

# The temperature-size rule is predicted to stabilise consumer-resource dynamics under warming

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## Contents

<b>1</b>	<b>Introduction</b>	<b>1</b>
<b>2</b>	<b>Methods and results</b>	<b>2</b>
2.1	The underlying consumer-resource dynamics . . . . .	2
2.2	Adding temperature dependence . . . . .	3
2.3	Adding mass dependence and the temperature size-rule . . . . .	3
2.4	Exploring asymmetric temperature-size responses . . . . .	4
2.5	Type-II functional response . . . . .	4
2.6	A functional response that depends on the body size ratio . . . . .	7
<b>3</b>	<b>Discussion</b>	<b>7</b>

## Abstract

**Keywords:** Metabolic theory, predator-prey, plant-herbivore, body size, allometry

## 1 Introduction

Temperature and body size determine many biological rates [9, 5]. How these factors individually influence consumer-resource dynamics has already been demonstrated [4, 2]. How they act in symphony has not yet been investigated.

Temperature also affects body size through the temperature-size rule [1]. Thus, temperature directly and indirectly affects ecosystem dynamics. These two pathways have the potential to reinforce or counteract one another, with population level consequences.

Here we model a simple consumer-resource interaction, with population dynamic parameters that depend on temperature and body size, and body sizes that depend on temperature.

We ask how including dependencies on both temperature and body size, as well as incorporating the temperature-size rule, affects the response of the consumer-resource dynamics to increasing temperature.

## 2 Methods and results

### 2.1 The underlying consumer-resource dynamics

We begin, like [4], with the Rosenzweig-MacArthur equations [8]

$$\begin{aligned}\frac{dR}{dt} &= rR \left(1 - \frac{R}{K}\right) - f(R)RC \\ \frac{dC}{dt} &= ef(R)RC - mC,\end{aligned}\tag{1}$$

which describe the rates of change in total resource  $R \in [0, K]$  and consumer  $C \geq 0$  biomass with time  $t$ .

In the absence of consumers,  $C = 0$ , the resource grows logistically, with intrinsic growth rate  $r \geq 0$  and carrying capacity  $K > 0$ . The intrinsic growth rate describes the rate at which resource biomass increases without consumers when the resource is rare,  $R \approx 0$ . The carrying capacity is the equilibrium biomass of the resource without consumers.

Resource biomass is consumed by consumers at a rate  $f(R)RC$ , where  $f(R) \geq 0$  is called the functional response. Of the biomass consumed, the unitless conversion efficiency parameter  $e \in [0, 1]$  determines the proportion of resource biomass that is directly converted into consumer biomass. Consumers die at constant per capita mortality rate  $m \geq 0$ .

An equilibrium is reached when the two rates of change in Equation (1) are zero, and solving the system at this point gives equilibrium resource  $\hat{R}$  and consumer  $\hat{C}$  biomass. There are three equilibria for this system: total extinction  $(R, C) = (0, 0)$ , consumer extinction  $(R, C) = (K, 0)$ , and coexistence  $(R, C) = (\hat{R}, \hat{C})$ , the latter with  $\hat{R} > 0$  and  $\hat{C} > 0$ . We are primarily concerned with the latter equilibrium, as that is presumably the equilibrium current consumer-resource systems are near. At this coexistence equilibrium one can calculate the ratio of consumer to resource biomass,  $\hat{C} : \hat{R}$ , and also perform a linear stability analysis to derive the leading (largest in absolute value) eigenvalue  $\lambda$ , which determines if (and how readily) the system, when perturbed a small amount from this equilibrium, will return to it (see the supplementary `Mathematica` file for details). Our measure of stability will be the negative of the real part of the leading eigenvalue. The system is stable if and only if this value is positive, and the system will return to equilibrium faster when this value is larger (i.e., larger positive values imply “more stable” systems). Together these two measures tell us how biomass is partitioned and how stable this partitioning is.

