperature to each water bath and returning it to the room after a number of days predetermined by time scale of the fluctuation being simulated.

6.1.2 Equations used in the simulation

The equations simulating the data and fluctuations can be implemented in an electronic spreadsheet or in e.g. R. The fluctuation was modeled as in the example of plasticity (Case 3 in main text) with time defined as the variable "x". Temperature, y(x) is modeled as an approximation to a solitary square wave, using the function:

$$y = (2m/\pi) \cdot atan(sin(2\pi x/2t)/\delta)$$

The parameter δ determines the flatness of the wave; m is the magnitude and t is the time scale (i.e. half the wave period $= 2t$). The function $atan$ is the arc-tangent ($= tan^{-1}$).

Developmental time, tolerance and body size are modelled using recursive formulas. Developmental time is simulated as depending on degree days. Organisms mature on the day where the cumulative temperature reaches or surpasses $800°C \cdot days$. The equation for this calculations is as follows:

$$\varphi = \sum_{x=1}^{100} y\,(x)/800 + \zeta_1$$

where φ is defined as the developmental state variable and ζ is a Gaussian error on mean=0 and variance=0.001. A small amount of Gaussian noise is added in all biological variables in order to simulate error but avoiding to produce highly noisy data. Developmental time (= D) is given by

$$1 = \sum_{x=1}^{D} y\,(x)/800 + \zeta_1(x)$$

The calculation is made through a loop where a $\varphi(x,t,m)$, accumulates the value of temperature per day until it reaches 800 C days. In a second step,$\varphi(x,t,m)$ is re coded,as binary indicating immature (=0) or mature (=1). The re-coding was preceded by a step ensuring that the developmental state variable is ever increasing (a condition that was violated after the introduction of Gaussian noise). The recording to binary is important because in the experiments one can only stage an animal as immature or mature.

The metric for tolerance is given by a physiological state variable $S(x,y)$, and the threshold temperature setting the tolerance range is $s = 0.5$. This would represent a case where the metric is the proportion of survivors or a physiological variable quantifying the state of the organism . The time course of $S(x,y)$ is modeled as an exponential decay using the difference equation:

$$S(x+1) = S(x) \cdot exp\big[a \cdot [y(x) - 5]\big] + \zeta_2(x)$$

where the exponential term drives the decrease in the physiological state and _{2} is a Gaussian error (mean=0, variance=0.001). The exponential term depends on the temperature on the day and a constant rate (a=0.001); a is set so as to produce a smooth decrease in S along the time range of the simulation (100 days), The exponential term is zero at the optimal temperature (=5C); hence, S remains constant after the fluctuation is experienced. The fluctuation components (m and t) drive S through the effect on $y(x,t,m)$.In this model, there is neither a recovery (S does not increase through time) nor time lag effects (S at a given time $x = x_f$ does not depend on temperatures at any time $x < x_f$). This model will however reflect the history of the fluctuation because longer t results in lower S at any chosen t^*.

The invariant response is represented as body size (=R). Body size is modeled as using the von Bertalanffy growth function. It is computed from a difference equation using a modification of the Ford-Waldford formulation.

$$R(x+1) = R_{inf} - exp(-k) \cdot \big[R(x) - R_{inf}\big] + \zeta_3(x)$$

where R_{inf} is the asymptotic size, k is the catabolic constant and _{3} is a Gaussian error (mean=0 , variance= 0.3). As in a realistic case, R increase over time also after the fluctuation is experienced.

Both k and R_{inf} decrease exponentially with temperature, $y(x)$, according to the functions:

$$k = 0.02exp(-0.02y)$$

$$R_{inf} = 20exp(-0.02y)$$

In both functions, the constants were chosen so as to produce smooth changes in body size along the time range considered. Those functions lead to a decrease in the invariante response (R) when the fluctuations are characterized by large m.

6.2. Preliminary data handling

Set working directory if needed

setwd("")

Libraries needed

```
library(dplyr)
library(lattice)
library(latticeExtra)
library(plot3D)
library(plot3Drgl)
library(mgcv)
library(nlme)
library(readr)
library(gridExtra)
library(tactile)
```

Uploading data: Column names and long names: x= time (in days) mag= magnitude of temperature tt= Time scale of thermal fluctuation y = temperature over time = y(x) Phi= binary variable: 0=immature; 1= mature. s= binary variable: 0= thermal threshold not reached; 1= thermal threshold reached. R= Invariant response (body size).All data should be numeric.

```
df <- data.frame(read_csv("workedexample.csv"))
```

The following figures show examples of thermal fluctuations and the biological variables covering the range of t and m in the example.

Thermal fluctuations:

```
color1<-c("blue","orange","#009E73")
color2<-c("#CCFFFF","#FFBF00","#CCFFCC")
mykey=list(text=list(c("t=10","t=25","t=50")),
           corner = c(0.02, 0.9),
           points=list(pch=21:23,col=color1,fill=color2))

xyplot(y~x|factor(mag),type="b", groups=factor(tt),grid=TRUE,
       key = mykey,pch=c(21,22,23),layout=c(3,1),
       strip=strip.custom(factor.levels=c("m=1","m=5","m=10")),
       xlab= "Time variable, x", ylab="Temperature, y",
       data=df[which(df$mag %in% c(1,5,10) & df$tt %in% c(10,25,50)),])
```

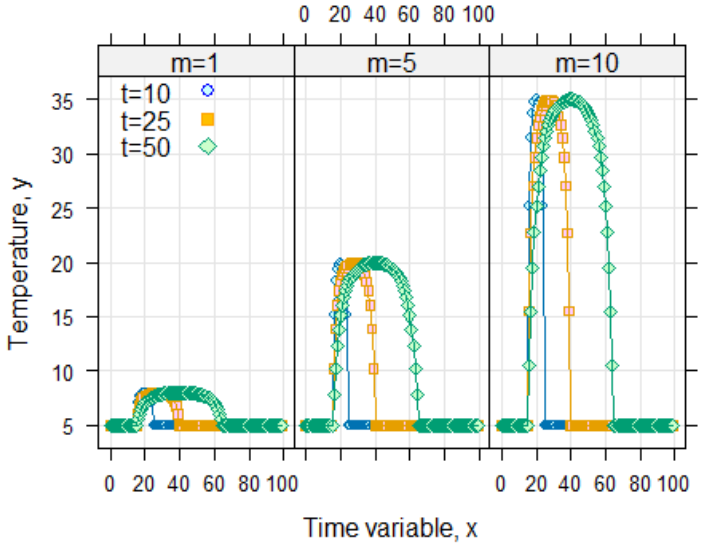


Figure S5. Time course of selected simulated thermal fluctuations characterized by different amplitude (m) and time scale (t).

```
xyplot(phi~x|factor(mag),type="b", groups=factor(tt),grid=TRUE,
       key = mykey,pch=c(21,22,23),layout=c(3,1),
       strip=strip.custom(factor.levels=c("m=1","m=5","m=10")),
       xlab= "Time variable, x", ylab="Developmental state,",
       data=df[which(df$mag %in% c(1,5,10) & df$tt %in% c(10,25,50)),])
```

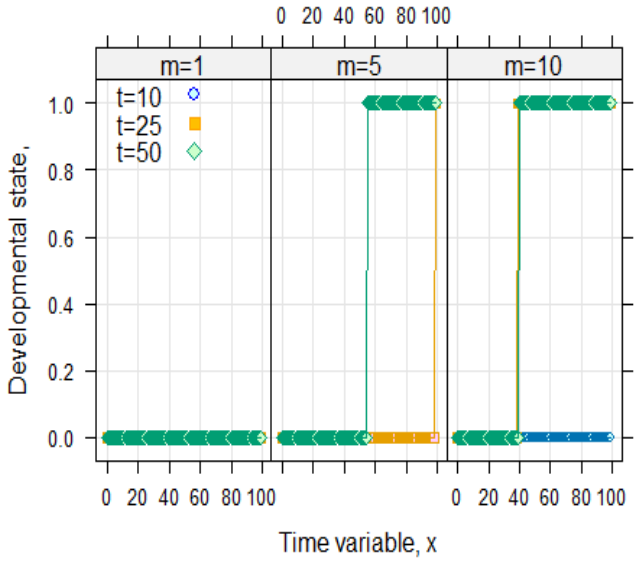


Figure S6. Time course of developmental state variable (0=immature, 1=mature) for selected simulated thermal fluctuations characterized by different amplitude (m) and time scale(t).

```
xyplot(s~x|factor(mag),type="b", groups=factor(tt),grid=TRUE,
       key=mykey,pch=c(21,22,23),layout=c(3,1),
       strip=strip.custom(factor.levels=c("m=1","m=5","m=10")),
       xlab= "Time variable, x", ylab="Physiological state,s",
       data=df[which(df$mag %in% c(1,5,10) & df$tt %in% c(10,25,50)),])
```

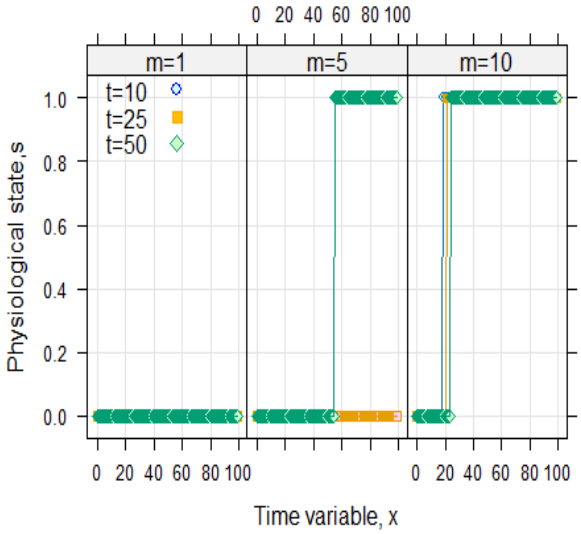


Figure S7. Time course of physiological state variable used to define the thermal tolerance limit (0=no response, 1=critical response) for selected simulated thermal fluctuations characterized by different amplitude (m) and time scale(t).

```
xyplot(R~x|factor(mag),type="b", groups=factor(tt),grid=TRUE,
       key=mykey,pch=c(21,22,23),layout=c(3,1),
       strip=strip.custom(factor.levels=c("m=1","m=5","m=10")),
       xlab= "Time variable, x", ylab="Body size, R",
       data=df[which(df$mag %in% c(1,5,10) & df$tt %in% c(10,25,50)),])
```

