The temperature-size rule is predicted to stabilize the response of consumer-resource dynamics under warming

or

Temperature-dependent body size alters the effects of temperature on consumer resource dynamics

Manuscript elements: Figure 1, figure 2?, figure 3?, supplementary `Mathematica` file.

Keywords: Metabolic theory, predator-prey, plant-herbivore, body size, allometry, functional response, mathematical model.

Manuscript type: Note.

Prepared using the suggested LaTeX template for *Am. Nat.*

Abstract

Body size influences the dynamical relationship between consumers and their resources. Mounting evidence suggests that body size declines with increasing temperature, a pattern called the temperature-size rule (TSR). The growing theory on temperature-dependent consumer resource interactions has yet to integrate the TSR into a general framework for how temperature affects consumer resource dynamics. We expanded an existing temperature-dependent consumer-resource model to include the indirect effects of warming, through changes in body size, and parameterized the model with data from data syntheses. We analyzed this model to answer the following questions: 1) How does including the TSR affect predictions for how temperature affects consumer-resource stability and biomass ratios? 2) Under what circumstances are the effects of the TSR most substantial? We found that including the TSR led to two qualitatively different predictions: under warming i) consumer-resource biomass is no longer expected to decline and ii) the dynamics are expected to become more stable, as opposed to the decline in stability predicted without the TSR. These qualitatively different predictions were strengthened by asymmetric temperature-size responses and type-II functional responses. Our analyses suggest that the effect of temperature on body size likely plays an important role in the response of consumer-resource systems to changing temperatures.

Introduction

Populations of consumers and their resources are joined across time by the fact that energy to the consumer comes from the resource, and the consumer determines mortality rates of the resource. In these systems, temperature-dependent consumption, growth and mortality rates can change the dynamics and their outcomes. Through the temperature-dependence of metabolism (**??**) and hence demographic vital rates, small changes in temperature that are not necessarily physiologically stressful for organisms can translate to changes in the stability and coexistence of consumers and their resources, producing predictable but non-intuitive effects of warming on simple food webs (**????**).

Demographic rates and consumer-resource interactions also depend on body size (**??**). Not only do rates of growth, mortality and consumption scale predictably with individual body sizes, but the consumption rates of consumer-resource systems can also depend on the ratio of body masses between consumers and prey (**?**). Changes in body size or body size ratios can therefore change demographic and interaction rates. Given the importance of body size to the dynamics and outcomes of consumer-resource interactions, frameworks for understanding how temperature affects consumer-resource dynamics have not considered the importance of changes in body size with temperature.

The frequently-observed negative relationship between temperature and body size, the temperature-size rule (TSR), has been called the third universal response to warming (**?**). For comparisons within populations, among species and across biogeographic gradients, body size of ectotherms tends to decline with increasing temperature (**????**). Although the mechanism for declining body size with warming varies among examples, including physiological plasticity, selection for smaller individuals, and turnover in species composition, the pattern is similar across levels of organization (**?**). **?** reported a mean slope of -3.65%/$^{\circ}C$ for aquatic organisms, ranging from -1.80%/$^{\circ}C$ for unicells, and becoming stronger (more negative) in increasingly large aquatic multicelled organisms.

Because body size is so central to consumer-resource dynamics, such a systematic pattern of changing body size with temperature could alter predictions for how temperature affects stability, persistence and coexistence in consumer-resource systems. We therefore integrated the temperature size rule into a general framework for temperature-dependent consumer-resource interactions to answer the following questions: 1) How does the TSR affect stability and consumer:resource biomass ratios over a temperature gradient?, 2) Does the effect of the TSR depend on whether consumer and resource body sizes respond similarly to temperature?, 3) Does the effect of the TSR depend on the form of the functional response?, And finally, 4) does the TSR itself induce a change in the functional response?

Methods and results

The underlying consumer-resource dynamics

We begin, like **?**, with the Rosenzweig-MacArthur equations (**?**)

$$\begin{aligned}\frac{\mathrm{d}R}{\mathrm{d}t} &= rR\left(1-\frac{R}{K}\right) - f(R)RC \\ \frac{\mathrm{d}C}{\mathrm{d}t} &= ef(R)RC - mC,\end{aligned} \tag{1}$$

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 (per unit biomass) in the absence of 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 biomass dies at a constant per unit biomass mortality rate $m \geq 0$.

