# Dimensionless numbers and life history evolution: age of maturity versus the adult lifespan

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#### Summary

Within many taxa the age of maturity is not simply positively correlated with the adult lifespan; the two variables are proportional to each other. The dimensionless number which is the constant of proportionality thus becomes something to be predicted by life history theory.

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A great many versions of life history evolution theory predict that the age of maturity should be positively correlated with the lifespan, and this qualitative prediction is met within many taxa (e.g., Williams, 1966; Tinkle, *et al.*, 1970; Charlesworth, 1980; Stearns and Crandall, 1981; Charnov, 1989, 1990). However, it is our contention that there is something much more interesting in the data than just the theoretically expected positive relation. To drive home this point, define  $\alpha$  as the age of maturity, and M as the average adult instantaneous mortality rate (i.e. survival for one time unit =  $e^{-M}$ ). Now note that  $\alpha \cdot M$  is a dimensionless number which neatly summarizes the relationship between lifespan and maturation. Indeed, the average length of the adult lifespan looks very much like 1/M; and of course  $\alpha \cdot M = \alpha/(1/M)$ ; thus the  $\alpha \cdot M (= x)$ 

Taxa	Μ·α	Method of estimation	Source
Fish	≃ 2	Regression of $\log_e M$ on $\log_e \alpha$ ( $r = -0.73$ all fish ( $n = 52$ ); $r = -0.84$ for Clupeomorpha ( $n = 26$ ))	Charnov and Berrigan, 1990 data from Beverton and Holt (1959), Beverton 1963 for Clupeomorpha
N. American walleye or pike perch (Stizostedion vitreum)	<b>≃</b> 2	Regression of $\log_{e} (1/T_m)$ on $\log_{e}\alpha$ for 13 pops ranging from Texas to N. Canada (r = -0.90)	Beverton, 1987
Pandalid shrimp (temperate to arctic waters, 5 species and 27 pops.)	≃ 2	$\alpha \cdot \bar{K} = 0.8$ for each of 3 $\alpha$ values (1989b) and $M = 2.7 \cdot K$ by fitted regression (1979) (r = 0.84)	Charnov, 1979, 1989

Table 1. The dimensionless number  $M \cdot \alpha$  for various taxa.

Temperate snakes	<b>≃</b> 1.5	Regression of $\log_e M$ on $\log_c \alpha$ for 16 species (r = -0.84)	Charnov and Shine 1990
Lizards	<b>≃</b> 1.3	Regression of $\log_e M$ on $\log_e \alpha$ for 20 species (r = -0.78)	Charnov and Shine, 1990
Mammals	<i>≃</i> 0.75	Regression of 'average adult lifespan' on $\alpha$ for 29 species ( $r = 0.96$ )	Charnov, 1990, data from Millar and Zammuto, 1983
Birds	<b>≃</b> 0.4	Regression of 'average adult lifespan' on $\alpha$ for 66 species ( $r = 0.91$ )	Unpublished analysis, data from many sources

number tells us the length of the prereproductive period ( $\alpha$ ) relative to the adult lifespan (1/M), or  $\alpha = x(1/M)$ . Should 1/M be proportional to  $\alpha$ , or M inversely proportional to  $\alpha$  within a group of species (or populations within one species), then the group shares a common value for the  $\alpha \cdot M$  number.

Our contention, defended in Table 1, is that  $1/M \propto \alpha$  within many taxa. For example, bony fish have  $\alpha \cdot M \approx 2$ , as do Pandalid shrimp (in a survey which covers the whole northern hemisphere). Temperate snakes have  $\alpha \cdot M \approx 1.5$ , while mammals have  $\alpha \cdot M \approx 0.75$ , a value much lower than the ectotherms. Lizards also show M to be inversely proportional to  $\alpha$ ; here  $\alpha \cdot M$  equals 1.3, right near the other ectotherm values and nowhere near the endotherms. Thus, for a given prereproductive period mammals and birds have average adult lifespans 3-5 times longer than fish, and 2-4 times longer than reptiles (see Fig. 1).

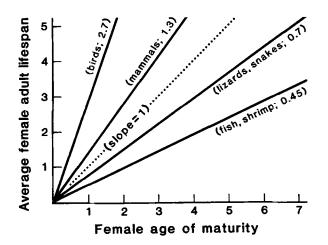


Figure 1. Average adult lifespan versus age of maturity. Y-axis is the 'expectation of further life at the age of maturity' estimated either by the area under the lx curve from age of maturity on (the best method) or by the inverse of the adult instantaneous mortality rate. Number on each line is the slope. See Table 1 for statistics.

#### Age of maturity versus the adult lifespan

So, the relation between lifespan and age of maturity is not just *positive*, it is often proportional. We consider it a major goal of life-history evolution theory to explain both the proportionality itself, and to attach meaning to the constant of proportionality – the dimensionless number  $\alpha \cdot M$ ; are the ectotherm/endotherm and terrestrial/aquatic differences shown in Table 1 related to some general features of the energetic/growth environment? Life history theorists have really just begun this exploration (Charnov, 1990; Charnov and Berrigan, 1990), although in one sense the scaling of maturation to lifespan is an old demographic technique; i.e., a 'dog's year represents  $\approx 7$  human years, etc.'

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