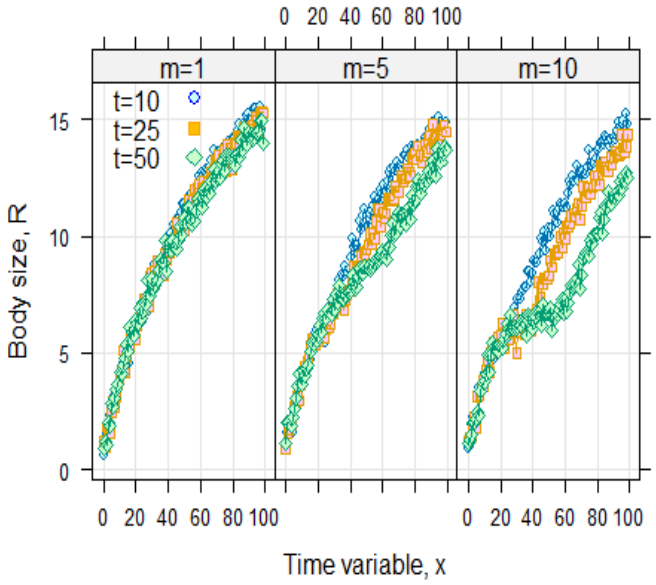


Figure S8. Growth in body size under selected simulated thermal fluctuations characterized by different amplitude (m) and time scale (t).

6.3. Compute τ and μ

6. 3.1 Steps for τ

The first step is the calculation of duration of development (DD) for each combination of fluctuation time scale (tt) and magnitude (mag). The loop below, extracts the time at which the binary variable switches from 0 to 1, for each combination of m and t. Calculations are stored in data frame dfDD

```
DD<-c1<-c2<-NULL
for(j in 1:10){
  for(k in seq(10,50,5)){
dfsub<-df[which(df$mag==j & df$tt==k),]
for (i in 1:nrow(dfsub)){
  datosi<-dfsub[i,]
  if(datosi$phi<1 & datosi$x<99){next} else {if(datosi$phi<1 & datosi$x==9
9){DDi<-NA
  DD<-c(DD,DDi)
  c1<-c(c1,j)
  c2<-c(c2,k)
  break}else {DDi<-datosi$x
  DD<-c(DD,DDi)
  c1<-c(c1,j)
  c2<-c(c2,k)
  break}
}}}}
```

```
dfDD<-data.frame(mag=c1,tt=c2,DD=DD)
dfDD<-arrange(dfDD,tt,mag)
```

For the calculation of τ^* (and τ), we must note that $\tau^* = 1$ corresponds to the time ($= x$) coinciding with the duration of development (D). Any fluctuation time scale must be scaled according to that the duration of development. The code below checks that the data are aligned properly, then places the D values in the original data frame and calculates τ^* (and τ).

```
df$tt2<-rep(dfDD$tt, each=100)
df$mag2<-rep(dfDD$mag, each=100)
range(df$mag-df$mag2)

## [1] 0 0

range(df$tt-df$tt2)

## [1] 0 0

df$DD<-rep(dfDD$DD, each=100)
df$tau<-df$tt/df$DD
df$taustar<-df$x/df$DD
```

6.3.2 Steps for μ

The point $\mu = 1$ occurs when the *s* variable switches from 0 to 1. Following the equation of μ, we get $\tau = 1 = m/E(t)$. Therefore, at that conditions we have that $m = E(t)$.

In each experiment, the response will switch from 0 to 1 at a given time x. Hence, points where $\mu = 1$ exist at many of the time slices defined by $x = t^*$. How μ varies through time depends on how the metric to calculate tolerance changes after the fluctuation is experienced. If the metric is the the proportion of survivors, tolerance might also decrease also after the fluctuation is experienced. Hence, μ will vary with the observation time $x = t^*$. In the worked example, the metric of tolerance does not change after the fluctuation.

```
mus<-tts<-xs<-mags<-mm1s<-NULL
dfE<-data.frame(x=rep(NA,900),tt=rep(NA,900),E=rep(NA,900))
# The double loop selects a time step and a  t-value
i=1
for(l in 0:99){
for(j in seq(10,50,5)){
    dfsub<-df[which(df$x==l & df$tt==j),]

# This loop finds mm1 = m at which tolerance switches to 1
```

```
  for(k in 1:10){
    ss<-dfsub$s[k]
  if(ss==1){mm1<-dfsub[k,2]
  break}else{mm1<-NA}
  }
dfE$x[i]<-l
dfE$tt[i]<-j
dfE$E[i]<-mm1
i=i+1
# Calculation : mu=m/mm1
mu<-dfsub$mag/mm1
# Storage of data
mm1s<-c(mm1s,mm1)
mus<-c(mus,mu)
tts<-c(tts,dfsub$tt)
xs<-c(xs,dfsub$x)
mags<-c(mags,dfsub$mag)
}}
```

```
# Output of loop
chequeo<-data.frame(x=as.numeric(xs),tt=tts,mag=mags,mu=mus)
# Output must be re-ordered according to the data frame df
chequeo<-arrange(chequeo,tt,mags,x)

df$mu<-chequeo$mu
rm(mus,mags,tts,xs)
rm(chequeo)
```

6.4. The invariant response

6.4.1 The mt-projection: space of existence and extreme fluctuations

We can now plot the invariant response, τ and μ. This will help us to identify the space of existence and the set of fluctuations categorized as extreme (using $\mu = 1$ as criterion). In the figure, we will mask values of body size outside the space of existence as they would not exist in a real case scenario. However, recall that in the example, the body size was still quantified after the time of maturation (after $\tau = 1$).

```
mag<-seq(1,10,1)
tt<-seq(10,50,5)

  dftstar<-subset(df, x==70)
  dfpoly<-dftstar[which(dftstar$mu==1),2:3]
  xcoord<-c(dfpoly$mag,10,10)
```

```
  ycoord<-c(dfpoly$tt,50,10)
sizemat<-matrix(data=dftstar$R, nrow=10, ncol=9)
mumat<-matrix(data=dftstar$mu, nrow=10, ncol=9)
taumat<-matrix(data=dftstar$tau, nrow=10, ncol=9)
taustarmat<-matrix(data=dftstar$taustar, nrow=10, ncol=9)
image2D(sizemat,mag,tt,colkey = TRUE, resfac = 6,
          #levels=seq(0.1,3.4,0.2),
          xlim=c(1,10),ylim=c(10,50),zlim=c(8,14),
        xlab="Magnitude", ylab="Time scale")

polygon2D(xcoord,ycoord, border ="black",col="white",add=TRUE)

contour2D(mumat,mag,tt,colkey = FALSE,
          col=c("black","black"),
          lty=1,lwd=2,
          levels=c(1), xlab="Magnitude", ylab="Time scale",
          xlim=c(1,10),ylim=c(10,50),
          add=TRUE)

contour2D(taumat,mag,tt,colkey = FALSE,
          col=c("dark blue"),lty=2,lwd=2,
          levels=c(1),
          xlab="Magnitude", ylab="Time scale",
          xlim=c(1,10),ylim=c(10,50),
          add=TRUE)
contour2D(taustarmat,mag,tt,colkey = FALSE,
          col=c("dark blue"),lty=1,lwd=2,
          levels=c(1),
          xlab="Magnitude", ylab="Time scale",
          xlim=c(1,10),ylim=c(10,50),
          add=TRUE)
abline(v =5, lty = 2)
abline(h=30,lty=2)
```

