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B. Survival analysis and Darwinian fitness

Survival* analysis is based on analyzing survival time X as a random variable [1], survivorship at age x, $\ell(x)$, being

$$\ell(x) = P(X \geq x). \tag{10.1}$$

The age-derivative of $\ell(x)$, $\ell'(x)$, is the additive inverse of the probability density function of the survival times, $f(x)$:

$$\ell'(x) = -f(x). \tag{10.2}$$

The mortality rate $\mu(x)$ is the change in survivorship conditioned on survivorship itself:

$$\mu(x) = -\frac{\ell'(x)}{\ell(x)}. \tag{10.3}$$

The rationale for analyzing the mortality rate is that the change in survivorship at age x comes down on those who survive up to age x, so that it expresses the change that pertains to survivors. Survivorship is directly related to the mortality rate through

$$\ell(x) = e^{-\int_0^x \mu(t)dt}. \tag{10.4}$$

Life expectancy from some age x onwards is calculated from $\ell(x)$ as

$$e(x) = \frac{1}{\ell(x)} \int_x^\infty \ell(t)dt, \tag{10.5}$$

with $e(0)$ life expectancy at birth. To die at age x, one has to survive to age x, and then die. Hence, $f(x)$ can be expressed as

$$f(x) = \ell(x)\mu(x). \tag{10.6}$$

Taking the integral over $f(x)$ yields

$$\int_0^\infty f(x)dx = 1. \tag{10.7}$$

The result of equation (10.7) makes sense. In intuitive terms, the chance of dying at some point in a lifetime is exactly one. In mathematical terms, $f(x)$ is a probability density function, integrating over which yields 1. This total mortality is incurred over $e(0)$ units of time. Hence, average mortality per time unit ($\bar{\mu}$) is $1/e(0)$, and vica versa:

$$e(0) = 1/\bar{\mu}. \tag{10.8}$$

Life expectancy and average mortality per time unit are inversely related. More generally, $\bar{\mu}(x)$ being average mortality from age x onwards,

$$\bar{\mu}(x) = \frac{\int_x^\infty \ell(t)\mu(t)dt}{\int_x^\infty \ell(t)dt}. \tag{10.9}$$

Knowing any one of the functions $\mu(x)$, $\ell(x)$ or $f(x)$, all others can be calculated.

Darwinian fitness is clearly a function of survival. The survivorship function indicates how long entities last, which is an indicator of future presence of the heritable material. Darwinian fitness is evenly clearly a function of reproduction. Reproduction leads to the creation of new entities, which contribute to the future presence of the heritable material. Reproduction and survivorship interact, in the sense that they determine each other's utility: The longer newly produced organisms survive, the greater their impact on the heritable material 'being there' in the future. Reversely, only organisms that are alive can reproduce, so survivorship augments reproductive output. Consequently, a measure of Darwinian fitness will depend on the product of survivorship and reproduction.

We can consider the instantaneous 'replacement rate' of organisms. To reproduce, an organism has to be alive. To die, it has to be alive as well. So at any moment, the instantaneous replacement rate is:

$$\ell(x)m(x) - \ell(x)\mu(x). \tag{10.10}$$

This is the rate at which new life is produced minus the rate at which life is lost, at an instance in time. However, organisms may defer reproduction and survival to later moments. For instance, during the first decade or so, humans do not reproduce, but do suffer mortality, so that the instantaneous replacement rate is negative. Early life processes, however, can have a large impact on later performance. Organisms grow and develop, which increases the vital rates at later points. This is not captured in equation 10.10, which is why equation 10.10 should be evaluated over all ages:

$$\int_0^\infty \left(\ell(x)m(x) - \ell(x)\mu(x)\right)dx = \int_0^\infty \ell(x)m(x)dx - \int_0^\infty \ell(x)\mu(x)dx. \tag{10.11}$$

Of the far right integral of equation (10.11) we know exactly what it is. It is the probability of an organism's death at some point during its lifetime, which is one per definition. There is therefore no surprise in this integral, and it can be left out of evolutionary considerations. The first integral on the right hand side of equation (10.11) is called the net reproductive rate, which is the expected value of number of offspring produced over an organism's lifespan [2,3].

The net reproductive rate has been used as a measure of fitness. It is, however, imperfect, because it does not account for *timing* of reproduction. An organism that replaces itself twice has a net reproductive rate of two. However, an organism that replaces itself twice every year will establish a population that grows much faster than a population established by an organism that replaces itself twice every ten years. Thus, it is necessary to extract a per time growth rate from a schedule of mortality and fecundity. This growth rate is conventionally indicated by r, and is called the intrinsic rate of increase, or the population growth rate. In the latter case, it should be kept in mind that the population that is referred to is the population established by the organism under study. Although a fitness measure should be an individual measure, otherwise competition cannot be accounted for, high individual fitness leads to a growing population of copies of that individual, so that we speak of "the population growth rate of the individual" [4]. The way to extract this population growth rate is to solve for r as the unique real root of the Euler-Lotka equation [2,3,5,6]:

$$\int_0^\infty e^{-rx}\ell(x)m(x)dx = 1. \tag{10.12}$$

The equation has many complex solutions, signifying potentially great oscillations initially. However, under some age-pattern of mortality and fecundity, eventually a stable population emerges, with asymptotic growth rate r. Lotka [5] was attentive enough to take ρ as a symbol for the unique real root of the equation, but it has become conventional to use r, keeping in mind that this is meant to refer to the unique real root of the equation.

Thus, we have obtained a valuable measure of Darwinian fitness, r, which passes the 'evolutionary stable strategy' (ESS) test [3]. This means that no organism that maximizes r under some constraints can be out-competed by organisms that choose a different strategy under the same constraints.

References

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