An equilibrium is reached when the two rates of change in Equation (**??**) 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 $(R, C) = (\hat{R}, \hat{C})$, 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 (we would not consider them consumer-resource systems if either the consumer or resource were absent). 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 λ, 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 **?**, two aggregates well describe the dynamics of this system. The first is $m/(ef(\hat{R}))$, which describes (the inverse of) consumer growth at equilibrium, is the slope of the consumer zero-net growth isocline, and is the abundance of the resource 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, $B_{CR} = ef(\hat{R})K/m$.

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 changes in the environment.

Adding temperature dependence

? discuss what is known about the temperature dependencies of the population dynamic parameters 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 metabolism B (in units of eV), k is Boltzmann's constant ($\approx 8.62 \times 10^{-5}$ eV/Kelvin), 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, S, 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, the prediction for carrying capacity becomes $K(T) = K_0 \exp(-(E_S - E_B)/(kT))$. Attack rate a depends on the temperature dependence of the body velocities ν in both species, both of which scale as Boltzmann-Arrhenius factors with activation energies $E_{\nu,i}$, for $i = \{R, C\}$. Attack rate is then $a(T) = a_0\sqrt{\sum_i \left[\nu_{0,i} \exp(-E_{\nu,i}/(kT))\right]^2}$, where $\nu_{0,i}$ 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 **??** 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, unlike Figure 3 in **?** where only K depends on temperature and the rest of the parameters are held constant. Comparing with Figure 3 in **?**, we see 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).

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 **?**, 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 **?** and **?** 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 (**?**). 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 β_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 $15°C$ 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 (**?**).

The red curves in Figure **??** 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 body 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 relatively larger consumer biomass. The increase in stability at high temperatures with the temperature-size rule is caused by the increase in the resource's intrinsic growth rate along with a decrease in attack rate with decreasing consumer body size. The indirect effects of temperature are acting in opposition to its direct effects. In the case of stability, the indirect effects are strong enough to override the direct effects, producing a qualitatively different prediction of how consumer-resource systems will respond to temperaure.

In the supplementary `Mathematica` file we explore how the strength of the temperature-size response $\beta_C = \beta_R = \beta$ affects our predictions (see also Figure **??**, green). We find that predictions for biomass ratio and stability at higher temperatures differ qualitatively from those of **?** for $\beta \geq 0.02$. The biomass ratio begins to increase with temperature around $\beta \sim 0.03$. Larger temperature-size responses cause both the biomass ratio and stability to increase faster with temperature (and decrease faster with declining temperature).

Exploring asymmetric temperature-size responses

In Figure **??** 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 (**?**). In Figure **??** (blue) 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 **??**) and ii) stability now increases even faster with increasing temperature. These effects are driven by the now larger decline in attack rate. Thus, expected asymmetries in the temperature-size response cause our predictions to deviate even further from those of without the temperature-size rule (**?**).

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 (the 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, $f(R) \approx b$ for $R << 1/(bh)$. At high resource biomass a type-II functional response implies that the rate of resource consumption per consumer biomass asymptotes at $\lim_{R\to\infty} f(R)R = 1/h$, describing satiation of the consumer.

Both capture rate and handling time are known to depend on temperature and body mass. In particular, **?** argue that 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 $h(T, M_R, M_C) = h_0 M_R^{h_R} M_C^{h_C} \exp(-E_h/(kT))$. Figure **??** shows how the functional response changes with temperature. Much of the difference in the response of the functional responses to temperature is due to the differing temperature- and mass- dependencies of attack rate a and capture rate b (compare black to red in Figure **??**), and not due to the form of the functional responses (i.e., setting $h = 0$ has little effect on the response of the type-II functional response to temperature). When capture rate has the same temperature- and mass-dependencies as attack rate (**?**), there is little difference between the response of the type-I and type-II functional responses to temperature (compare black to blue in Figure **??**).

With the parameter values given in **?**, we can plot B_{CR}, $\hat{C} : \hat{R}$, and stability as functions of temperature when there is a type-II functional response (see 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 to temperature when $E_S > E_B$), ii) makes equilibrium biomass ratios increase with temperature, and iii) makes stability increase more quickly with temperature, despite the fact that a type-II functional response decreases stability at our reference temperature (15°C, i.e., without a direct or indirect temperature response). Thus, a type-II functional response, like asymmetric temperature-size responses, causes our predictions to vary further from those without the temperature-size rule (**?**).