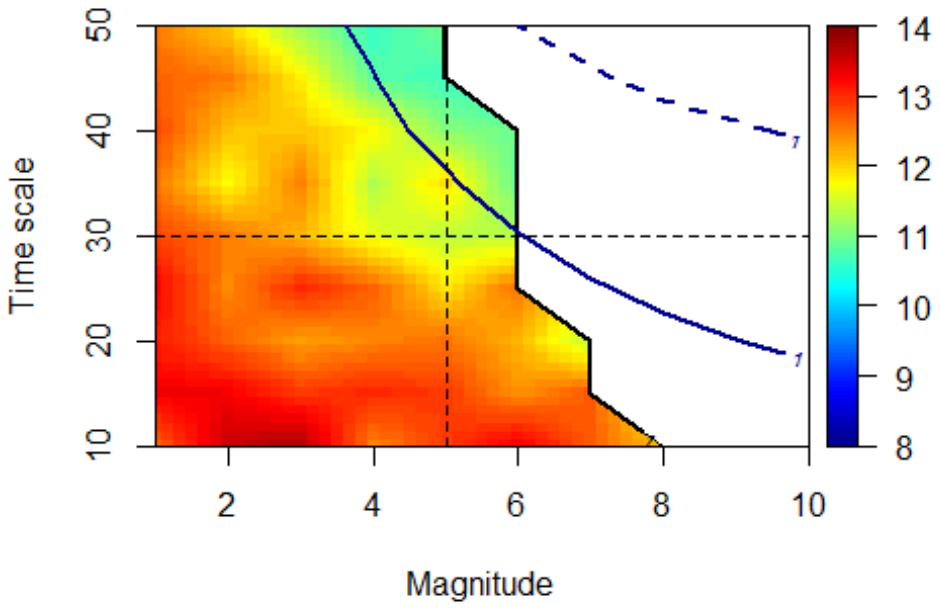


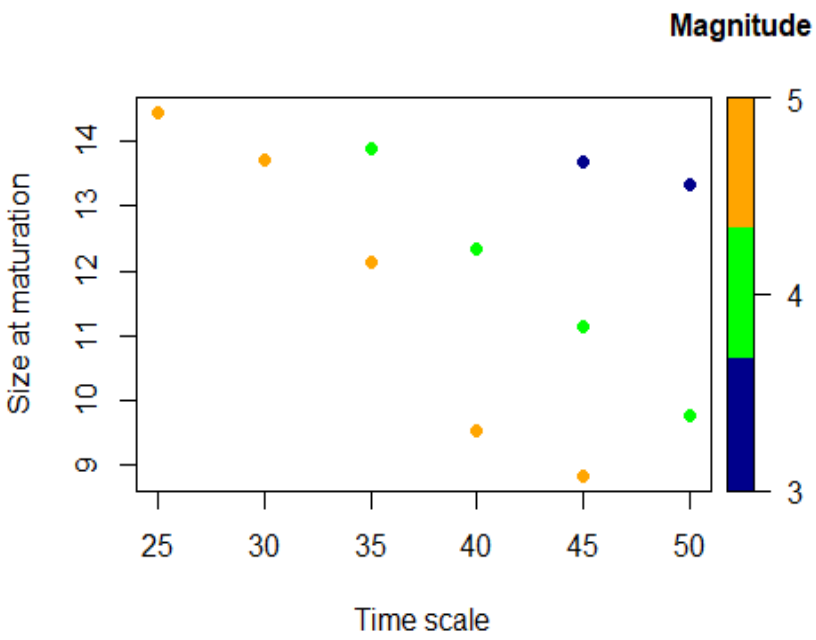
Figure S9. The (mt)-projection of the invariant response at t^*=70. The black continuous line corresponds to $\mu = 1$, defining the region of existence. The black dashed line delimit the region (m<5) where the tolerance becomes independent of the time scale of the fluctuation. The horizontal black dashed line indicate the region (t>30) where fluctuations enable maturation. The blue line corresponds to tau star=1 and the blue dashed line is $\tau = 1$. The line of $\tau^* = 1$ gives the time of maturation. In the example, the time of maturation was simulated also for m$\mu > 1$ in order to show the region the fluctuation magnitude is high enough to elicit a response before the organisms reach maturation ($\tau = 1$ line lies in the region where mu>1). The line of $\tau = 1$ gives the set of fluctuations with time scales equal to that of the time of maturation. In this case, fluctuations of such length are located in the region of mu >1 showing that such type of fluctuations would not be tolerated (within the region defined in the diagram).

6.4.2 The response at maturation in the mt-projection

The code below produces the response at $\tau^* = 1$ as two different scatter plots o. The command rgl() will create a separate window and enable to rotate the image and better appreciate the pattern.

```
dfRtau<-df[which(df$taustar==1 & df$mu<1),c(2,3,7)]

scatter2D(dfRtau$tt,dfRtau$R, pch=20, cex=1.5,
          xlab="Time scale", ylab="Size at maturation",
          colvar = as.integer(dfRtau$mag),
          col=c("dark blue", "green", "orange"),
          colkey = list(at = c(3, 4, 5), side=4,
          labels = c("3", "4", "5")), clab = "Magnitude" )
```

```
scatter3D(dfRtau$mag,dfRtau$tt,dfRtau$R, phi=0, bty ="g",
          xlab="Magnitude", ylab="Time scale",
          zlab="Size at maturation",ticktype="detailed",
          pch=20, cex=2,
          colkey=FALSE )
```



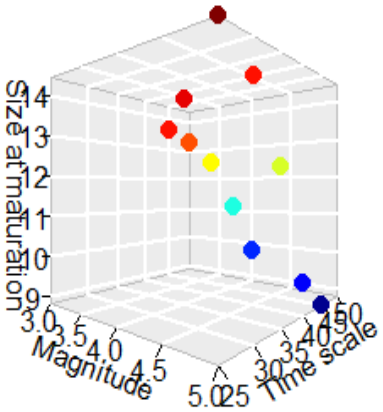


Figure S10. Two representations of the mt-projection of the invariant response at τ^*=1. Because of the sparsity of data I was not able to create a heatmap. A projection as heatmap is

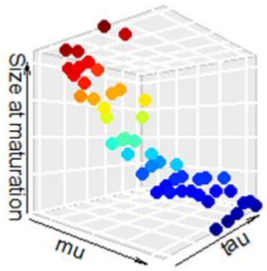
shown after model fitting (Figure S19). Note that in the extra-window one can rotate the scatterplot.

6.4.3 The (μ, τ)-projection

The figure that we need to create can be based on a scatter or on an image. In the latter case, the best option is to fit a general additive model (gam) and represent the predictions.

```
dfmutau<-df[which(df$taustar==1),c(7,11,13)]

# Image based on smoothed data
g1<-gam(R~te(mu,tau),data=dfmutau)
summary(g1)

##
## Family: gaussian
## Link function: identity
##
## Formula:
## R ~ te(mu, tau)
##
## Parametric coefficients:
##             Estimate Std. Error t value Pr(>|t|)
## (Intercept)  9.57716    0.05659   169.3   <2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Approximate significance of smooth terms:
##              edf Ref.df     F p-value
## te(mu,tau) 11.14  13.65 180.6  <2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adj) =  0.981   Deviance explained = 98.6%
## GCV = 0.20575  Scale est. = 0.15369   n = 48

range(dfmutau$tau)

## [1] 0.1595745 1.2500000

range(dfmutau$mu)

## [1] 0.600000 1.666667

scatter3D(dfmutau$mu,dfmutau$tau,dfmutau$R, phi=0, bty ="g",
          xlab="mu", ylab="tau", zlab="Size at maturation",
          pch=20, cex=2,
          colkey=FALSE )
```

```
mu<-seq(min(dfmutau$mu),1,length.out=20)
tau<-seq(min(dfmutau$tau),max(dfmutau$tau),length.out=20)
dfmutau2<-data.frame(expand.grid(mu=mu,tau=tau))
dfmutau2$R<-predict(g1, newdata=dfmutau2)
mutaumat<-matrix(dfmutau2$R,nrow=20,ncol=20) # mu varies with row

image2D(mutaumat,mu,tau,colkey = TRUE, resfac = 6,
          #levels=seq(0.1,3.4,0.2),
          #xlim=c(0,1),
        #,ylim=c(10,50),
        xlab=expression(paste(mu)), ylab=expression(paste(tau)))
```



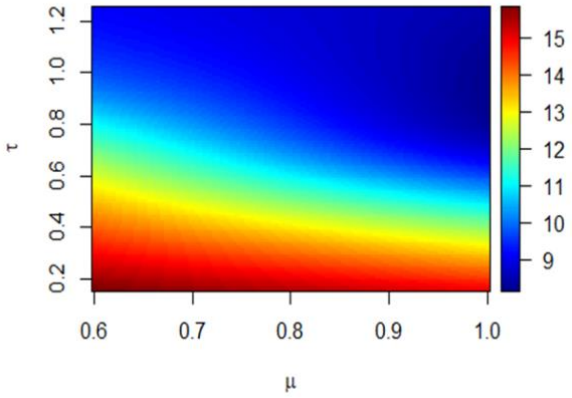


Figure S11. Two different representations of the $\mu\tau$-projection of the invariant response at the time of maturation ($\tau^* = 1$). As expected, the invariant response is much less responsive to μ than to τ especially, at low (or high) τ values, i.e. when the time scale of the fluctuations are short (or long) relative to the time of maturation.

6.5 Statistical analysis

The study of the role of different fitting methods is outside the scope of this paper; I refer to Zuur et al. (2009) for an overview and to Kreyling et al. (2018) for more details on gradient analysis. Briefly, I use backward model selection based on the Akaike Information Criterion (AIC). In addition, because the data is modeled with Gaussian errors, I focus on regression and do not include here the analysis of residuals; such analysis can be reproduced by the user adding appropriate code. The code contains however a check that the fitted and observed values follow a linear trend (plot and correlation).

For the models, I consider three points: (1) Parametric vs non-parametric models. I choose a parametric method (nonlinear regression) because SOFiA requires that we obtain equations. (2) Mechanistic vs phenomenological model. I opt for a phenomenological description assuming that the level of knowledge of the system is not sufficient to develop a mathematical theory. (3) Depending on the nature of the invariant response, it may be possible to study (3a) its time evolution from the start of the experiment, (3b) only over a few time points or (3c) only once (e.g. only a maturation). The choice depends on the cost of making an observation, on consequences of disturbing the environmental conditions being manipulated and on whether measurements are invasive (e.g. organisms must be killed). Here, I assume that the response can be observed two times: at a fixed clock time after all fluctuations are experienced ($t^* = 70 days$) at the time of maturation (τ^*=1). This assumption has also a third reason, which is to illustrate how the response change depended on the coordinate used to measure time.

Statistical models are fitted only to data falling inside the region of existence (including at times when $\mu = 1$, as animals can be still measured at that time).