As explained in [4], two aggregates well describe the dynamics of this system. The first is  $m/(ef(R))$ , which describes (the inverse of) consumer growth, is the slope of the consumer zero-net growth isocline, and is the equilibrium abundance of resources at the coexistence equilibrium. The second aggregate is  $K$ , the equilibrium resource biomass in

the absence of consumers. Dividing the second aggregate by the first gives a measure that defines the biomass potential of the resource that is converted into consumer biomass,  $B_{CR} = ef(R)K/m$ .

In what follows we will examine how our three measures,  $B_{CR}$ ,  $\hat{C} : \hat{R}$ , and stability, change with temperature. We start by assuming a type-I functional response,  $f(R) = a$ , where  $a$  is called the attack rate, which describes the rate of resource consumption per resource biomass. We later explore the effect of a type-II functional response and the potential for the functional response to change with temperature.

## 2.2 Adding temperature dependence

Gilbert *et al.* [4] discuss what is known about the temperature dependencies of  $r$ ,  $K$ ,  $a$ ,  $m$ , and  $e$ , and give equations and parameter estimates in their Table 1. Briefly, resource growth rate  $r$  is expected to scale with metabolism as a Boltzmann-Arrhenius factor,  $r(T) = r_0 \exp(-E_B/(kT))$ , where  $E_B$  is the activation energy of the metabolism  $B$  (in units of eV),  $k$  is Boltzmann's constant ( $\approx 8.62 \times 10^{-5}$  eV/K), and  $T$  is the temperature (in Kelvins). Resource carrying capacity  $K$  is determined by the ratio of the supply rate of nutrients into the system and the rate of uptake of nutrients by the resource,  $r$ . With supply rate also scaling as a Boltzmann-Arrhenius factor with activation energy  $E_S$ , carrying capacity is  $K(T) = K_0 \exp(-(E_S - E_B)/(kT))$ . Attack rate  $a$  depends on the temperature dependence of the body velocities  $\nu$  in both species, which both scale as Boltzmann-Arrhenius factors with activation energies  $E_{\nu,i}$ , with  $i = \{R, C\}$ . Attack rate is then  $a(T) = a_0 \sqrt{\sum [\nu_{0,i} \exp(-E_{\nu,i}/(kT))]^2}$ , where the sum is over  $i = \{R, C\}$  and  $\nu_{0,i}$  are rate-constants. Consumer mortality is also expected to scale as a Boltzmann-Arrhenius factor,  $m(T) = m_0 \exp(-E_m/(kT))$ . Conversion efficiency is assumed to be independent of temperature  $e(T) = e_0$ .

The black curves in Figure 1 show  $B_{CR}$ , equilibrium consumer to resource biomass ratio  $\hat{C} : \hat{R}$ , and stability of the coexistence equilibrium as functions of temperature  $T$  (plotted in Celsius). In these plots  $r$ ,  $K$ ,  $a$ , and  $m$  all depend on temperature as discussed above, unlike Figure 3 in [4] where only  $K$  depends on temperature and the rest of the parameters are held constant. Comparing with Figure 3 in [4] shows that adding temperature dependence in  $r$ ,  $a$ , and  $m$  causes equilibrium consumer:resource biomass to decline with temperature (instead of increasing) and stability to decrease at a slower rate with increasing temperature. These changes are largely driven by the temperature dependence of consumer mortality: increasing temperature increases consumer mortality, lowering equilibrium consumer biomass and increasing stability at high temperatures (relative to the case where mortality  $m$  does not depend on temperature).

## 2.3 Adding mass dependence and the temperature size-rule

We next allow the population dynamic parameters to depend on the body size of the interacting species. Following [2], each parameter can be written as a power law function of the body

mass of resource  $M_R$  or consumer  $M_C$ . Here we combine [2] and [4] by letting the parameters depend on both temperature and mass:  $r(T, M_R) = r(T)M_R^\rho$ ,  $K(T, M_R) = k(T)M_R^\kappa$ ,  $a(T, M_C) = a(T)M_C^\alpha$ ,  $e(T, M_C) = e(T)M_C^\epsilon$ , and  $m(T, M_C) = m(T)M_C^\mu$ .

