

## The Distribution of Wearout over Evolved Reliability Structures

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A multiple-integral equation, termed the wearout equation, describes the distribution of wearout (or aging) over evolved reliability structures, such as organisms and self-replicating machines, and thus statistically governs virtually all aging properties of the systems. The equation is applied to the computation of *ab initio* ("from the beginning") life tables for four natural populations of ungulates—wild boar, Dall sheep, African buffalo, and hippopotamus—which represent a broad range of survival characteristics. The good agreement of the *ab initio* and empirical tables, the best available for testing the theory, demonstrates the basic realism of the wearout equation. If the equation withstands further experimental testing, its analysis may provide insight into fundamental questions in the biology of aging.

### 1. Introduction

The distribution of wearout over evolved reliability structures tells almost everything of interest about the evolution of aging in organisms and self-replicating machines. The study of the evolution of wearout (or aging) is part of a new branch of reliability theory called evolutionary reliability theory (Miller, 1987). In general, both the reliability structure‡ and the component reliabilities of evolutionary systems are functions of time. A multiple-integral equation (equation 33), called the wearout equation, describes the distribution of evolved wearout for a given structure. The importance of this equation and the central place of structure in the evolution of wearout is illustrated by the following analogy with organic chemistry: The process of evolution gives rise to a reliability structure and associated distribution of wearout

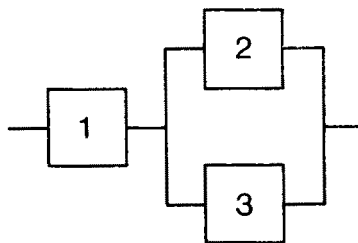


FIG. 1. The simplest non-trivial series-parallel system.

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‡ An example of a reliability structure is the three-component series-parallel structure shown in Fig. 1. At the gross anatomical level, organisms are series-parallel systems, e.g., the heart is in series with two lungs, each in parallel, and in series with two kidneys, each in parallel. At the organ level, they are probably *k*-out-of-*n* systems (see below), i.e., an organ functions as long as any *k* of its *n* cells (or other subunits) function.

that determines its wearout properties analogously to the way that the process of chemical reaction gives rise to a chemical structure, or molecule, and associated electron-density that determines its chemical properties. The wearout equation describes how wearout is distributed over the evolved reliability structure in the same way that the wave equation (Schrödinger equation) describes how an electron is distributed over the chemical structure. The solution of the wearout equation for a species of organisms is the reliability equivalent of molecular orbitals for a chemical species. Thus, knowing the reliability structure and solution of the wearout equation is as important to understanding the aging of organisms as knowing the chemical structure and molecular orbitals is to understanding the properties of a chemical species such as benzene. Accordingly, I believe that the wearout equation is an important new departure for the biology of aging.

The fundamental property intuitively described above as the “distribution of wearout” is more descriptively termed the *heterogeneous wearout distribution*. Consider the wearout failure-time distribution for an infinite population of genetically homogeneous components  $i$  ( $i = 1, 2, \dots, n$ ) from an  $n$ -component system in a constant environment. [Wearout, or aging, is defined as a failure process having an increasing failure rate (Birnbaum *et al.*, 1966)]. The distribution for non-biological components is known generally (Barlow & Proschan, 1981; Smith, 1983) to be approximately normal with mean lifetime  $w_i$  and standard deviation  $s_i$ , which is non-zero only because the components are not completely homogeneous due to manufacturing errors (or analogous developmental errors in the biological case) and because the environment is not perfectly uniform and constant. Since for evolutionary systems these sources of variation are of minor importance compared with a much greater source, genetic heterogeneity, we will neglect the homogeneous variation and let  $s_i = 0$ . Now consider the wearout failure distribution of genetically heterogeneous components  $i$  for an evolutionary system. This distribution, a function of the population’s distribution of genotypes affecting the reliability of component  $i$ , is determined by natural selection. Let continuous random variable  $W_i$  be the wearout failure-time of genetically heterogeneous components  $i$ ; each value  $W_i = w_i$  corresponds to the above mean wearout lifetime  $w_i$  of a genetically homogeneous component subpopulation with  $s_i = 0$ . The heterogeneous wearout distribution of the system, or what we mean by the “distribution of wearout” over the reliability structure, is the probability density  $f$  of the random vector  $\mathbf{W} = (W_1, W_2, \dots, W_n)$ , where  $\mathbf{w}$  belongs to the Euclidean  $n$ -space

$$\mathcal{W} = \{\mathbf{w}: w_1 > 0, w_2 > 0, \dots, w_n > 0\}. \quad (1)$$

Any particular system, or homogeneous subpopulation of systems, is represented as a point  $\mathbf{w} = (w_1, w_2, \dots, w_n)$  in wearout space  $\mathcal{W}$ .

