

Interactive effects of oxygen and temperature on ectotherms

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1 Setting up the model

1.1 Key assumptions

- Animals will adapt activity levels to optimise available energy
- Growth is limited either by food capture, food processing capacity, or by available oxygen
- Temperature acts directly on rates that are determined by enzymatic activity: digestive activity (via maximum consumption) and metabolic cost. The scaling with temperature (determined by the activation energy E_a) is assumed the same for these processes. Consequently, temperature only acts on ecological rates (food acquisition) via optimisation given temperature driven changes in enzymatic rates.

1.2 Adaptive activity model

In the adaptive activity model, ectotherms adjust the relative amounts of time (τ) spent foraging and resting to optimise the net energy/mass gain P_C . Since both energy gain and loss are sensitive to temperature and oxygen limitations, both the activity level and the net energy gain will be subject to these environmental constraints. Their interplay thus determines available energy for growth, reproduction, and, ultimately, organisms final size.

The model is written in terms of carbon (or energy) and oxygen balance equations:

$$f_C = \frac{\tau}{\tau + \frac{hc_T w^q - p}{\gamma \Theta}} \quad (1)$$

$$P_C = S_C - D_C \quad (2)$$
$$= (1 - \beta - \phi) f_C h c_T w^q - (1 + \tau \delta) c_T k w^n \quad (3)$$

$$P_{O_2} = S_{O_2} - D_{O_2} \quad (4)$$

$$= f_{O_2} w^n - \omega (\beta f_C h c_T w^q + (1 + \tau \delta) c_T k w^n) \quad (5)$$

where f is the feeding level ($[0,1]$), determined by the fraction of time spent foraging (or proportion of maximum attack rate) τ , consumption rate $\gamma w^p \Theta$ (search rate γw^p times prey availability Θ) and maximum consumption hw^q . In the following, we will refer to τ as the activity fraction for sake of generality. Maximum consumption, being determined by digestive (enzymatic) processes, is assumed to scale with temperature as $c_T = e^{E_a(T-T_0)/kTT_0}$. Available carbon P_C is determined by supply (S_C) from prey consumption ($f_C h c_T w^q$), with $\beta \approx 0.15$ a loss due to specific dynamic action (SDA, or heat increment; the energy spent absorbing food), and $\phi \approx 0.25$ is the fraction of food excreted and egested. Metabolic costs (D_C) are those of standard metabolism (kw^n), as well as active metabolism (scaled in units of standard metabolism as δkw^n), with the activity fraction τ determining the fraction of time that the active metabolism cost applies.

The oxygen budget determines the metabolic scope S_{O_2} . Metabolic scope is the difference between oxygen supply $S_{O_2}/w^n = f_{O_2}$, the amount of oxygen supplied per unit weight, and oxygen demand. Demand (D_{O_2}) is the sum of oxygen used for SDA ($\beta f_C h c_T w^q$) and catabolism ($[1 + \tau\delta]c_T kw^n$), with ω determining amount of oxygen required per unit of metabolised carbon (note: oxygen is measured in the same units as the carbon. To find the actual amount of oxygen used multiply by the amount of oxygen used to respire one unit of carbon).

The maximum oxygen consumption—usually called the maximum metabolic rate (MMR), or active metabolic rate—is the oxygen consumption during maximal activity level that can be sustained over some time. This level is determined by oxygen delivery to organs and muscles. At constant temperature, oxygen supply as a function of ambient oxygen is assumed, in line with experimental evidence, to follow a saturating function. We specify P_{50} as the point where the MMR (or oxygen supply) has dropped by 50% relative to the saturation level l ¹. Oxygen supply, and hence the MMR, are usually found to be temperature dependant (CITE), with a peak in MMR at an optimal temperature. We follow Lefrancois & Claireaux (2003) and Strasbaka & Gnauck (1985) and use a dome shaped function that peaks at the optimal temperature. Thus:

$$f_{O_2} = l(1 - e^{O_2 \log(0.5)/P_{50}}), \quad (6)$$

$$l = \zeta \left(\frac{T_{\max} - T}{T_{\max} - T_{\text{opt}}} \right)^\eta \times \exp\left(-\eta \frac{T_{\max} - T}{T_{\max} - T_{\text{opt}}}\right), \quad (7)$$

with f_{O_2} the oxygen supply (MMR), T_{\max} the lethal temperature for the species, T_{opt} the temperature at which the MMR is optimised and η determines the width of the dome-shape, and ζ its height (Figure 1).