If mass does not change with temperature then adding these mass dependencies does not change the response of the consumer-resource dynamics to temperature. However, mass is expected to change with temperature, according to the temperature-size rule [1]. We incorporate a simple form of the temperature-size rule here for illustrative purposes. In particular, we assume body mass declines linearly with temperature,  $M_i(T) = M_i(T_{ref})(1 - \beta_i(T - T_{ref}))$ , where  $\beta_i$  is the fraction that mass is reduced as temperature is increased by one degree and  $T_{ref}$  is a reference temperature, which we set to  $15^\circ\text{C}$  throughout. This linear decline best approximates the response of organisms with a dry mass of less than  $10^{-3}$  mg, whereas larger organisms experience a faster than linear decline [3].

The red curves in Figure 1 depict our main results: adding mass dependencies and the temperature-size rule modifies our prediction of how consumer-resource dynamics respond to changes in temperature. While there is little change in  $B_{CR}$ , the equilibrium consumer to resource biomass ratio is no longer expected to decline with increasing temperature and stability is now expected to increase. These changes are brought on by the indirect effect of temperature, through mass, on the population dynamic parameters. In particular, the lack of decline in the consumer to resource biomass ratio with the temperature-size rule, relative to the case without it, is primarily driven by changes in consumer conversion efficiency and the intrinsic growth rate of the resource. Both of these rates increase with declining body mass, supporting a larger consumer biomass, relative to resource biomass. The indirect effects of temperature, through body size, act in opposition to the direct effects of temperature, and in the case of stability the indirect effects override the direct effects to produce a qualitatively different prediction.

## 2.4 Exploring asymmetric temperature-size responses

In Figure 1 we assumed both resource and consumer body mass declined with temperature at the same rate,  $\beta_C = \beta_R = 0.02$ , i.e., both decline 2% per degree increase. However, larger organisms often experience larger declines in body size with temperature [3]. In the supplementary `Mathematica` file we let consumer body size decline twice as fast as the resource,  $2\beta_R = \beta_C = 0.04$ . The main effect of the asymmetric temperature-size response is that i) the  $B_{CR}$  with  $E_S > E_B$  now asymptotes at higher temperatures (compare with the dark solid curves in Figure 1) and ii) stability now increases even faster with increasing temperature.

## 2.5 Type-II functional response

The consumption of resources in some systems may be better described by a type-II functional response,  $f(R) = b/(1 + bhR)$ , where  $b$  is sometimes called the capture rate (per resource biomass per consumer biomass rate of resource biomass consumption) and  $h$  is the handling time. This collapses to a type-I functional response at low resource biomass,  $f(R) \approx b$