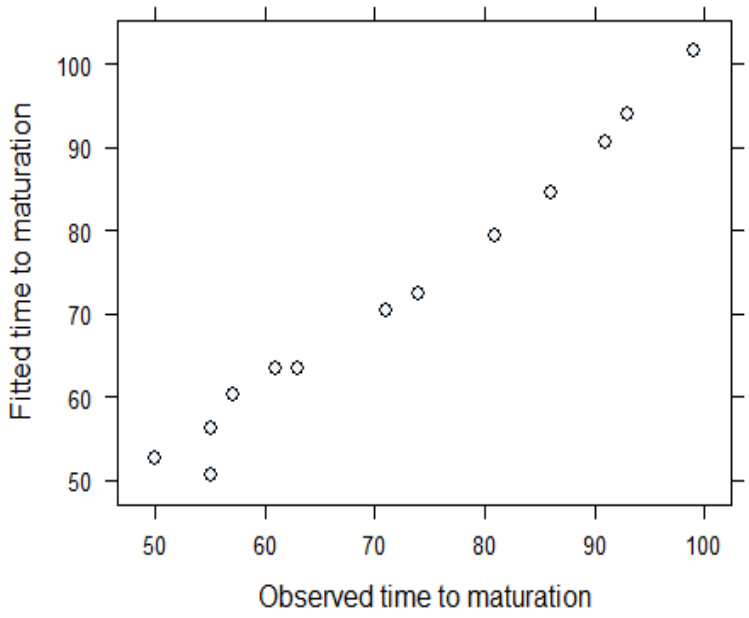
6.5.1 Developmental time and τ

The first step is to find a model for time to maturation. In the code below, the first line selects the data, using the time slice of $x = t^* = 70$ (the values of DD are repeated over each time slice). The subsequent lines run model selection using non-linear regression from the package *nlme* (Pinheiro et al. 2023). The choice of model includes those used in Case 1 and 2, in addition to other candidate models. The starting value of the parameter "a" is based on the maximum duration developmental time. The starting value of "b" is obtained by trial and error, starting with *b=1*.

```
dfDD2<-df[which(!is.na(df$DD) & df$mu<=1 & df$x==70),]

max(dfDD2$DD)

## [1] 99

d1<-nls(DD~a/(mag*tt)^b, start=list(a=90,b=1),data=dfDD2)
d2<-nls(DD~a/(1+mag*tt)^b, start=list(a=90,b=1),data=dfDD2)
d3<-nls(DD~a*exp(b/mag*tt),start=list(a=90,b=0.1),data=dfDD2)
```

```
d4<-nls(DD~a*exp(-b*mag*tt),start=list(a=90,b=0.01),data=dfDD2)
AIC(d1,d2,d3,d4)

##    df       AIC
## d1  3  77.05104
## d2  3  77.00644
## d3  3 146.78126
## d4  3  79.53617

dfDD2$fitd<-fitted(d1)
cor.test(dfDD2$fitd,dfDD2$DD)

##
##  Pearson's product-moment correlation
##
## data:  dfDD2$fitd and dfDD2$DD
## t = 29.872, df = 15, p-value = 8.855e-15
## alternative hypothesis: true correlation is not equal to 0
## 95 percent confidence interval:
##  0.9765171 0.9970807
## sample estimates:
##       cor
## 0.9916998

summary(d1)

##
## Formula: DD ~ a/(mag * tt)^b
##
## Parameters:
##    Estimate Std. Error t value Pr(>|t|)
## a 1.315e+04  2.367e+03   5.554 5.52e-05 ***
## b 1.007e+00  3.544e-02  28.410 1.86e-14 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 2.082 on 15 degrees of freedom
##
## Number of iterations to convergence: 9
## Achieved convergence tolerance: 2.125e-07

xyplot(fitd~DD,cex=1, pch=21, col="black",fill="aliceblue", data=dfDD2, yl
ab="Fitted time to maturation",
       xlab="Observed time to maturation")

xyplot(DD~I(mag*tt),cex=1, pch=21, col="black",fill=" dark blue", data=dfD
D2, ylab="Time to maturation",
       xlab="tm")+
```

```
  xyplot(fitd~I(mag*tt),pch=21,cex=0.5, col="black",fill="aliceblue", data
=dfDD2)
```



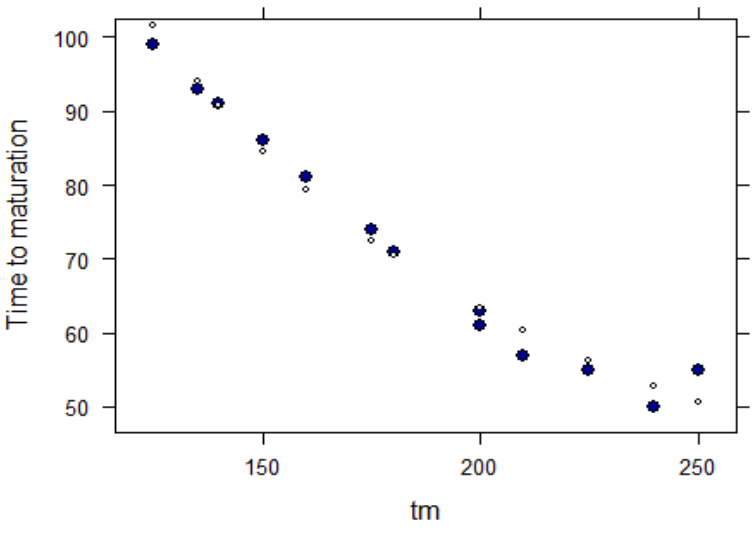


Figure S12. Two different graphs showing fitted vs observed time to maturation based in model d1 which showed the lowest AIC (with $\Delta AIC > 10$ vs the subsequent model). In the first panel, blue symbols: observed; light blue: fitted.

The next step is to reproduce τ from fitted model. The first loop adds the fitted duration of development to the data frame dfDD, including the NAs. In the second step, the fitted $\tau - values$ are calculated.

```
j=1
dfDD$mu<-df$mu[which(df$x==70)]
dfDD$Dfit<-NA
for (i in 1:nrow(dfDD)){
if(is.na(dfDD$DD[i])==TRUE|dfDD$mu[i]>1){next
  }else{dfDD$Dfit[i]<-dfDD2$fitd[j]
j=j+1}
}

# Calculation of fitted tau
df$Dfit<-rep(dfDD$Dfit, each=100)
df$taufit<-df$tt/df$Dfit
df$taustarfit<-df$x/df$Dfit
```

6.5.2 Tolerance and μ

Tolerance is defined as the magnitude of thermal fluctuation at which there is a critical response (coded as a switch of s from 0 to 1 in the data table). In the example, tolerance depends on t, but not on the time after the fluctuation is experienced (t^*). Recall that in the example, measurements were made also after maturation, because at t^*=70 some individuals already matured. Hence, the data set is not restricted to $\tau^* < 1$. An alternative scenario would be that tolerance is quantified before or at (but not after) maturation. In such case, μ and τ can only be calculated in complementary data sets.

```
dfE2<-dfE[which(!is.na(dfE$E) & dfE$x==70),]
max(dfE2$E)

## [1] 8

dfE2<-dfE[which(dfE$x==70),]

e1<-nls(E~a*(tt)^b, start=list(a=10,b=1),data=dfE2)
e2<-nls(E~(a+b*log(tt)), start=list(a=10,b=1),data=dfE2)
e3<-nls(E~a*exp(b/tt),start=list(a=10,b=0.1),data=dfE2)
e4<-nls(E~a*exp(-b*tt),start=list(a=10,b=0.01),data=dfE2)
AIC(e1,e2,e3,e4)

##    df       AIC
## e1  3  8.462066
## e2  3  7.938269
## e3  3 13.404193
## e4  3  9.616453
```

```
dfE2$fit<-fitted(e2)

xyplot(fit~E, data=dfE2)

xyplot(E~tt, pch=21, col="black",fill="blue", data=dfE2,
       ylab="Tolerance", xlab="Time scale of fluctuation,t") + xyplot(fit~
tt,cex=0.5,type="b", data=dfE2)
```

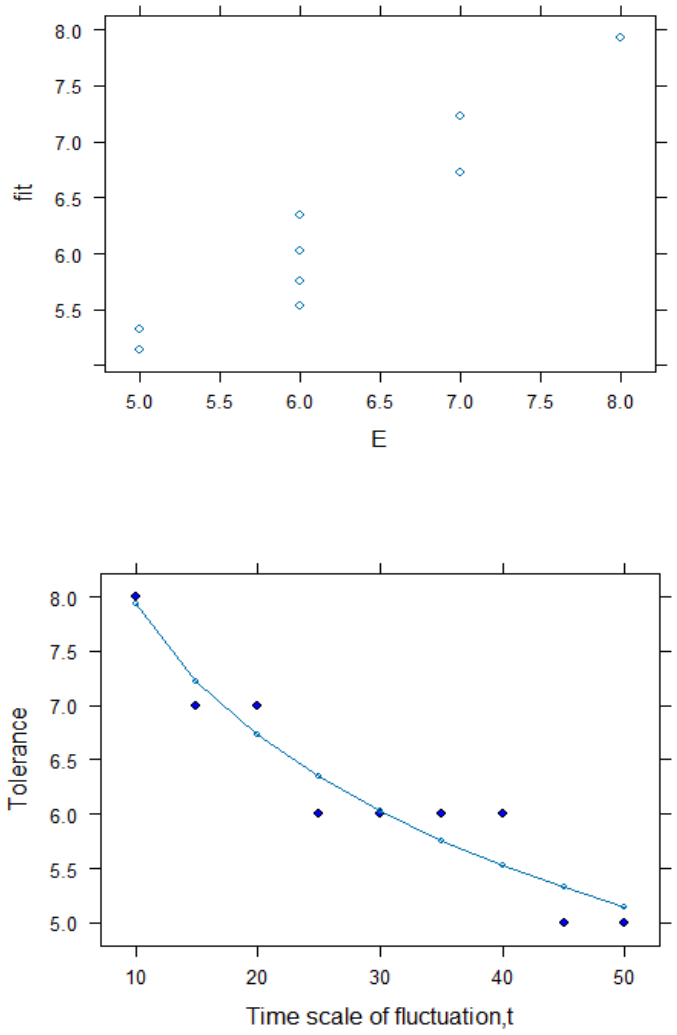


Figure S13. Top panel: Fitted vs observed tolerance. Bottom panel: fitted (line) vs observed tolerance limit (blue circles). All panels are based in model *e*2 which showed the slightly lowest AIC (than competing models with the same number of parameters.

The next step is the calculation of fitted μ. First, fitted tolerance range is stored in the time slice $x = 70$. Then, fitted μ is calculated as the ratio of fitted tolerance and m. Finally, both μ-values calculated from fitted model and observations are plotted in the space of fluctuations.

```
  dftstar<-subset(df, x==70)
dftstar$Efit<-rep(dfE2$fit, each=10)
dftstar$mufit<-dftstar$mag/dftstar$Efit


mufitmat<-matrix(data=dftstar$mufit, nrow=10, ncol=9)


contour2D(mumat,mag,tt,colkey = FALSE,
          col=c("dark blue"),lty=2,lwd=2,
          levels=c(1),
          xlab="Magnitude", ylab="Time scale",
          xlim=c(1,10),ylim=c(10,50),
          add=FALSE)
contour2D(mufitmat,mag,tt,colkey = FALSE,
          col=c("red"),lty=1,lwd=2,
          levels=c(1),
          xlab="Magnitude", ylab="Time scale",
          xlim=c(1,10),ylim=c(10,50),
          add=TRUE)
```

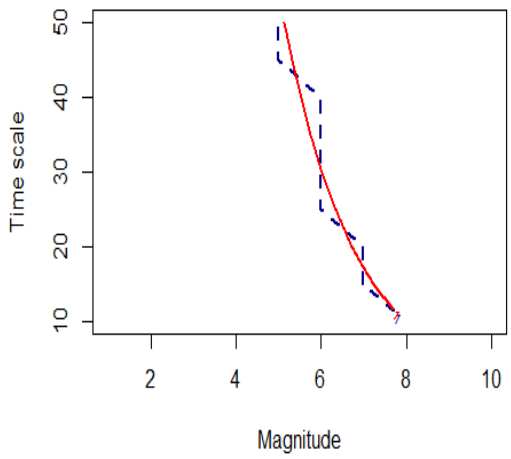


Figure S14. Curves showing μ-values calculated from fitted model (red line) and observations (blue dashed line) at the time slice $t^* = 70$.

