Interactive effects of oxygen and temperature on ectotherms

Philipp Neubauer   Ken H. Andersen

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1   Setting up the model

1.1   Key assumptions

- Animals will adapt acitivty 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 aquisition) 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:

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

$$P_C = S_C - D_C \tag{2}$$

$$= (1 - \beta - \phi) f_C h c_T w^q - (1 + \tau \delta) c_T k w^n \tag{3}$$

$$P_{0_2} = S_{O_2} - D_{O_2} \tag{4}$$

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

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 avalibility 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 metabolsim 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_{0_2}. Metabolic scope is the difference between oxygen supply $S_{O_2}/w^n = f_{O_2}$, the amount of oxgygen 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). Oxygen supply as a function of ambient oxygen is assumed to follow a saturating function, with P_{50} the point where supply has dropped by 50% relative to the saturation level l. Assuming an asymptotic functional form, we can write $f_{O_2} = l(1 - e^{O_2 \log(0.5)/P50})$ [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

$$\tau_{opt} = \frac{w^{-n-2p}\sqrt{(1-\beta-\phi)\gamma^3\delta kc_T h^2 w^{n+3p+2q}}}{\gamma^2 \delta k} - \frac{c_T hw^{q-p}}{\gamma}. \qquad (6)$$

We assume that 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_{0_2}. Solving for τ_{max}, the expression is far less elegant:

$\tau_{max} = \dfrac{1}{2\gamma\delta c_T k\omega}m^{-n-p}$

$\qquad ((-\gamma f_{O_2}m^{n+p} + \gamma c_T km^{n+p} + \delta kc_T^2 h\omega m^{n+q} + \beta c_T \gamma h\omega m^{p+q})^2 -$

$\qquad 4\gamma\delta c_T k\omega m^{n+p}(khc_T^2\omega m^{n+q} - f_C hc_T m^{n+q}))^{0.5}$

$\qquad \gamma f_C m^{n+p} - \gamma k\omega c_T m^{n+p} - \delta khc_T^2\omega m^{n+q} - \beta\gamma hc_T\omega m^{p+q})$

Both temperature and oxygen will influence τ, such that at a given temperature and oxygen concentration, $\tau_{T,O_2} = \min(\tau_{opt}, \tau_{max})$, 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}).

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

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	$h \approx 5g_{WW}^{1-n}$/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 and order-of-magnitude estimate of the product $\Theta\gamma$.

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 m 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.