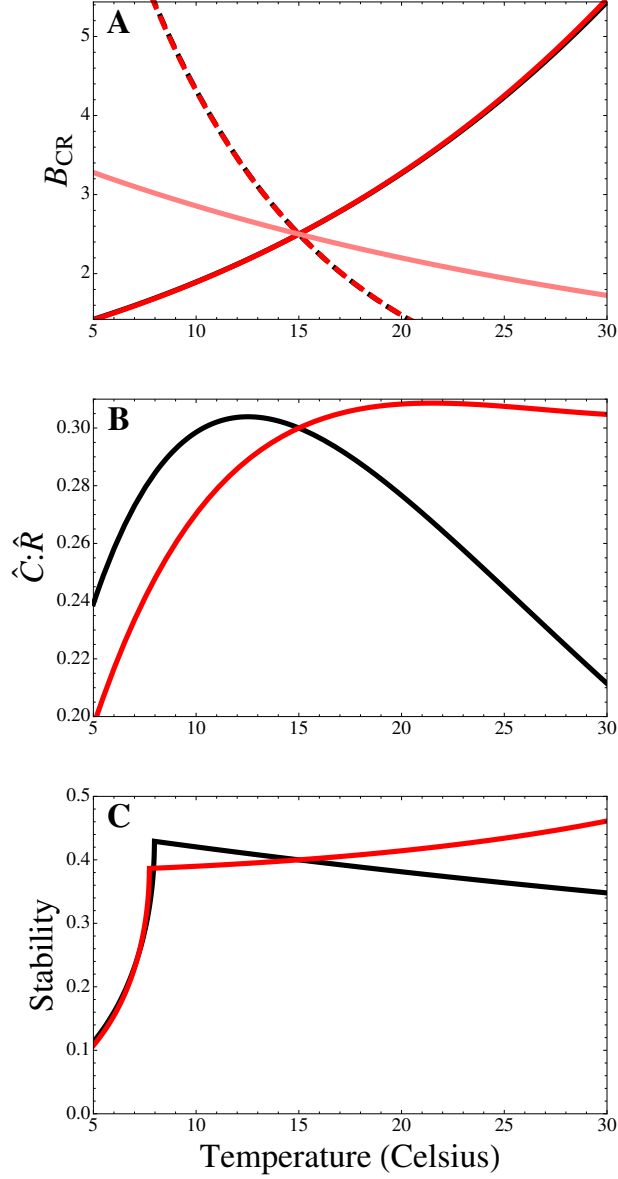


Figure 1:  $B_{CR}$ , equilibrium consumer to resource biomass ratio  $\hat{C} : \hat{R}$ , and stability of the coexistence equilibrium as functions of temperature  $T$  (plotted in Celsius) with (red) and without (black) mass dependencies and the temperature-size rule. Rate-constants (e.g.,  $r_0$ ) were chosen to make  $r = 2$ ,  $K = 100$ ,  $a = 0.1$ ,  $m = 0.6$ , and  $e = 0.15$  at  $15^\circ C$  (as in [4]). Other parameters as in [4, 2]:  $E_B = 0.32$  (solid dark),  $E_B = 0.9$  (dashed and solid light),  $E_S = 0.9$  (solid),  $E_S = 0.32$  (dashed),  $E_m = 0.65$ ,  $E_{\nu,i} = 0.46$ ,  $\nu_{0,i} = 1$ ,  $\kappa = -0.81$ ,  $\alpha = 1$ ,  $\epsilon = -0.5$ ,  $\mu = -0.29$ ,  $\rho = -0.81$ ,  $\beta_i = 0.02$  (red),  $\beta_i = 0$  (black).

for  $R \ll 1/(bh)$ . And at high resource biomass a type-II functional response implies that the rate of resource consumption per consumer biomass asymptotes at  $\lim_{R \rightarrow \infty} f(R)R = 1/h$ ,