As an aside, in this analysis we set b_0 to give $f(R) = 0.1$ at $15°C$, to remain consistent with **?**. 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 (roughly $h_0 < 10^{-12}$) we find that stability increases exponentially with temperature (see supplementary `Mathematica` for details). Thus, even though a type-II functional response decreases stability at the reference temperature (because of the lags induced by handling time), stability is increased at higher temperatures. The increased stability at higher temperatures with a type-II functional response is caused by the temperature dependence of the capture rate (**?**), which differs from the temperature dependence of the type-I attack rate (**?**). Giving capture rate the same temperature dependence as attack rate (**?**), with a small enough handling time at the reference tempeture ($h_0 <\sim 10^{-13}$) stability still increases exponentially with temperature, from the reference temperature, but the square root in the expression now allows the temperature dependence of other parameters to slow and revert this increase at higher temperatures. Larger handling times prevent the exponential increase in stability with temperature, and the increase in handling time with temperature can even cause stability to decrease with temperature (see supplementary `Mathematica` file for details).

? complied a large database on capture rates and handling times and compared the data to their theoretical predictions. They found that 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 (see supplementary `Mathematica` file for details), and hence may help explain the discrepancies observed.

A functional response that depends on the body size ratio

Functional responses tend to be roughly type-II when consumers and resources have similar body sizes, but become 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 (**?**). Without the temperature-size rule, the body mass ratio remains constant with temperature, and therefore the form of the functional response is not expect 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. Hence the temperature-size rule can be said to destabilize the consumer-resource dynamics at high temperatures through by promoting type-II functional responses (it can also be said that the temperature-size rule stabilizes the dynamics at lower temperatures by promoting type-III functional responses). 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).

Discussion

Possible experiment to test the effect of the TSR: Our main predictions: equilibrium consumer to resource biomass ratio is expected to increase with temperature (due to increases in consumer conversion efficiency and the growth rate of the resource associated with declining body sizes). Could test this by comparing two systems: one where body size is allowed to decrease with temperature, and another where the smallest individuals are removed (or the opposite).

Stability is expected to increase because decreasing consumer body size lead to decreased attack rates and increase resource growth rates.

-talk about which areas are ripe for experimental exploration – temperature dependencies of handling time/capture rate vs. magnitude and potential asymmetry of TSR

References

Atkinson, D. 1994. Temperature and organism size - a biological law for ectotherms? Advances in Ecological Research 25:1–58.

Daufresne, M., K. Lengfellner, and U. Sommer. 2009. Global warming benefits the small in aquatic ecosystems. Proceedings of the National Academy of Sciences 106:12788–12793.

DeLong, J. P. 2012. Experimental demonstration of a ' rate – size ' trade-off governing body size optimization. Evolutionary Ecology Research 14:343–352.

DeLong, J. P., B. Gilbert, J. B. Shurin, V. M. Savage, B. T. Barton, C. F. Clements, A. I. Dell, H. S. Greig, C. D. G. Harley, P. Kratina, K. S. McCann, T. D. Tunney, D. A. Vasseur, and M. I. O'Connor. 2015. The body size dependence of trophic cascades. The American Naturalist 185:354–366.

Forster, J., A. G. Hirst, and D. Atkinson. 2012. Warming-induced reductions in body size are greater in aquatic than terrestrial species. Proceedings of the National Academy of Sciences 109:19310–19314.

Gardner, J. L., A. Peters, M. R. Kearney, L. Joseph, and R. Heinsohn. 2011. Declining body size: a third universal response to warming? Trends in Ecology and Evolution 26:285–291.

Gilbert, B., T. D. Tunney, K. S. Mccann, J. P. Delong, D. A. Vasseur, V. Savage, J. B. Shurin, A. I. Dell, B. T. Barton, C. D. G. Harley, H. M. Kharouba, P. Kratina, J. L. Blanchard, C. Clements, M. Winder, H. S. Greig, and M. I. O'Connor. 2014. A bioenergetic framework for the temperature dependence of trophic interactions. Ecology Letters 17:902–914.

Gillooly, J. F., J. H. Brown, and G. B. West. 2001. Effects of size and temperature on metabolic rate. Science 293:2248–2252.

Kalinkat, G., F. D. Schneider, C. Digel, C. Guill, B. C. Rall, and U. Brose. 2013. Body masses, functional responses and predator-prey stability. Ecology Letters 16:1126–1134.

O'Connor, M. I., B. Gilbert, and C. J. Brown. 2011. Theoretical predictions for how temperature affects the dynamics of interacting herbivores and plants. The American Naturalist 178:626–38.

