PERSPECTIVES: EVOLUTIONARY BIOLOGY

Sex and Death

David N. Reznick and Cameron Ghalambor

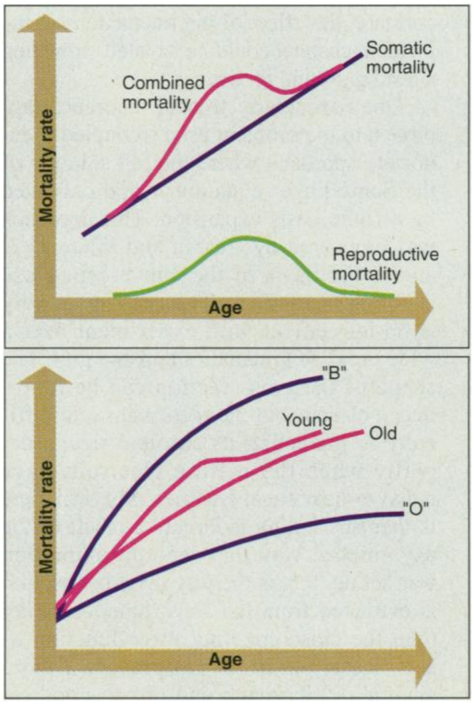
Inexorable facts of life in Western society are birth, death, and taxes. For organisms in nature, life's trinity is instead birth, death, and reproduction. It is the task of evolutionary biologists to work out how these three components of an organism's life history are related. For example, theories that seek to explain how life histories of organisms evolve often assume that an increase in the number of offspring produced results in a shortening of life-span. But the empirical evaluation of this reproductive cost has proven far more difficult than the assumption of its existence. This reflects inconsistencies among the different methods used to evaluate the cost of reproduction (*1*). Now, on page 2521, Sgró and Partridge (*2*) elegantly combine two experimental approaches to show that in the fruit fly *Drosophila* reproduction has a delayed impact on mortality that becomes evident long after the onset of egg production. They developed two lines of fruit flies ("young" and "old") that differed in longevity and evaluated how abrogation of egg-laying altered mortality rate. By analyzing mortality in young and old flies that could or could not lay eggs, the investigators were able to provide a superior definition of cause-and-effect. Their approach also yielded some surprising dividends in the characterization of the evolution of aging.

The authors created five replicate young and old lines of fruit flies. Each generation of the young line was initiated with eggs laid by very young adults; each generation of the old line was initiated with eggs from much older (21 to 28 days) parents. After 31 generations of selection, the old lines produced fewer eggs early in life, but had longer life-spans (*3*). The mortality rates of the young and old fly lines were similar up to 30 days of age. Then, the young line experienced a wave of higher mortality that peaked at 40 to 50 days of age (see the figure, top).

The investigators compared how the mortality rates of young and old lines changed in response to two types of manipulation that abrogated egg laying. First, they irradiated larvae, inducing sterility. Second, they ablated reproduction by creating young and old lines that contained a mutation in the *ovo* gene. This gene is only expressed in the ovary, and mutants cease egg production at an early stage in development. With either x-irradiation or mutation the higher mortality in the young lines disappeared, yielding very similar mortality rates in the young and old lines. The authors' interpretation of this finding is that the fly death rate has two components. The first component, shared by the young and old lines, is an acceleration in death rate as the flies age. The second component is a reproduction-induced surge in mortality at the onset of aging after egg laying has ceased. It is the second component that is "removed" by the experimental abrogation of reproduction. This removal erases much of the difference in mortality schedule and life-span between the young and old lines (see the figure, top).

Medawar (*4*) proposed that aging is caused by the interaction between accumulated deleterious mutations and mortality due to extrinsic causes, such as disease or predation. Populations that experience lower extrinsic mortality will accumulate fewer such mutations because they will be removed by natural selection. The aging disparities in this study are not caused by the accumulation of deleterious mutations; if they were, then the difference in mortality rates between the young and old lines would persist even when they were unable to reproduce. Instead the different mortality rates can be attributed to antagonistic pleiotropy: that is, genes that alter the cost-benefit balance at different stages in the life cycle through their affect on both early life fecundity and longevity (*5*). The investigators' success in selecting for flies with increased longevity lies in the selection of alleles that both suppressed reproduction early in life and the wave of mortality that this reproduction causes later in life. Conversely, in young lines, the evolution of increased reproduction early in life comes at the cost of reduced longevity.

An unanticipated dividend of the Sgró and Partridge study is their explanation for one of the most surprising results to emerge from aging research. Evolutionary theory predicts that mortality rates should continue to accelerate with age. But, instead, mortality rates plateau or decelerate in organisms as diverse as yeast, nematodes, insects, and humans (*6*). This leveling off can be caused by nongenetic differences in frailty or susceptibility to mortality among individuals (*7*). Sgró and Partridge suggest that the deceleration in mortality at greater ages might also reflect the waning of the wave of mortality induced by reproduction (see the figure, top).



Death-defying flies (Top) Mortality can be separated into two components. The first ("somatic mortality") refers to the progressive increase in mortality rate with age. The second ("reproductive mortality") applies to the wave of mortality that follows long after the onset of reproduction. The actual mortality rate is the sum of these two components. When combined, the mortality rate appears to level off at advanced ages. Sgró and Partridge (*2*) propose that it is the "reproductive mortality" component that is reduced as a consequence of selection for egg laying late in life. **(Bottom)** Differences in the mortality rates of "B" and "O" lines versus "young" and "old" lines of flies (*2*, *8*). The mortality rate of the B line increases more steeply than that of the O line early in life, but this difference is reduced as mortality rates level off later in old age (*2*). The mortality rate of the young line is similar to that of the old line until 30 days of age when it shows a transient increase, presumably as a consequence of the higher fecundity early in life of the young line flies.