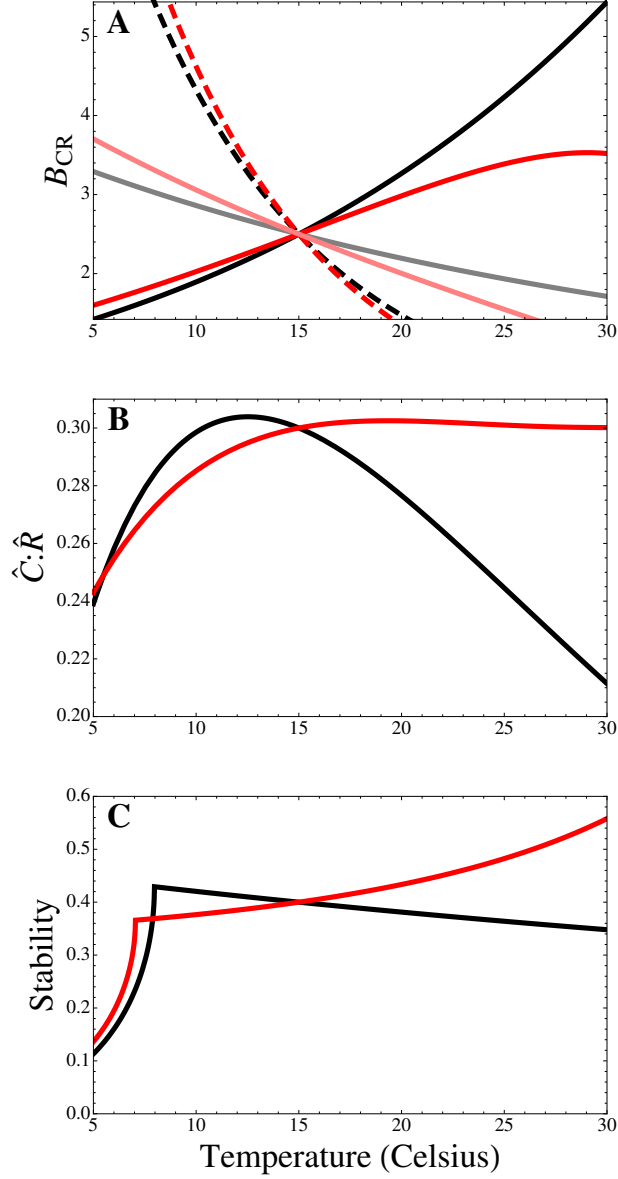


Figure 2: SUPPLEMENTARY FIGURE.  $B_{CR}$ , equilibrium consumer to resource biomass ratio  $\hat{C} : \hat{R}$ , and stability of the coexistence equilibrium as functions of temperature  $T$  (plotted in Celsius) with (red) and without (black) mass dependencies and the temperature-size rule. Rate-constants (e.g.,  $r_0$ ) were chosen to make  $r = 2$ ,  $K = 100$ ,  $a = 0.1$ ,  $m = 0.6$ , and  $e = 0.15$  at  $15^\circ C$  (as in [4]). Other parameters as in [4, 2]:  $E_B = 0.32$  (solid dark),  $E_B = 0.9$  (dashed and solid light),  $E_S = 0.9$  (solid),  $E_S = 0.32$  (dashed),  $E_m = 0.65$ ,  $E_{\nu,i} = 0.46$ ,  $\nu_{0,i} = 1$ ,  $\kappa = -0.81$ ,  $\alpha = 1$ ,  $\epsilon = -0.5$ ,  $\mu = -0.29$ ,  $\rho = -0.81$ ,  $\beta_R = 0.02$  and  $\beta_C = 0.04$  (red),  $\beta_i = 0$  (black).

describing satiation of the consumer.

Both capture rate and handling time are known to depend on temperature and body mass. In particular, capture rate scales like  $b(T, M_R, M_C) = b_0 M_R^{b_R} M_C^{b_C} \exp(-E_b/(kT))$  and handling time like  $h(T, M_R, M_C) = h_0 M_R^{h_R} M_C^{h_C} \exp(-E_h/(kT))$  [7]. Using these dependencies and the parameter values in [7] we can again plot  $B_{CR}$ ,  $\hat{C} : \hat{R}$ , and stability as functions of temperature, this time with a type-II functional response. We do this in the supplementary **Mathematica** file. The main conclusions are: in comparison to a type-I functional response, a type-II functional response i) makes the  $B_{CR}$  slopes more positive (increasing the response temperature when  $E_S > E_B$ ), ii) makes equilibrium biomass ratios increase with temperature, and iii) makes stability increase more quickly with temperature.

