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Adaptive value, entropy and survivorship curves

NATURAL survivorship curves fall into three main types^{1,2}. Type I, or rectangular distribution, describes the situation in which all individuals attain the maximum physiological longevity of the species. Here the maximum age at death and the mean life expectancy coincide. The Type II life table describes a mortality which is independent of age; that is, no single age group is favoured at the time of dying. The Type III table is characterised by a high mortality early in life and a life expectancy which increases with the age of survivors. The three types of curve are illustrated in Fig. 1. The general shape of the survivorship curve is fixed for each species, however, the convexity of the curve is highly sensitive to environmental conditions and the genetic constitution of the population. This fact suggests that the general shape of the life table may provide information about the genetic variability in the population, the range of environmental factors that impinge on the population or the incidence of random events in the lifetimes of different individuals³. This note characterises in terms of two new demographic parameters the relative effect genetic and environmental factors play in the evolution of the life table. The analysis we give revolves around two demographic variables, the entropy of a population and the adaptive value. Entropy H measures the variability of the mortality distribution. The measure of variability also describes the convexity of the life table. The adaptive value ψ is a measure of the correlation between the variability of the mortality distribution and the environmental variability. Thus the adaptive value reduces to the entropy when the environment is constant.

We give two distinct characterisations of life-history curves in terms of optimisation arguments. In the first characterisation, we assume that the survivorship curves are completely determined by the genetic constitution. The life tables are derived by maximising H subject to constraints which are given a genetic interpretation. In the second description, we assume that the environmental effects are the only significant influence. The three life tables are derived in terms of maximising ψ subject to constraints on the environmental parameters. We

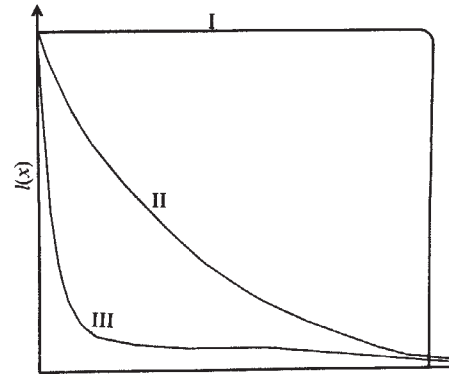


Fig. 1 The theoretically possible distinct types of life table. For Type I, $H = \log e^0$; for Type II, $H = 1 + \log e^0$ and $l(x) = \exp -(x/e^0)$; for Type III, $H = \frac{1}{2} + \log e^0$ and $l(x) = \exp -(\pi/4e^{02})x^2$.

also discuss the corresponding biological mechanisms which generate the life tables. Note that the genetic and environmental constraints which are imposed in the optimisation arguments correspond to initial conditions in the mechanistic description. These biological mechanisms can be mathematically described in terms of a birth and death process. This mathematical model together with a precise description of the correspondence between constraints and initial conditions is discussed elsewhere⁶.

Let $l(x)$ be the probability that an individual born at age zero survives to age x , and let $m(x)$ be the age-specific fecundity. The net reproductive rate R_0 is given by

$$R_0 = \int_0^{\infty} l(x)m(x) dx$$

The expectation of life of an individual aged x is

$$e^0 = \int_0^{\infty} l(x) dx$$

The entropy of the population⁴ is given by

$$H = - \int_0^{\infty} q(x) \log q(x) dx$$

where $q(x) = l(x)m(x)/R_0$ is the probability density function of the age of reproducing individuals. The expression H is a measure of the variability of the contribution of the different age-classes to the stable age-distribution. It also measures the convexity of the net-maternity function $V(x) = l(x)m(x)$. Fixing the fecundity, say $m(x) = 1$, we obtain

$$H = - \int_0^{\infty} \frac{l(x)}{e^0} \log \frac{l(x)}{e^0} dx \\ = - \frac{\int_0^{\infty} l(x) \log l(x) dx}{\int_0^{\infty} l(x) dx} + \log e^0$$

Normalising, we obtain

$$H^* = - \frac{\int_0^{\infty} l(x) \log l(x) dx}{\int_0^{\infty} l(x) dx}$$

The expressions H and H^* measure the convexity of the survivorship curve. For the Type I life table, $H^* = 0$ and $H = \log e^0$. For the Type II life table, $H^* = 1$, and $H = 1 + \log e^0$.

An interesting application of our entropy parameter to the study of male-female mortality patterns is given in ref. 5.

The notion of an adaptive value of a population⁶ generalises the entropy concept to incorporate the effects of environmental forces on the life-history distribution. We refer to ref. 6 for a precise mathematical definition. In this note we give an intuitive account. We consider the population as a stationary stochastic process whose phase space, the set of all life histories is subject to perturbations by an environmental process. There

are thus two stochastic processes at work, the process described by the population and the process described by the distorting effects of the environmental action. We can therefore identify two entropies, H , the entropy of the population in the case when no environmental forces interfere, and \hat{H} , the conditional entropy, that is, the entropy of the perturbed process given that the unperturbed mortality distribution is known. The adaptive value ψ is defined to be

$$\psi = H + \hat{H}.$$

This function measures the correlation between the variability of the mortality distribution and environmental variability. Thus, in a constant environment, ψ is precisely the entropy H of the population.