6.5.3 Model for the invariant response (body size)

For model fitting, we take the realistic scenario that the invariant response is not observed at $\mu > 1$. The response at $t^* = 70$ is modeled using exponential and polynomial functions, considering a multiplicative term. The selection leads to two different candidate models and I choose the linear model. Notice that I had silenced some code in order to focus on the main output.

```
dftstar$R2<-ifelse(dftstar$mu>1, NA,dftstar$R)
dftstar2<-dftstar[which(!is.na(dftstar$R2)),]
# Exponential model
# Step by step processes used to find initial parameter values:
# Step 1: estimate a and b
rt<-nls(R2~a*exp(c*tt), start=list(a=10,c=-0.1),data=dftstar2)
#Step 2: use estimated a and b as starting values
rtm<-nls(R2~a*exp(b*mag+c*tt), start=list(a=13,b=-0.1,c=-0.003),
         data=dftstar2)
#Step 3: use estimated a,b and c, to find d.

rtmexp<-nls(R2~a*exp(b*mag+c*tt+d*mag*tt), start=list(a=14,b=-0.02,c=-0.00
4,d=-0.0005),
          data=dftstar2)

rtmexp2<-nls(R2~a*exp(b*mag+c*tt), start=list(a=14,b=-0.02,c=-0.004),
          data=dftstar2)

rtmexp3<-nls(R2~a*exp(c*tt+d*mag*tt), start=list(a=14,c=-0.004,d=-0.0005),
          data=dftstar2)

rtmexp4<-nls(R2~a*exp(b*mag+d*mag*tt), start=list(a=14,b=-0.02,d=-0.0005),
          data=dftstar2)

rtmexp5<-nls(R2~a*exp(d*mag*tt), start=list(a=14,d=-0.0005),
          data=dftstar2)

AIC(rtmexp,rtmexp2,rtmexp3,rtmexp4,rtmexp5) # Keep rtmexp3
```

```
##         df      AIC
## rtmexp   5 49.10956
## rtmexp2  4 69.39824
## rtmexp3  4 47.17395
## rtmexp4  4 49.18062
## rtmexp5  3 53.31589
```

```
# Linear model
rtmlin<-lm(R2~tt+mag+I(tt*mag), data=dftstar2)
rtmlin2<-lm(R2~tt+mag, data=dftstar2)
rtmlin3<-lm(R2~mag+I(tt*mag), data=dftstar2)
rtmlin4<-lm(R2~tt+I(tt*mag), data=dftstar2)# best linear model
rtmlin5<-lm(R2~I(tt*mag), data=dftstar2)
AIC(rtmlin,rtmlin2,rtmlin3,rtmlin4,rtmlin5)
```

```
##         df      AIC
## rtmlin   5 49.02313
## rtmlin2  4 66.95880
## rtmlin3  4 49.82108
## rtmlin4  4 47.02611
## rtmlin5  3 53.28650
```

```
AIC(rtmlin4,rtmexp3)
```

```
##         df      AIC
## rtmlin4  4 47.02611
## rtmexp3  4 47.17395
```

```
# There are two different models with similar fit.
cor.test(fitted(rtmlin4),dftstar2$R2, na.rm=TRUE)
```

```
##
##  Pearson's product-moment correlation
##
## data:  fitted(rtmlin4) and dftstar2$R2
## t = 15.019, df = 54, p-value < 2.2e-16
## alternative hypothesis: true correlation is not equal to 0
## 95 percent confidence interval:
##  0.8317671 0.9393256
## sample estimates:
##       cor
## 0.8982463
```

```
cor.test(fitted(rtmexp3),dftstar2$R2, na.rm=TRUE)
```

```
##
##  Pearson's product-moment correlation
##
## data:  fitted(rtmexp3) and dftstar2$R2
## t = 14.994, df = 54, p-value < 2.2e-16
## alternative hypothesis: true correlation is not equal to 0
## 95 percent confidence interval:
##  0.8313141 0.9391526
## sample estimates:
##       cor
## 0.8979623
```

```
#qqnorm(resid(rtmexp3))
#qqnorm(resid(rtmlin4))

#xyplot(fitted(rtmlin4)~dftstar2$R2)
#xyplot(fitted(rtmexp3)~dftstar2$R2)
summary(rtmlin4)

##
## Call:
## lm(formula = R2 ~ tt + I(tt * mag), data = dftstar2)
##
## Residuals:
##      Min       1Q   Median       3Q      Max
## -0.68535 -0.22472 -0.02086  0.24723  0.78522
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept) 13.536600   0.114992 117.718  < 2e-16 ***
## tt          -0.012861   0.004431  -2.902  0.00539 **
## I(tt * mag) -0.009608   0.000926 -10.376 2.28e-14 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 0.3524 on 53 degrees of freedom
## Multiple R-squared:  0.8068, Adjusted R-squared:  0.7996
## F-statistic: 110.7 on 2 and 53 DF,  p-value: < 2.2e-16


xyplot(R2~I(tt+mag*tt), pch=21, col="black",fill="aliceblue",
      data=dftstar2,
       ylab="Size, R", xlab="t + mt") +
  xyplot(fitted(rtmlin4)~I(tt+mag*tt),cex=0.7,pch=20,
         col="black", data=dftstar2)+
  xyplot(fitted(rtmexp3)~I(tt+mag*tt),cex=0.7,col="red",pch=20,
         data=dftstar2)
```

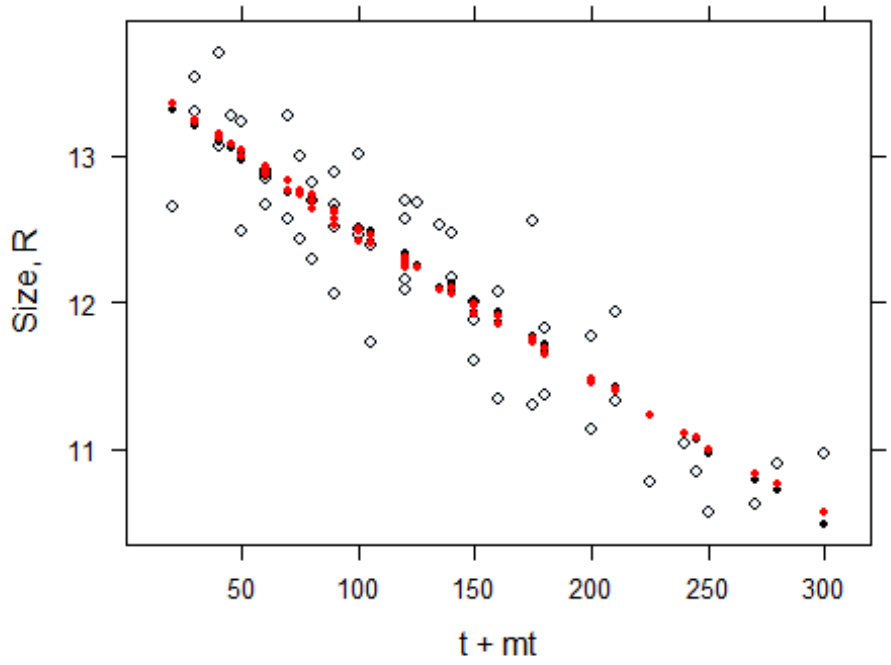


Figure S15. Observed body size (light blue symbols) at $t^* = 70$ and the fitted values for the linear and exponential models in response to the predictors (both models are fitted to the same set of predictors).

We now use the linear model to predict response in clock time:

```
dfpred<-data.frame(expand.grid(mag=seq(1,10,0.2),tt=seq(10,50,2)))
dfpred$x<-rep(70,nrow(dfpred))
dfpred$DD<-predict(d1,newdata=dfpred)
dfpred$taustar<-dfpred$x/dfpred$DD
dfpred$tau<-dfpred$tt/dfpred$DD

dfpred$E<-predict(e2, newdata=dfpred)
dfpred$mu<-dfpred$m/dfpred$E
dfpred$R<-predict(rtmlin4,newdata=dfpred)
```

The following code allows to visualize predictions. The first step is to create data matrices and then the plots

```
mag=seq(1,10,0.2)
tt=seq(10,50,2)
```

```
sizemat<-matrix(data=dfpred$R, nrow=46, ncol=21)
mumat<-matrix(data=dfpred$mu, nrow=46, ncol=21)
taumat<-matrix(data=dfpred$tau, nrow=46, ncol=21)
taustarmat<-matrix(data=dfpred$taustar, nrow=46, ncol=21)

# Plots
image2D(sizemat,mag,tt,colkey = TRUE, resfac = 6,
          #levels=seq(0.1,3.4,0.2),
          xlim=c(1,10),ylim=c(10,50),zlim=c(8,14),
        xlab="Magnitude", ylab="Time scale")

image2D(mumat,mag,tt,colkey = FALSE,
        contour=list(TRUE,nlevels=1, col="black"),
        resfac = 6,
        col="transparent",
        #breaks=c(0,1,2),
        #lty=1,lwd=1,
        xlab="Magnitude", ylab="Time scale",
        xlim=c(1,10),ylim=c(10,50),zlim=c(0,1),
        add=TRUE)
contour2D(mumat,mag,tt,colkey = FALSE,
        levels=c(1),
        lty=1,lwd=1,
        xlab="Magnitude", ylab="Time scale",
        xlim=c(1,10),ylim=c(10,50),
        add=TRUE)


contour2D(taumat,mag,tt,colkey = FALSE,
          col=c("dark blue"),lty=2,lwd=2,
          levels=c(1),
          xlab="Magnitude", ylab="Time scale",
          xlim=c(1,10),ylim=c(10,50),
          add=TRUE)
contour2D(taustarmat,mag,tt,colkey = FALSE,
          col=c("dark blue"),lty=1,lwd=2,
          levels=c(1),
          xlab="Magnitude", ylab="Time scale",
          xlim=c(1,10),ylim=c(10,50),
          add=TRUE)

rect2D(x0=1,y0=10,x1=10,y1=50, col="transparent",add=TRUE)
abline(v =5.1, lty = 2)
abline(h =30, lty = 2)
```