Rall, B. C., U. Brose, M. Hartvig, G. Kalinkat, F. Schwarzmuller, O. Vucic-Pestic, and O. L. Petchey. 2012. Universal temperature and body-mass scaling of feeding rates. Philosophical Transactions of the Royal Society B: Biological Sciences 367:2923–2934.

Rall, B. C., O. Vucic-Pestic, R. B. Ehnes, M. EmmersoN, and U. Brose. 2010. Temperature, predator-prey interaction strength and population stability. Global Change Biology 16:2145–2157.

Rosenzweig, M. L., and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. The American Naturalist 97:209–223.

Vasseur, D. A., and K. S. McCann. 2005. A mechanistic approach for modeling temperature-dependent consumer-resource dynamics. The American Naturalist 166:184–198.

West, G. B., J. H. Brown, and B. J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. Science 276:122–126.

Yodzis, P., and S. Innes. 1992. Body size and consumer-resource dynamics. The American Naturalist 139:1151–1175.

Figure legends

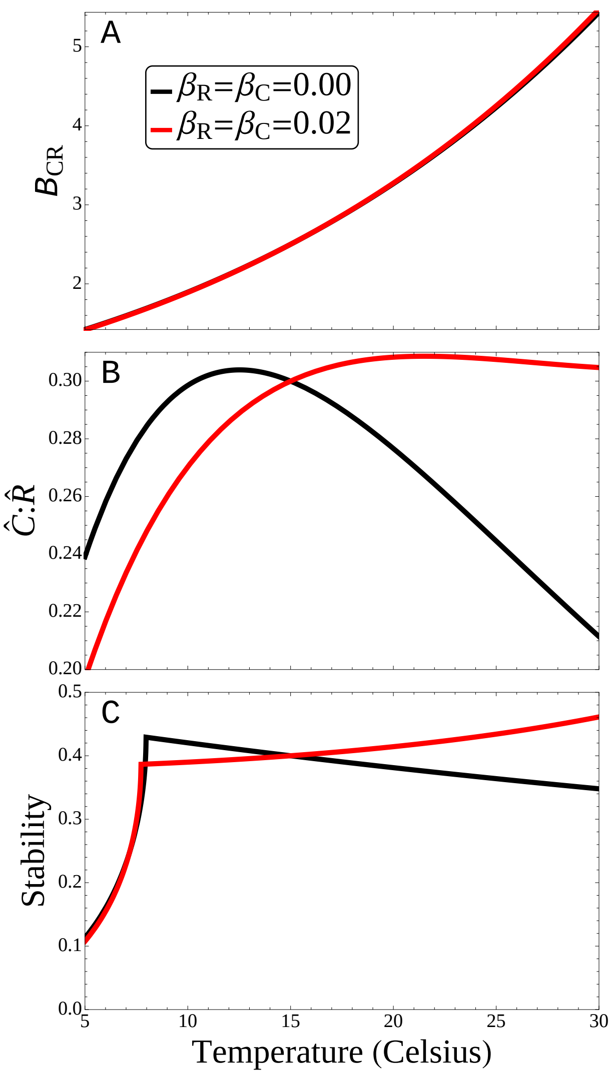

Figure 1: B_{CR}, equilibrium consumer to resource biomass ratio $\hat{C} : \hat{R}$, and stability of the co-existence equilibrium as functions of temperature T (plotted in Celsius) with (red) and without (black) mass dependencies and the temperature-size rule. Rate-constants were chosen to make $r = 2$, $K = 100$, $a = 0.1$, $m = 0.6$, and $e = 0.15$ at $15°C$ (as in Figure 3 of **?**). Other parameters as in **?** and **?**: $E_B = 0.32$, $E_S = 0.9$, $E_m = 0.65$, $E_{\nu,i} = 0.46$, $\nu_{0,i} = 1$, $\kappa = -0.81$, $\alpha = 1$, $\epsilon = -0.5$, $\mu = -0.29$, $\rho = -0.81$, $\beta_i = 0$ (black), $\beta_i = 0.02$ (red). Note that we allow all population dynamic parameters to depend on temperature and mass, unlike Figure 3 in **?**, where only K varies.

