

Begin with the equation for reserve dynamics: assimilation minus mobilization.

$$\frac{dE}{dt} = \dot{p}_A - \dot{p}_C \quad (1)$$

Using the chain rule, we can derive the equation for reserve density  $[E] = E/V$ :

$$\frac{d[E]}{dt} = \frac{\dot{p}_A}{V} - \frac{\dot{p}_C}{V} - [E] \left( \frac{1}{V} \frac{dV}{dt} \right). \quad (2)$$

Following standard DEB notational convention, when a rate is written inside brackets it means that the rate is divided by structure  $V$ . So the equation for reserve density is typically written as:

$$\frac{d[E]}{dt} = [\dot{p}_A] - [\dot{p}_C] - [E]\dot{r}, \quad (3)$$

where  $\dot{r} = (1/V)(dV/dt)$  is the specific growth rate.

We also know that a fraction  $\kappa$  of the mobilization flux is allocated towards somatic growth ( $\dot{p}_G$ ) and maintenance ( $\dot{p}_M$ ), so that the specific growth rate can be written as

$$\dot{r} = \frac{1}{V} \frac{\dot{p}_G}{[E_G]} = \frac{\kappa[\dot{p}_C] - [\dot{p}_M]}{[E_G]}, \quad (4)$$

where  $[E_G]$  is the specific cost of growth.

Once we specify forms for mobilization rate  $\dot{p}_C$  and somatic maintenance rate  $\dot{p}_M$ , the dynamics of the state variables (energy reserves  $E$  and structure  $V$ ) will be completely determined.

The equation for reserve dynamics can be reexpressed more generally as

$$\frac{d[E]}{dt} = [\dot{p}_A] - g([E], V), \quad (5)$$

where  $g$  is some function of  $[E]$  and  $V$  that captures all of the ways that reserve density might decrease. Note that we know that  $g$  must depend only on  $[E]$  and  $V$  (the individual state variables) and not on  $f$  (the food availability) because mobilization and growth are independent of the external environment. We use two assumptions of DEB theory, those of partitionability and weak homeostasis, to derive the dependence of  $g$  on  $[E]$  and  $V$ .

The assumption of partitionability implies that the composition of  $g$  must be identical to the composition of the entire reserve. More precisely, for any compound  $E_i$  making up a constant fraction  $\lambda_i$  of the reserve, the amount of  $E_i$  in  $g$  must also be a constant fraction  $\lambda_i$  of  $g$ . That is

$$g_i([E_i], V) = g_i(\lambda_i[E], V) = \lambda_i g([E], V) \quad (6)$$

Mathematically, this implies that  $g$  must be linear in  $[E]$ , so we can rewrite  $g$  as

$$g([E], V) = h(V)[E] \quad (7)$$

where  $h(V)$  is some as-yet-undetermined function of  $V$ .

We can use the assumption of weak homeostasis to determine the dependence of  $h$  on  $V$ . Weak homeostasis states that under constant food there is a reserve density  $[E]^*$  which remains constant. This reserve density must be independent of structure, since the individual

will maintain this reserve density over growth. So when  $[E] = [E]^*$ ,  $d[E]/dt = 0$ , and

$$[\dot{p}_A] = h(V)[E]^* \quad (8)$$

Recall that  $[\dot{p}_A] = \{\dot{p}_{Am}\}f/L$ . Therefore, in order for  $[E]^*$  to be independent of structure,  $h(V)$  must have the same dependence on structure as does  $[\dot{p}_A]$ . Thus,

$$h(V) = \frac{\dot{v}}{L}, \quad (9)$$

where  $\dot{v}$  is a parameter, termed the energy conductance. Therefore, we have that

$$g([E], V) = \frac{\dot{v}[E]}{L} \quad (10)$$

The dynamics of reserve density are as follows:

$$\frac{d[E]}{dt} = \frac{\{\dot{p}_{Am}\}f}{L} - \frac{\dot{v}[E]}{L} \quad (11a)$$

$$= \frac{\dot{v}}{L} \left( \frac{\{\dot{p}_{Am}\}}{\dot{v}}f - [E] \right) \quad (11b)$$

$$= \frac{\dot{v}}{L} ([E_m]f - [E]), \quad (11c)$$

where  $[E_m]$  is the maximum reserve density.

To determine mobilization rate, recall that  $g([E], V) = [\dot{p}_C] - [E]\dot{r}$  (from equations 3 and 5). Substituting equations 4 and 10 into this expression, you can derive the equation for mobilization rate as:

$$[\dot{p}_C] = [E] \left( \frac{\dot{v}/L + [\dot{p}_M]/[E_G]}{1 + \kappa[E]/[E_G]} \right). \quad (12)$$