

## Delayed costs and their effect on adaptive growth rates

Jonathan M. Yearsley<sup>1</sup>, Ilias Kyriazakis<sup>2</sup> and Iain J. Gordon<sup>3</sup>.

It is widely recognised that growth can carry a mortality risk, and that these costs of growth can influence an animal's growth rate [3, 2, 6]. The adaptive significance of costs upon an animal's growth rate has been extensively modelled [7, 8, 9, 4, 1], but all studies have assumed that growth costs are instantaneous. In contrast, data suggest that the costs of growth need not always be instantaneous, but can act over a range of time-scales [5].

We present an adaptive growth model in which the costs of growth are delayed for period of time, with the time-delay defining the time-scale of the growth cost. The model is generally applicable to any two parameter growth curve, and is used to look at the effects of time-scale upon the adaptive growth strategy. The optimal growth rates are calculated assuming one of two possible fitness measures; the reproductive rate,  $R_0$  and the intrinsic population growth rate  $r$ .

The effect of an increasing time-delay in the costs of growth is to weaken the strength of selection on growth rate. A second implication of a time-delay is to suggest a new explanation for the strategy of compensatory growth following a period of growth limitation. It is shown that the time taken to reach maturity is a threshold time-delay: if the costs of growth are delayed until maturity then growth compensation can be an adaptive strategy, even if the environment is unchanging. The results are depen-

<sup>1</sup>The Macaulay Institute, Craigiebuckler, Aberdeen, U.K., AB15 8QH (e-mail: J.Yearsley@macaulay.ac.uk).

<sup>2</sup>Animal Nutrition and Health Department, Scottish Agricultural College, West Mains Road, Edinburgh, U.K., EH9 3JG (e-mail: I.Kyriazakis@ed.sac.ac.uk).

<sup>3</sup>The Macaulay Institute, Craigiebuckler, Aberdeen, U.K., AB15 8QH (e-mail: I.Gordon@macaulay.ac.uk).

dent upon the measure fitness, indicating that the form of the population regulation plays a role in determining adaptive growth strategies.

## References

- [1] Abrams PA, Leimar O, Nylin S, Wiklund C, 1996. The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. *American Naturalist* 147: 381–395.
- [2] Arendt JD, 1997. Adaptive intrinsic growth rates: and integration across taxa. *Quarterly Review of Biology* 72: 149–177.
- [3] Case TJ, 1978. On the evolution and adaptive significance of post-natal growth rates in the terrestrial vertebrates. *Quarterly Review of Biology* 53: 243–282.
- [4] Ludwig D, Rowe L, 1990. Life-history strategies for energy gain and predator avoidance under time constraints. *American Naturalist* 135: 686–707.
- [5] Metcalfe NB, Monaghan P, 2001. Compensation for a bad start: grow now, pay later? *Trends in Ecology and Evolution* 16: 254–260.
- [6] Nylin S, Gotthard K, 1998. Plasticity in life-history traits. *Annual Review of Entomology* 43: 63–83.
- [7] Sibly R, Calow P, Nichols N, 1985. Are patterns of growth adaptive? *Journal of Theoretical Biology* 112: 553–574.
- [8] Stearns SC, 1992. *The evolution of life histories*. Oxford: Oxford University Press.
- [9] Werner EE, Anholt BR, 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist* 142: 242–272.