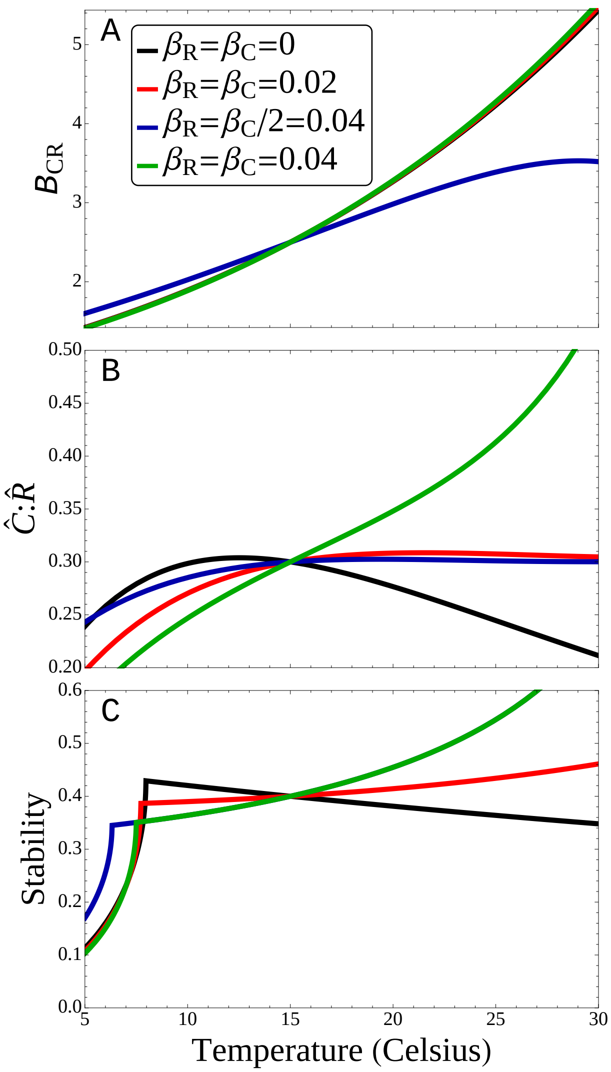

Figure 2: B_{CR}, equilibrium consumer to resource biomass ratio $\hat{C} : \hat{R}$, and stability of the coexistence equilibrium as functions of temperature T (plotted in Celsius) without the temperature-size rule (black), with a relatively weak, symmetric temperature size rule (red), with an asymmetric temperature-size rule (green), and with a relatively strong, symmetric temperature-size rule (blue). Rate-constants were chosen to make $r = 2$, $K = 100$, $a = 0.1$, $m = 0.6$, and $e = 0.15$ at $15°C$ (as in Figure 3 of **?**). Other parameters as in **?** and **?**: $E_B = 0.32$, $E_S = 0.9$, $E_m = 0.65$, $E_{\nu,i} = 0.46$, $\nu_{0,i} = 1$, $\kappa = -0.81$, $\alpha = 1$, $\epsilon = -0.5$, $\mu = -0.29$, $\rho = -0.81$.

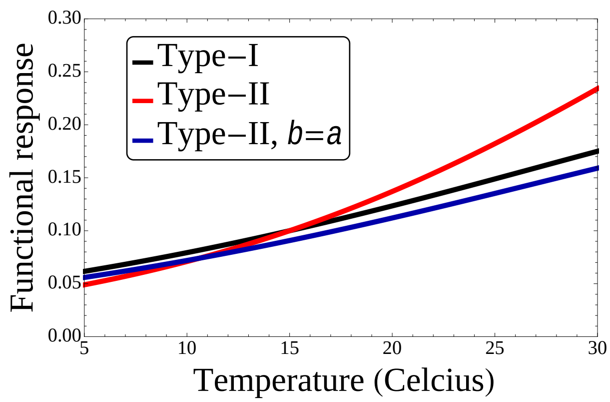

Figure 3: Functional response as a function of temperature. Shown are a type-I functional response (black), a type-II functional response with temperature- and mass-dependencies of capture rate and handling time from **?** (red), and a type-II functional response with temperature- and mass-dependencies of capture rate like that of attack rate in **?** (blue). Rate-constants were chosen to make $r = 2$, $K = 100$, $a = 0.1$, $m = 0.6$, and $e = 0.15$ at 15°C (as in Figure 3 of **?**). Other parameters as in **?**, **?**, and **?**: $E_B = 0.32$, $E_S = 0.9$, $E_m = 0.65$, $E_{\nu,i} = 0.46$, $\nu_{0,i} = 1$, $\kappa = -0.81$, $\alpha = 1$, $\epsilon = -0.5$, $\mu = -0.29$, $\rho = -0.81$, $\beta_i = 0.02$, $a_C = 1/4 + 2/3$, $a_R = 1/3$, $h_C = -2/3$, $h_R = 0.5$, $E_a = 0.65$, $E_h = -0.65$, $h_0 = 10^{-13}$.