We now describe the various distributions that maximise H subject to various constraints. We suggest biological interpretations of these constraints by specifying mechanisms which implement these adaptive strategies.

(1) The distribution that maximises H subject to the constraint

$$\int_0^{\omega} l(x) dx = 1$$

where ω is the maximum life expectancy, yields the Type I life table.

The mechanisms implementing this strategy can be described in terms of a mortality which is the end result of senescence or wearing out of the individual, the senescent process going on at the same time and at the same rate in each individual.

(2) The distribution that maximises H subject to the constraint on the mean of the distribution $l(x)$ is given by

$$l(x) = \exp\left(\frac{-x}{e_0}\right)$$

This yields the Type II life table. This curve describes great interindividual variation in the age at death. The variation can arise exclusively from interindividual genetic variability. In the Type I curve, there is no genetic variability, hence the senescent process is the same in each individual. This implies that the life expectancy and the maximum longevity of the species coincide. For the Type II curve, there is genetic variability, hence senescence is less uniform. The degree of genetic variability of the population is measured by the constraint on the mean of the mortality distribution.

(3) The distribution that maximises H subject to a constraint on the variance is given by

$$l(x) = \exp\left[\frac{-\pi}{4e_0^2}\right] x^2$$

Of the three curves described, Type III represents the greatest individual variability in the time of dying. The constraint on the variance is a measure of the genetic variability in the population. The senescent process in this case is much less uniform than that which generates the Type II life table.

It is important to note that these distributions can also be derived as a result of maximising the adaptive value ψ , subject to environmental constraints. Thus an environmental agent that is lethal to individuals irrespective of their genetic constitution and that kills off all individuals at some prescribed age ω will yield a life table whose variability is maximally correlated with the environmental action, that is, a Type I curve.

An environmental agent that acts randomly on the individuals of different ages and is indifferent to the ages of the individuals will yield a Type II curve. Finally, an environmental agent that is age-specific and selectively removes younger individuals will yield a Type III table.

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Egocentric orientation is influenced by trained voluntary cyclorotary eye movements

A CYCLOROTARY eye movement is a motor response of the eye made around the visual axis. Counter-rolling of the eye, for example, occurs during lateral head tilt^{1–5}; conjugate rotary nystagmus can be induced by a large rotating field^{6–9}; and disjunctive cyclorotations can occur during ordinary convergence^{10,11}. Because none of these torsional eye movements can be produced as an isolated voluntary response, eye torsion has always been classified as an involuntary response, a reflex. Using a visual-feedback procedure, however, we have trained humans to make conjugate voluntary cyclorotary eye movements up to 30 degrees in magnitude¹². We have also demonstrated that these large torsional movements are not visually induced and can be made in the absence of any visual stimulus. Accompanying the training and performance of these eye movements were a number of striking illusions related to one's own sense of body orientation. Because these newly trained eye movements are unprecedented, it is of interest to characterise accompanying illusions in detail, comparing them with other illusions of self rotation induced through vestibular¹³ and visual^{14,15} inputs. In this paper we compare the effects of trained cyclorotary eye movements with head and whole body tilts, showing a quantitatively similar change in egocentric orientation for each type of tilt. As such, our findings suggest the possibility of shared mechanisms affecting the stability of one's internal frame of reference, both for eye and body movements.

The exact method of training and testing of voluntary torsion using visual biofeedback has been detailed elsewhere¹². A subject was seated in a dark room with head movements fixed by a full mouth bite plate. A vertical $11 \times 0.25^\circ$ flash was presented monocularly to generate a vertical afterimage. This afterimage was then imaged in space next to a line of light of equal colour, brightness and size (real line stimulus). The subject was instructed to keep this afterimage line matched parallel to the real line only by cyclorotating the eyes. With practice, the subject gradually acquired the ability to rotate the eye(s) to match greater and greater inclinations of the real line. These cyclorotations were trained at the rate of about $0.8^\circ \text{h}^{-1} \text{d}^{-1}$ for 35 d (Fig. 1a). Using similar methods for 5–10 h of additional training, subjects were trained to make torsional slow pursuit (Fig. 1b) and torsional saccades (Fig. 1c). Individual frame analysis of 35-mm slides or 16-mm motion pictures filmed simultaneously were used to objectify the cyclorotary eye movements. Measurements from photographs used radial iris markings or limbal-scleral blood vessel junctions in relation to a visible and stable reference marker. Accuracy of measurements was ± 10 min.

During initial training, but not during final experimentation, subjects often felt that their heads and bodies were 'rolling laterally' and sometimes experienced associated visual illusions. Accompanying these changes in egocentric orientation were intermittent sensations of stomach nausea, headache and general body fatigue. The most dramatic of these illusions occurred as a distinct 'hallucinatory barrage' at least twice to each subject during initial training. Associated with eyelid tremor, the nearly vertical and parallel lines would appear to move independently, becoming almost horizontal and also appearing curved or wiggly. Accompanying these peculiar visual illusions were very powerful sensations of body flotation