# Ageing and typical survivorship curves result from optimal resource allocation

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#### ABSTRACT

Ageing is a general feature of higher organisms. Evolutionary theories of ageing rest on a gradual decline of fitness sensitivity to changes in survival and fecundity with age, so traits expressed late in life are less favoured by natural selection than those expressed early in life. From the life-history perspective, ageing may result from a scheme of optimal resource allocation in which investment in repair is lower than that required for removing all experienced damage. Here, we report the results of a dynamic programming model based on the disposable soma theory of ageing, which optimizes resource allocation to growth, reproduction and repair. The optimal allocation strategy responds to externally imposed mortality, and repair intensity varies with age, being highest early in life. Because the level of repair varies, the rate of ageing is highest under high extrinsic mortality and lowest under low mortality. The allocation strategy shapes the survivorship curve and maximum lifespan. The model results provide an explanation of the variety of survivorship curves and maximum lifespans observed in nature. The results are discussed alongside empirical data from studies using mainly comparative approaches.

*Keywords*: ageing, disposable soma theory, life history, longevity, mortality, resource allocation, survivorship curves.

#### **INTRODUCTION**

Ageing has attracted considerable attention from scientists in different disciplines. It is a process of decline in physiological functioning that results in increasing mortality and decreasing reproduction with age. From the life-history perspective, ageing means restriction of the life-history options open to an organism over time (Partridge and Barton, 1996). Because ageing appears non-adaptive, it is puzzling to evolutionary biologists. The commonly accepted explanation is that ageing occurs because natural selection acts less strongly on traits expressed late in life than on those expressed early in life (Medawar, 1952; Williams, 1957; Hamilton, 1966; Charlesworth, 1994). Two classes of mechanisms are based on this assumption (see Rose, 1991; Partridge and Barton, 1993): (1) the non-adaptive explanation, according to which late-acting deleterious mutations accumulate in

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