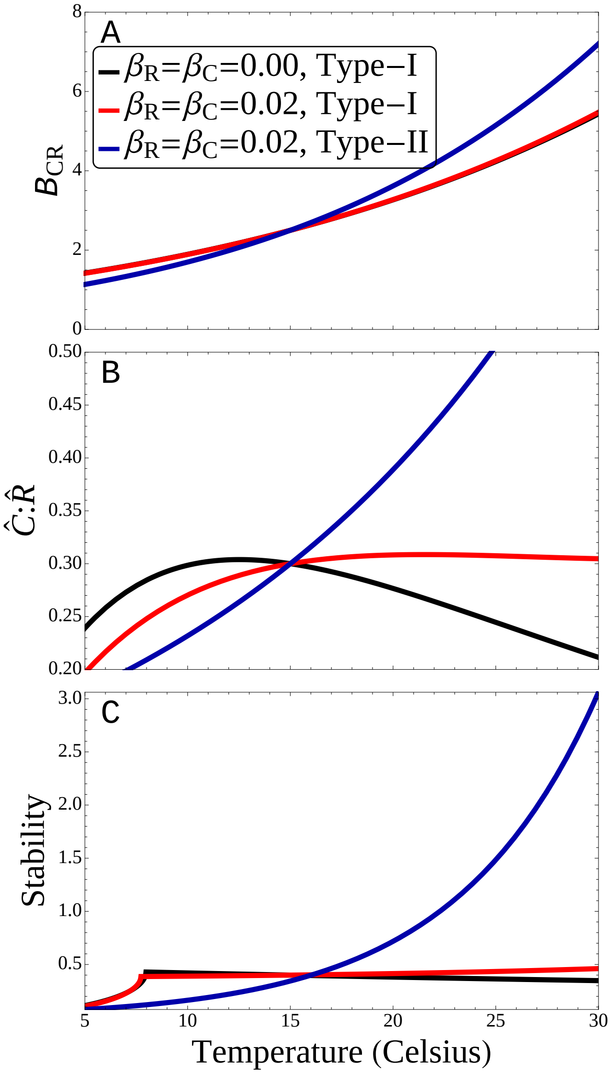

Figure 4: SUPPLEMENTARY FIGURE. B_{CR}, equilibrium consumer to resource biomass ratio $\hat{C} : \hat{R}$, and stability of the coexistence equilibrium as functions of temperature T (plotted in Celsius) with (red and blue) and without (black) mass dependencies and the temperature-size rule. Type-II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

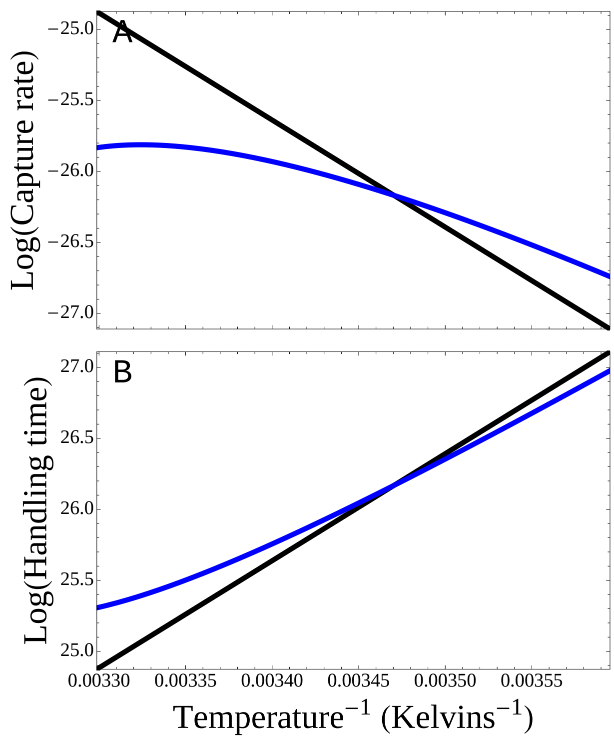

Figure 5: SUPPLEMENTARY FIGURE. The sensitivity of capture rate and handling time to temperature with (blue) and without (black) the temperature-size rule. Plotted are (A) $\log(b/b0)$ and (B) $\log(h/h0)$. Parameters as in **?**: $a_C = 1/4 + 2/3$, $a_R = 1/3$, $h_C = -2/3$, $h_R = 0.5$, $E_a = 0.65$, $E_h = -0.65$.