As an aside, in this analysis we set  $b_0$  to give  $f(R) = 0.1$  at  $15^\circ\text{C}$ , to remain consistent with [4]. This leaves  $h_0$  as a free parameter. However, this free parameter only influences the results in the case of stability. When  $h_0$  is small enough to allow a stable coexistence equilibrium ( $h_0 < 1 \approx 0^{-12}$ ) we find that stability increases exponentially with temperature (see supplementary **Mathematica** for details).

[7] compiled a large database on capture rates and handling times and compared the data to their theoretical predictions. They were surprised to find capture rate and handling time responded less strongly to temperature than expected (see their Figure 2a,d). Interestingly, we found that the temperature-size rule reduces the sensitivity of both capture rate and handling time to temperature, and hence may explain the discrepancies observed between data and theory in [7].

## 2.6 A functional response that depends on the body size ratio

The functional response tends to be more type-II when consumers and resources have similar body sizes, but becomes more sigmoidal and hence more type-III when consumers are much bigger than their resource, as resources are then better able to hide when rare [6]. Without the temperature-size rule, the body mass ratio remains constant with temperature, and therefore the form of the functional response is not expected to change. However, with the temperature-size rule body sizes change. When the temperature-size responses are asymmetric, the ratio of body sizes will change and influence the form of the functional response. Because consumers are often larger than their resource, and because larger organisms are expected to have greater reductions in body size with temperature, the ratio of consumer to resource body size will often decrease with temperature. As stated above, lower consumer to resource body size ratios produce functional responses more like type-II, which are less stable than type-III functional responses, and hence the temperature-size rule can be said to destabilize the consumer-resource dynamics at high temperatures through this mechanism (and stabilize the dynamics at lower temperatures). However, the amount by which the shape of the functional response is adjusted by the temperature-size rule does not appear to be large and therefore the stabilizing effects discussed in previous sections will likely prevail (see supplementary **Mathematica** file for details).