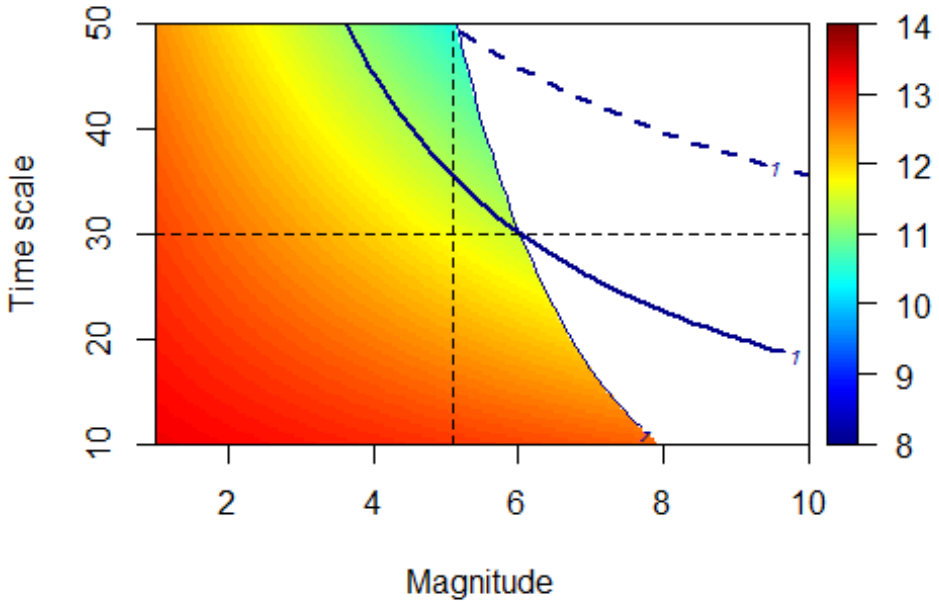


Figure S16. The predicted response in the mt-projection. The black continuous line corresponds to $\mu = 1$, defining the region of existence. The black dashed line delimits the region ($m < 5$) where the tolerance becomes independent of the time scale of the fluctuation. The horizontal black dashed line indicates the region ($t > 30$) where fluctuations enable maturation. The blue line corresponds to $\tau^* = 1$ and the blue dashed line is $\tau = 1$. The line of $\tau^* = 1$ gives the time of maturation. In the example, the time of maturation was simulated also for $\mu > 1$ in order to show the region the fluctuation magnitude is high enough to elicit a response before the organisms reach maturation (the $\tau = 1$ line lies in the region where $\mu > 1$). The line of $\tau = 1$ gives the set of fluctuations with time scales equal to that of the time of maturation. In this case, fluctuations of such length are located in the region of $\mu > 1$ showing that such type of fluctuations would not be tolerated (within the region investigated in the experiment).

6.5.4 Modelling the response at maturation

Because individuals still grow after the fluctuation is experienced, we cannot use the previous model fit (valid only for $t^* = 70$). Because body size is measured only 2 times, we cannot model size as $R = f(t^*, t, m)$. Instead, we have to create separate models for $R(t, m|t^* = 1)$ and $r(t, m|\tau^* = 1)$ considering $\mu \leq 1$).

```
dfRtau<-df[which(df$taustar==1 & df$mu<=1),c(2,3,7)]

m1<-lm(R~tt+mag+I(tt*mag), data=dfRtau)
```

```
m2<-lm(R~tt+mag, data=dfRtau)
m3<-lm(R~tt+I(tt*mag), data=dfRtau)
m4<-lm(R~mag+I(tt*mag), data=dfRtau)
m5<-lm(R~I(tt*mag), data=dfRtau)
m6<-lm(R~1, data=dfRtau)
AIC(m1,m2,m3,m4,m5,m6)
```

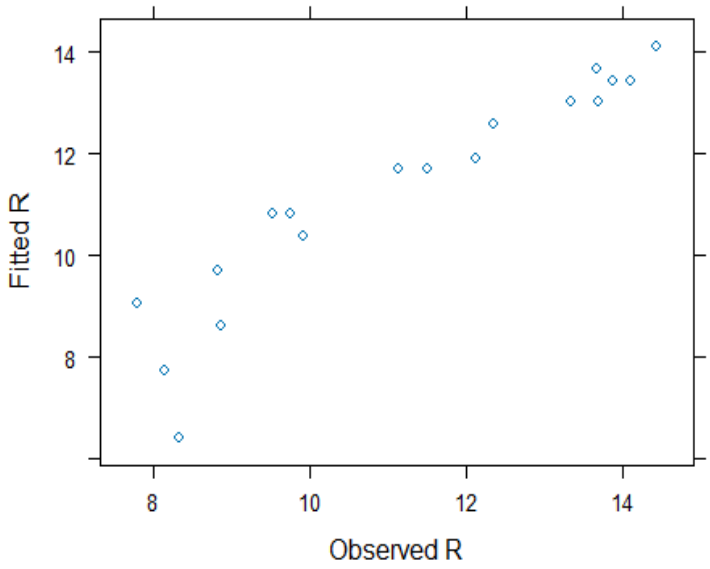
```
##    df      AIC
## m1  5 53.38721
## m2  4 55.99130
## m3  4 51.39432
## m4  4 51.49063
## m5  3 50.41331
## m6  2 89.14155
```

```
summary(m5)
```

```
##
## Call:
## lm(formula = R ~ I(tt * mag), data = dfRtau)
##
## Residuals:
##     Min      1Q  Median      3Q     Max
## -1.2827 -0.5057  0.2119  0.4230  1.9221
##
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept) 19.619552   0.757138   25.91 4.19e-15 ***
## I(tt * mag) -0.044027   0.003891  -11.31 2.46e-09 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 0.8232 on 17 degrees of freedom
## Multiple R-squared:  0.8828, Adjusted R-squared:  0.8759
## F-statistic:   128 on 1 and 17 DF,  p-value: 2.462e-09
```

```
dfRtau$fit<-fitted(m5)



xyplot(fit~R, data=dfRtau,ylab="Fitted R", xlab="Observed R")
```

```
 xyplot(R~I(mag*tt), pch=21, col="black",fill="aliceblue", data=dfRtau,
       ylab="Size, R", xlab="mt") +
  xyplot(fit~I(mag*tt),cex=0.7,pch=20, type="b",
         col="black", data=dfRtau)
```



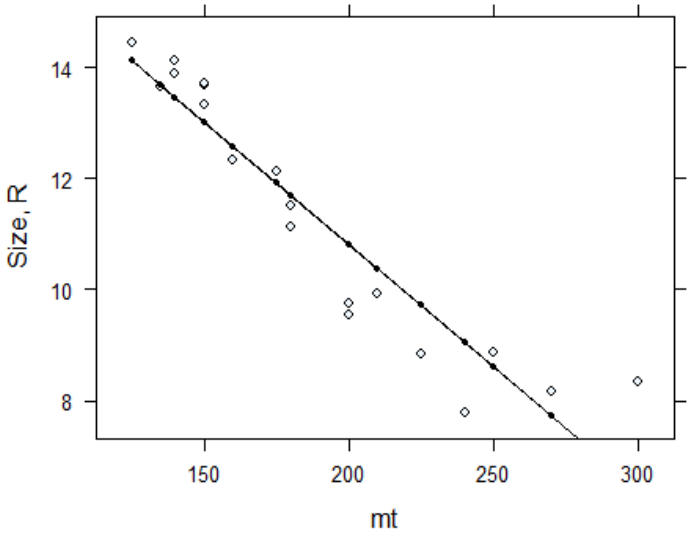


Figure S17. Observed and fitted body size at maturation $\tau^* = 1$ for the best model in response to the predictors.

Representation of size at maturation:

```
mag=seq(min(dfRtau$mag),max(dfRtau$mag),length.out=25)
tt=seq(min(dfRtau$tt),max(dfRtau$tt),length.out=25)
dfpredtau<-data.frame(expand.grid(mag=mag,tt=tt))
dfpredtau$R<-predict(m5, newdata=dfpredtau)
```

```
sizemat<-matrix(dfpredtau$R,nrow=25,ncol=25)

image2D(sizemat,mag,tt,colkey = TRUE, resfac = 6,
        xlim=c(3,7),
        xlab="Magnitude", ylab="Time scale")
```

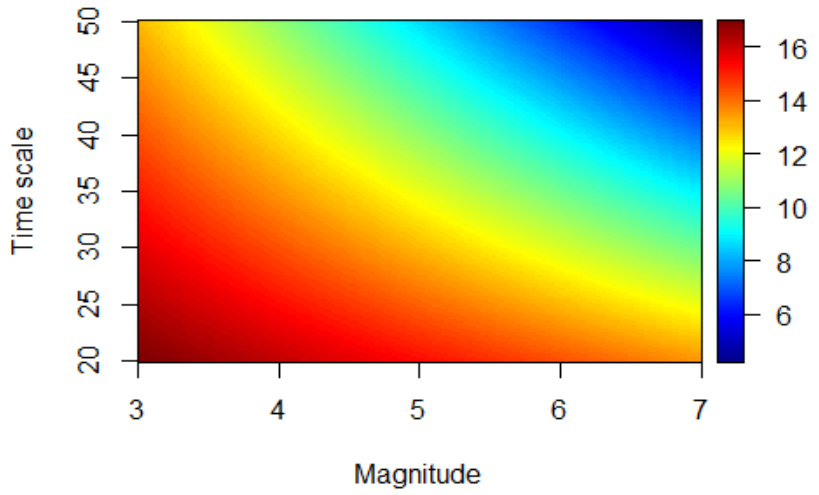


Figure S18. Predicted response at maturation, $\tau^* = 1$ in the mt-projection, for $\mu < 1$. The predictions correspond to the observations shown as scatterplot in Fig 6. Both the observed and predicted size at maturation lie on a surface that crosses the time slice $t^* = 70$ and hence do not use the same data.