We now assume that organisms will adjust their activity level to maximise available energy under energetic and oxygen constraints. Energetically, the optimal activity level (τ_{opt}) is found at $\frac{dP}{d\tau} = 0$, which gives

¹Could also use the same functional form as the consumption of food for simplicity: $f_{O_2} = \Gamma \Theta_{O_2} / (\Gamma \Theta_{O_2} + h_{O_2} = \Theta_{O_2} / (\Theta_{O_2} + P_{50}))$.

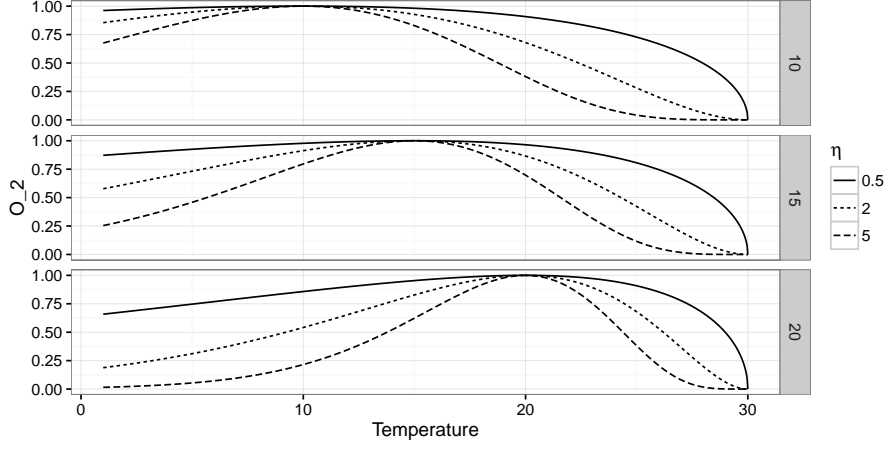


Figure 1: Maximum metabolic rate as a function of temperature, for three different optimal temperatures (panels—see panel label for optimal temperature in degrees celsius), and increasing values of η .

$$\tau_{\text{opt}} = \frac{w^{-n-2p} \sqrt{(1-\beta-\phi)\gamma^3 \delta k c_T h^2 w^{n+3p+2q}}}{\gamma^2 \delta k} - \frac{c_T h w^{q-p}}{\gamma}. \quad (8)$$

We assume that the metabolic scope dictates the upper limit of this activity, such that at τ_{max} , oxygen demand D_{O_2} equals total supply S_{O_2} . Solving for τ_{max} , the expression is far less elegant:

$$\begin{aligned} \tau_{\text{max}} = & \frac{1}{2\gamma\delta c_T k \omega} m^{-n-p} \\ & ((-\gamma f_{O_2} m^{n+p} + \gamma c_T k \omega m^{n+p} + \delta k c_T^2 h \omega m^{n+q} + \beta c_T \gamma h \omega m^{p+q})^2 - \\ & 4\gamma\delta c_T k \omega m^{n+p} (k h c_T^2 \omega m^{n+q} - f_C h c_T m^{n+q}))^{0.5} \\ & \gamma f_C m^{n+p} - \gamma k \omega c_T m^{n+p} - \delta k h c_T^2 \omega m^{n+q} - \beta \gamma h c_T \omega m^{p+q} \end{aligned}$$

Both temperature and oxygen will influence τ , such that at a given temperature and oxygen concentration, $\tau_{T,O_2} = \min(\tau_{\text{opt}}, \tau_{\text{max}})$, meaning we assume that animals will adapt their effort to optimise energy gain ($P_C^{\tau_{T,O_2}}$, the net production at τ_{T,O_2}).

Assuming a constant investment r in reproduction with weight ($D_{C_r} = rm$), the energy available for growth is directly proportional to $P_C^{\tau_{T,O_2}}$, and is thus a function of temperature and oxygen. Furthermore, organism size m_∞ , determined as the mass where $S_C^{\tau_{T,O_2}} = D_C^{\tau_{T,O_2}} + D_{C_r}^{\tau_{T,O_2}}$, is also determined by environmental factors.

Table 1: Parameters

Description	Value
Specific dynamic action	$\beta = 0.15$
Egestion and excretion	$\phi = 0.25$
Consumption rate ¹	$\Theta\gamma \approx hw^{p-q}$ (g _C /time)
Coef. for maximum consumption rate	$h \approx 5g_W^{1-n}/\text{yr}$
Critical feeding level	$f_c \approx 0.1$
Activity coefficient	$\delta \approx 1$
Exponent for max. consumption	$q = 0.75$
Exponent for clearance rate	$p = 0.8$
Exponent for std. metabolism	$n = 0.75$

¹ This is under the assumption that the amount of encountered food Θ is roughly independent of body size. This gives an order-of-magnitude estimate of the product $\Theta\gamma$.