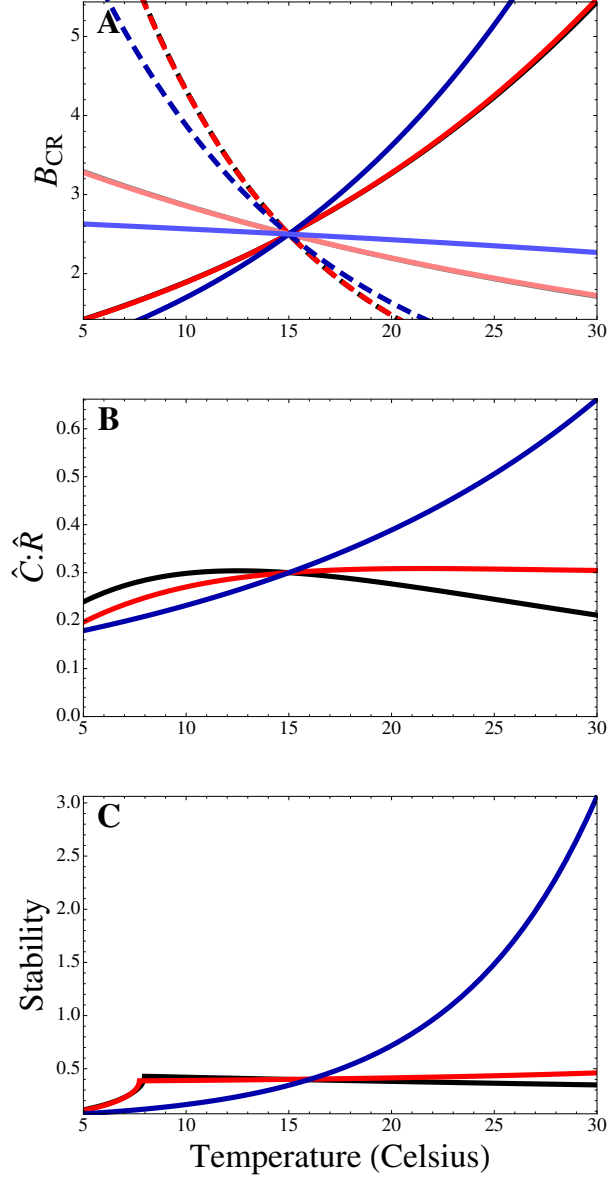


Figure 3: SUPPLEMENTARY FIGURE.  $B_{CR}$ , equilibrium consumer to resource biomass ratio  $\hat{C} : \hat{R}$ , and stability of the coexistence equilibrium as functions of temperature  $T$  (plotted in Celsius) with (red and blue) and without (black) mass dependencies and the temperature-size rule. Type-II functional response in blue. Rate-constants (e.g.,  $r_0$ ) were chosen to make  $r = 2$ ,  $K = 100$ ,  $f(R) = 0.1$ ,  $m = 0.6$ , and  $e = 0.15$  at  $15^\circ\text{C}$  (as in [4]). Other parameters as in [4, 2, 7]:  $E_B = 0.32$  (solid dark),  $E_B = 0.9$  (dashed and solid light),  $E_S = 0.9$  (solid),  $E_S = 0.32$  (dashed),  $E_m = 0.65$ ,  $E_{\nu,i} = 0.46$ ,  $\nu_{0,i} = 1$ ,  $\kappa = -0.81$ ,  $\alpha = 1$ ,  $\epsilon = -0.5$ ,  $\mu = -0.29$ ,  $\rho = -0.81$ ,  $\beta_i = 0.02$  (red and blue),  $\beta_i = 0$  (black),  $a_C = 1/4 + 2/3$ ,  $a_R = 1/3$ ,  $h_C = -2/3$ ,  $h_R = 0.5$ ,  $E_a = 0.65$ ,  $E_h = -0.65$ ,  $h_0 = 10^{-13}$ .



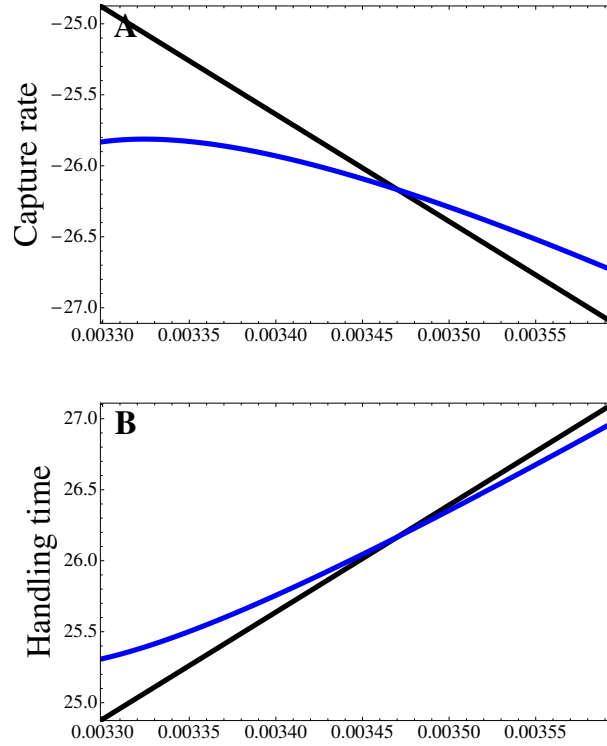


Figure 4: SUPPLEMENTARY FIGURE. The sensitivity of capture rate and handling time to temperature with (blue) and without (black) the temperature-size rule. Plotted are (A)  $\log(b/b_0)$  and (B)  $\log(h/h_0)$ . Parameters as in [7]:  $a_C = 1/4 + 2/3$ ,  $a_R = 1/3$ ,  $h_C = -2/3$ ,  $h_R = 0.5$ ,  $E_a = 0.65$ ,  $E_h = -0.65$ .

### 3 Discussion

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