6.5.5 Modeling and simulating interactive effects

The difference between the response at a fixed time clock vs fixed biological time is given by the form of the equations:

$$r = R_1(t, m|\tau^* = 1) = 19 - 0.04tm$$

$$R_2(t, m; t^* = 70) = 13 - 0.013t - 0.01mt$$

The above equations also help us to understand the difference in the interactive effects of m and t on body size, at both clock and biological time. In both cases there is a negative synergistic effect but the one at maturation is stronger than the one at a fixed clock time. Hence size at maturation is more responsive than size at a fixed clock time.

Mathematically the interaction is obtained by differentiating the equations above and finding that the partial derivative with respect to any of the above components depends on the other component. For example

$$dr/dt = -0.04m$$

$$dR/dt = -0.013 - 0.01m$$

The following simulation shows the response at similar levels as it would be seen in a box & whisker plot.

```
dfsim1<-dftstar2[,c(2,3)]
dfsim<-data.frame(NULL)
for (i in 1:100){
  sR<-simulate(rtmlin4,n=1)
dfsim1$sR<-sR$sim_1
dfsim1$N<-i
dfsim<-rbind(dfsim,dfsim1)
}

dfsim2<-dfRtau[,c(1:2)]
dfsimtau<-data.frame(NULL)
for (i in 1:100){
  sR2<-simulate(m5,n=1)
dfsim2$sR<-sR2$sim_1
dfsim2$N<-i
dfsimtau<-rbind(dfsimtau,dfsim2)
}
```

Both responses coincide in a narrow range of values and the interaction effect is not very clear.

```
colNPars <- list(superpose.polygon = list(col = c("aliceblue","green")),
                    superpose.symbol = list(fill = c("aliceblue","green"))
)

dfsimsub<-subset(dfsim,mag %in% c(4,6) & tt %in% c(35,40))
dfsimsubtau<-subset(dfsimtau,mag %in% c(4,6) & tt %in% c(35,40))

bwplot2(sR~factor(mag), groups=factor(tt), data=dfsimsub,
        ylab="Size at t*=70", xlab="Fluctuation magnitude",
        fill=c("aliceblue","green"),
        auto.key=list(text=c("t=35","t=40")),
         par.settings=colNPars)

bwplot2(sR~factor(mag), groups=factor(tt), data=dfsimsubtau,
        ylab="Size at \u03C4*=1", xlab="Fluctuation magnitude",
        fill=c("aliceblue","green"),
        auto.key=list(text=c("t=35","t=40")),
         par.settings=colNPars)
```

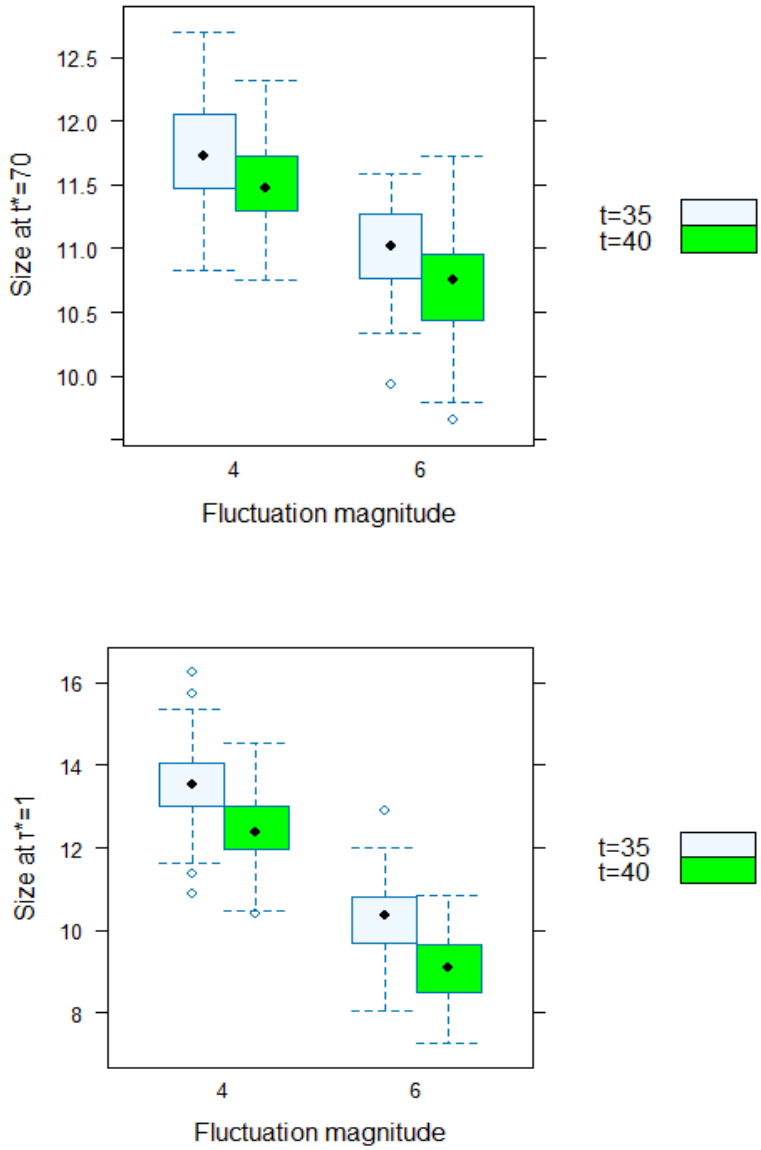


Figure S19. Simulations of an experiment comparing responses to m and t at a fixed clock time (top panel) vs at maturation (bottom panel). Note that the range of m and t values is too narrow to visualize the interaction. However, it is clear that the effect of t is stronger at maturation than at $t^* = 70$.

The following simulation highlights the difference in the sensitivity to m and t by covering a wider range of values.

```
dfsimsub<-subset(dfsim,mag %in% c(2,4,6) & tt %in% c(10,30))
bwplot2(sR~factor(mag), groups=factor(tt), data=dfsimsub,
        ylab="Size at t*=70", xlab="Fluctuation magnitude",
        fill=c("aliceblue","green"),
        auto.key=list(text=c("t=10","t=30")),
         par.settings=colNPars)
```

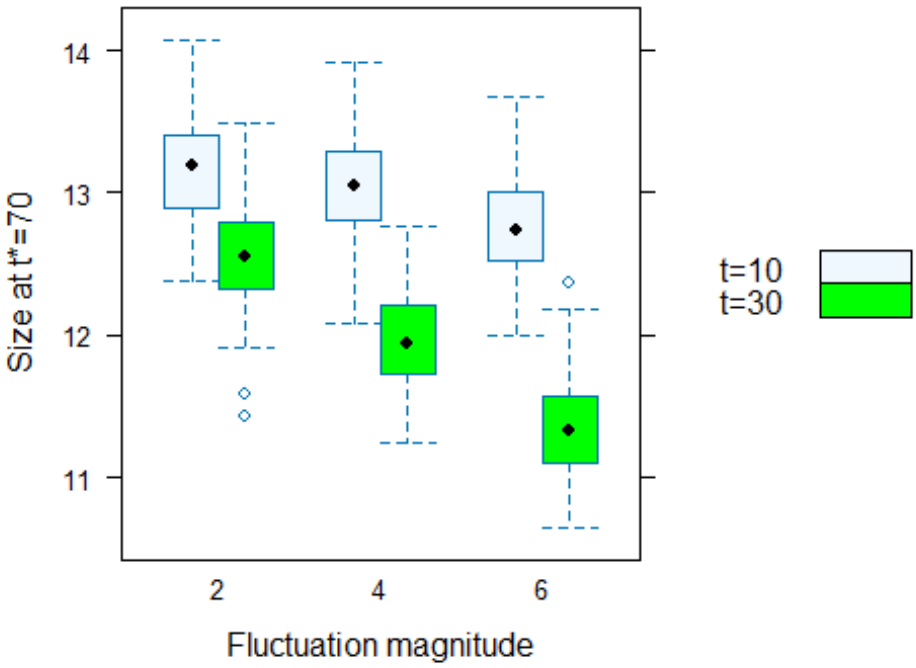


Figure S20. Simulations of an experiment comparing responses to m and t at a fixed clock time $t^* = 70$.