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The results of the Sgró and Partridge study differ from those of a similar study by Service and colleagues (*7*, *8*). Service's group compared "B" and "O" lines of fruit flies (*9*), which are analogous to the young and old lines, respectively, in the Sgró and Partridge study. The B lines have a steeper increase in mortality rate than O flies early in life and higher mortality rates throughout their lives (*7*) (see the figure, bottom). This is in contrast to the wave of increased mortality among young fly lines at the onset of aging found in the new study (*2*). Service's group (*8*) compared the longevities of mated and unmated B and O lines of fruit flies. They found that unmated, nonreproducing flies lived longer than mated flies, but that the difference in longevity remained the same for both lines whether they were mated or not.

There are three possible explanations for the differences between the B and O and young and old lines. First, the lines themselves were derived from different baseline stocks of *Drosophila*, so the way in which they "evolved" may reflect genetic differences that were there from the start. Second, the flies in Service's experiments (*8*) had normal intact ovaries, whereas those in the new study did not. In fact, many of the unfertilized flies in the Service study still produced some eggs, thus incurring some reproductive cost. Third, there were differences in the mode and intensity of selection for young and old lines. In terms of mode, Sgró and Partridge's selection regime more effectively isolated age-specific egg production as the agent of selection. In terms of intensity, the Service group progressively increased the intensity of selection by increasing the difference in B and O line generation times from two- to fivefold (*9*). In contrast, Sgró and Partridge sustained a steady twofold difference in generation time between young and old lines throughout selection.

The effects of the mode of selection can be evaluated by adopting a selection regime similar to that used by Service and colleagues (*9*), and by selecting for new derivatives from the young and old lines. The effects of the intensity of selection can be evaluated by first increasing the intensity of selection on the derivatives of the young and old lines, and then by repeating the experimental manipulations that abrogate reproduction. If the differences between the two studies can be attributed to the baseline population or selection regime, then this diversity in outcomes may be giving us a glimpse of the true complexity of the genetics of aging and the diverse mechanisms by which a changing life-span evolves. Regardless of whether the disparities between these findings are resolved, the Sgró and Partridge study has provided a new means for understanding the evolutionary relationship between reproduction and mortality.

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PERSPECTIVES: APPLIED PHYSICS

Semiconductor Lasers Lose Their Cool

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Semiconductor lasers are used widely in applications ranging from telecommunications to compact disc (CD) players to atmospheric chemistry. A relatively new concept in semiconductor laser technology, the quantum cascade (QC) laser, promises to revolutionize laser technology in the mid- to far-infrared spectrum. Vertical cavity surface emitting lasers (VCSELs) are also promising because the perpendicular beam they emit allows arrays of lasers to be packed closely on a wafer surface, thus enabling large arrays of lasers to be manufactured at low cost. Three recent papers (*1*–*3*) explain how some of the remaining technical obstacles to the wider applicability of QC and VCSEL lasers may be overcome.

Traditional semiconductor lasers are diodes and can operate at or above room temperature. They are also capable of continuous, as opposed to pulsed, operation. "Pump" power is delivered by an electric current injected into the junction region of the diode. In contrast, QC and VCSEL lasers have until recently been restricted to low temperatures. The three papers (*1*–*3*) describe QC and VCSEL lasers operating at room temperature, although none demonstrates continuous operation and only one (*1*) describes devices pumped by electrical current injection.

Initial demonstrations of a new type of semiconductor laser typically involve optical rather than electrical pumping. Optical pumping by short excitation pulses avoids substantial heating and bypasses the engineering challenges inherent in delivering high electric current densities into the active region. Such device engineering is a major issue in VCSELs, in blue lasers based on nitrides, and in quantum cascade lasers where the potential drop across the device implies much heat generation. Krestnikov *et al.* (*2*) and Someya *et al.* (*3*) use a vertical cavity device geometry for their blue nitride-based lasers, thus combining two forms of device engineering difficulty when attempts are made to extend them to electrical pumping. Most new semiconductor lasers also do not begin as room temperature devices, their obvious operating regime. The standard approach has been to start with optical pumping at cryogenic temperatures and low duty-cycle excitation by short pulses. Cryogenic cooling has also been used with electrically pumped lasers, because the threshold current for lasing increases exponentially with temperature. Optical pumping is generally much less efficient than electrical pumping, but this is not necessarily a problem because high instantaneous power pulses are readily obtained, for example, from mode-locked titanium-sapphire lasers or, at shorter wavelengths, from nitrogen gas lasers. In (*2*) and (*3*), the instantaneous pump level is about 1 MW cm^{-2}; by contrast, the best semiconductor lasers have threshold power densities of well below 100 W cm^{-2}.

Most semiconductor lasers are based on direct band gap III-V compounds. Active structures are grown epitaxially on single-crystal substrates of gallium arsenide (GaAs) or indium phosphide (InP). A notable exception is the blue semiconductor laser (*4*, *5*), which is usually grown on insulating substrates of single-crystal sapphire. QC lasers (*6*) retain the use of substrates of GaAs or InP but involve the growth of remarkably complex and precise epitaxial structures. QC lasers are unusual in their use of a single type of current carrier (electrons), instead of the traditional *p-n* diode in which light is generated through electron-hole recombination. Traditional laser technology does not easily enable coherent laser emission in the infrared, but the advent of the QC laser is likely to change this situation radically.

The paper by Müller *et al.* on QC

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