The figure below illustrates the interaction by plotting the response as a function of the time scale of the fluctuation at fixed values of the magnitude (3 and 5).

```
p1<-xyplot(R~tt, groups=factor(dfpred$mag, levels=c(3,5)), data=dfpred,yla
b="R(t,m,t*=70)", xlab="Clock time scale",
           pch=21, col="black",fill=c("aliceblue","green"),
            xlim=c(25,49), ylim=c(8,18))
p2<-xyplot(R~tt, groups=factor(dfpredtau$mag, levels=c(3,5)), data=dfpredt
au,ylab="r(t,m,\u03C4=1)", xlab="Clock time scale",
           pch=21, col="black",fill=c("aliceblue","green"),
            xlim=c(25,49),ylim=c(8,18))

grid.arrange(p1,p2, nrow=1)
```

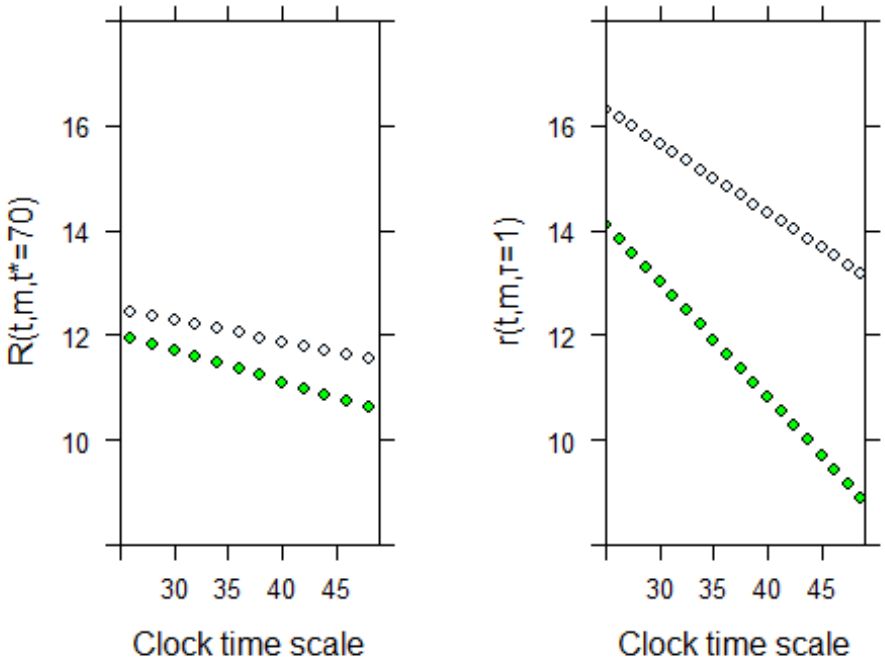


Figure S21. Comparison of responses at a fixed clock time vs at maturation. Note that the response at maturation is more sensitive to t than it is at a fixed clock time. These results show that we need to be clear about the choice of metric for time.

6.6 Scale transition theory

In this section, a set of fluctuations (e.g. heatwaves) are presented and the objective is to estimate the average response triggered by the fluctuations. There are three options for predictions: (1) model simulations, (2) scale transition theory, (3) mean field approach.

The field data is represented by the file mapping the heatwaves. The interest is in predicting the average response to those heatwaves with time scales larger than 10 days, that may be considered as extreme and at the limit of the region of existence. The reference temperature (no fluctuation) is set to 15°C, so that m is calculated as the difference between the maximum temperature and 15°C.

```
mhw <- data.frame(read_csv("heatwavescaledvf.csv"))

mhw$tt<-mhw$duration
mhw$mag<-mhw$MaxTemperature-15

xyplot(tt~mag, data=mhw)
```

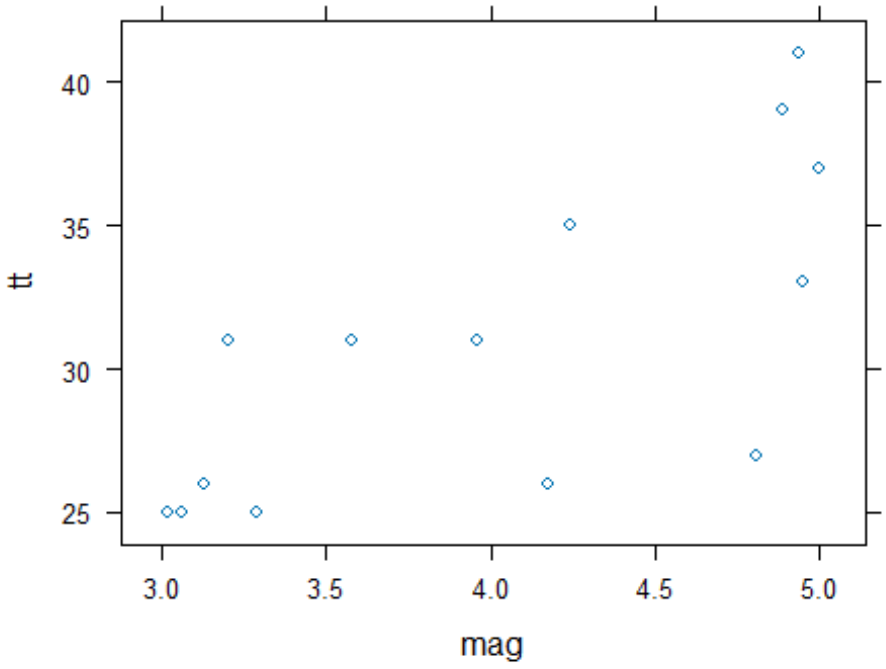


Figure S22. A set of fluctuations mapped according to their components in the extrinsic frame (tt= time scale, mag=magnitude).

The calculations below will lead to three different types of prediction 1. From model 2. From mean heatwave 3. Scale transition theory. For scale transition theory, the equation needed is given in Koussoroplis et al. (2017). In the following, and to simplify the notation, I will consider that R is quantified at a fixed time (either clock or biological) and will drop the indices t^* and τ^*. I take the following notation:

$$R(\overline{m},\overline{t}) = R_0$$

$$d^2R(m,t)/dm^2|_{\overline{m},\overline{t}} = R''_{11}$$

$$d^2R(m,t)/dt^2|_{\overline{m},\overline{t}} = R''_{22}$$

$$d^2R(m,t)/dmdt|_{\overline{m},\overline{t}} = R''_{12}$$

$$Var(m) = a_{11}$$

$$Var(t) = a_{22}$$

$$Cov(m,t) = a_{12}$$

The scale transition equation can be re-written as:

$$\overline{R(m,t)} = R_0 + 0.5a_{11}R''_{11} + 0.5a_{22}R''_{22} + a_{12}R''_{12}$$

For calculation purposes, I find it better to express the equation using matrix algebra notation, as an inner product of two vectors:

$$\overline{R(m,t)} = AR'$$

where the symbol ’ denotes transposition and where A and R are the following row vectors:

$$A = [1, 0.5a_{11}, 0.5a_{22}, a_{12}]$$

$$R = [R_0, R''_{11}, R''_{22}, R''_{12}]$$

Given the equations obtained above the mixed derivatives are constants and the second derivatives are zero; hence we obtain:

$$R = [R_0, 0, 0, -0.01] \text{ for } t^* = 70 \text{ days}$$

$$R = [R_0, 0, 0, -0.04] \text{ for } \tau^* = 1$$

With R_0 depending on whether the response is calculated at $t^*=70$ days or $\tau^*=1$

Calculations:

```
# 1 From model
mhw$Rtstar<-predict(rtmlin4,newdata=mhw)
mhw$Rtaustar<-predict(m5, newdata=mhw)
# 2 From mean field
media1<-predict(rtmlin4,newdata=data.frame(mag=mean(mhw$mag),tt=mean(mhw$t
t)))
media2<-predict(m5,newdata=data.frame(mag=mean(mhw$mag),tt=mean(mhw$tt)))

# 3 From scale transition theory

# I am calculating it as an inner product between vectors
# Vector of derivatives and other terms
A.tstar<-c(1,0,0,rtmlin4$coefficients[3])
A.taustar<-c(1,0,0,m5$coefficients[2])
# Vector of Means, variances and covariance for field data
R.tstar<-c(media1,I(0.5*var(mhw$mag)),I(0.5*var(mhw$tt)),cov(mhw$tt,mhw$ma
g))
R.taustar<-c(media2,var(mhw$mag),var(mhw$tt),cov(mhw$tt,mhw$mag))
# Inner products
stt1<-A.tstar%*%R.tstar
stt2<-A.taustar%*%R.taustar



#Results
resu<-data.frame(Coordinate=c("Clock", "Biological"),
           Time=c("70 days","maturation"),
           Model = c(mean(mhw$Rtstar),mean(mhw$Rtaustar)),
```

```
           Mean.MHW=c(media1,media2),
           STT=c(stt1,stt2))
knitr::kable(resu,
             caption="Table S2. Average response to marine heatwaves of mo
re than 10 days long, estimated from model, mean field components and scal
e transition theory up to second order.")
```

Table S2. Average response to marine heatwaves of more than 10 days long, estimated from model, mean field components and scale transition theory up to second order.

Coordinate	Time	Model	Mean.MHW	STT
Clock	70 days	11.92024	11.94870	11.91805
Biological	maturation	14.03158	14.16197	14.02155

End of code

Section S7: The space of fluctuation from the perspective of a second species

Here I use the models in cases 1 and 2 to show that one can add a second species or organism and obtain a set of coordinate frames completely independent human metrics of time and tolerance. I start by recalling the mapping functions for the two species with numbers 1,2 indexing the respective mapping functions:

$$\mu_1 = m(S_0 + k_\mu t)$$

$$\tau_1 = t(D_{min} + k_\tau/m)^{-1}$$

$$\mu_2 = \frac{m}{[M_{crit} - M_0 - z \cdot \log(t)]}$$

$$\tau_2 = tL_{max} \cdot e^{\frac{-A}{(m+273)}}$$

An easy way to get rid of *m* and *t* is to work with the coordinates of system 1.

$$m = (\mu_1 - k_\mu k_\tau \tau_1)/(S_0 + k_\mu D_{min} \tau_1)$$

$$t = \tau_1 \frac{(\mu_1 D_{min} + S_0 k_\tau)}{(\mu_1 - k_\mu k_\tau \tau_1)}$$

Then we can plug the expression of *m* and *t* into those of μ_2 and τ_2. The resulting equations do not have *m* and *t*.

$$\mu_2 = \frac{(\mu_1 - k_\mu k_\tau \tau_1)}{\left\{M_{crit} - M_0 - z log\left[\frac{\tau_1(\mu_1 D_{min} + S_0 k_\tau)}{(\mu_1 - k_\mu k_\tau \tau_1)}\right]\right\}(S_0 + k_\mu D_{min} \tau_1)}$$

$$\tau_2 = \tau_1 \frac{(\mu_1 D_{min} + S_0 k_\tau)}{(\mu_1 - k_\mu k_\tau \tau_1)} L_{max} \cdot \exp\left(\frac{-A}{(\mu_1 - k_\mu k_\tau \tau_1)/(S_0 + k_\mu D_{min} \tau_1) + 273}\right)$$

Section S8. Supplementary References

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