From ten simple assumptions, I will derive the wearout equation, whose solution is the heterogeneous wearout distribution  $f$  for a species. We will then use the equation in a significant application: computation of basically accurate theoretical life tables for four natural populations of ungulates—wild boar, Dall sheep, African buffalo, and hippopotamus—which represent a wide range of survival characteristics. Such theoretical tables, because they derive from the fundamental heterogeneous

wearout distribution, are called *ab initio*, i.e. "from the beginning". The good agreement of the *ab initio* tables with the known empirical tables, the best available for testing a theory of the evolution of aging (Miller, 1988), demonstrates the basic realism of the wearout equation.

## 2. Theory

### (A) ASSUMPTIONS

(1) *The population consists of binary, coherent, order- $n$ , isomorphic systems of fixed structure* (Barlow & Proschan, 1981). Being coherent implies that a system fails only because one or more of its components fails. Isomorphic systems have the same reliability structure.

(2) *There are two independent, superimposed modes of component failure: (a) random failure having a constant failure rate and (b) wearout failure having an increasing failure rate.* A constant failure rate implies an exponential failure distribution. Random failure of components arises from accidents, competition, predation, disease, and other random events. Early failure, or infant mortality, is neglected.

(3) *The failure of components is statistically independent.*

(4) *All components have the same exponential (random) failure rate  $\lambda$  ( $\lambda > 0$ ), assumed given.*

(5) *The standard deviation  $s_i$ , ( $i = 1, 2, \dots, n$ ) for the wearout failure-time of homogeneous components is zero.* This is equivalent to the distribution's being degenerate with mean  $w_i$ , or to a deterministic wearout life for a given system. As is characteristic of wearout, the component failure rate is increasing (it has the value zero before age  $w_i$  and infinity at  $w_i$ ).

(6) *Probability density function  $f$ , the heterogeneous wearout distribution, is stationary in evolutionary time  $t$ .* Since this requires that the probability of birth always equals the probability of death at each  $w \in \mathcal{W}$ , reproduction must be a continuous process.

(7) *The population size is infinite.*

(8) *At any time  $t$ , all systems for which age  $Y \geq r > 0$ , where  $Y$  is a continuous random variable and  $r$  is a real parameter of the population, have equal probability of self-reproduction.* Since all individuals for which  $Y \geq r$  have a finite probability of reproduction, we will refer to them as parents. Because  $Y \geq r$  is the only condition for reproduction, a given individual can reproduce repeatedly, and fecundity is independent of age (after age  $r$ ).

(9) *Reproduction, occurring component-wise, is described statistically as follows: Let random variable  $W'_i$  be the wearout life of component  $i$  ( $i = 1, 2, \dots, n$ ) of an offspring and  $v_i$  be that of the parent. Then there exists a probability density function  $\tau_w$ , assumed given, such that*

$$P(a \leq W'_i \leq b) = \int_a^b \tau_w(w_i, v_i) dw_i, \quad w_i > 0, \quad v_i > 0 \quad (2)$$

where  $a$  and  $b$  are positive real numbers. Variable  $v_i$  is a parameter of the density; however, since it will be a variable of integration in the derivation below, it is treated as an independent variable.

(10) Random variables  $W'_i$  ( $i = 1, 2, \dots, n$ ) are statistically independent.

(B) RELIABILITY AT A POINT

Derivation of a formula for the wearout equation will require a function called the *reliability at a point*, i.e., at a point  $w$  of wearout space  $\mathcal{W}$ . The reliability at a point,  $R_{X|w}$ , is the conditional probability

$$R_{X|w}(x|w) = P(X > x | W = w) \tag{3}$$

where continuous random variable  $X$  is the age of system failure from either random or wearout failure and  $w \in \mathcal{W}$ . Prior to deriving expressions for  $R_{X|w}$ , consider the following quantities at point  $w$  (see Fig. 2). Order the component wearout lifetimes  $w_i$  ( $i = 1, 2, \dots, n$ ) of any system at  $w$  so that  $w^{(j)}$  is the  $j$ th failure age and where  $w^{(1)} \leq w^{(2)} \leq \dots \leq w^{(n)}$ . Let  $c^{(j)}$  be the component  $i$  of the intact system (i.e., before any component failures) having wearout life  $w^{(j)}$ . Define  $w^{(0)} = 0$  and  $c^{(0)} = \phi$ . Let  $\omega(w)$  be the system wearout life at  $w$ . Structure function  $\omega$  is a composition of order statistics; for example, for the order-3 series-parallel system shown in Fig. 1,  $\omega(w) = \min [w_1, \max (w_2, w_3)]$ . Generally, index  $j$  will not attain values as large as  $n$  because at some value, denoted  $J$ ,  $w^{(j)} = \omega(w)$  and the system fails of wearout before all components have failed. Finally, let  $I_j$  be the real interval  $[w^{(j-1)}, w^{(j)})$  for  $j = 1, 2, \dots, J$ . Assuming that the homogeneous failure distribution is degenerate ( $s_i = 0$ ),  $I_j$  at  $w$  is a fixed deterministic interval—the interval between the  $(j - 1)$ th and  $j$ th component wearout failures. Failure events at  $w$  have a mixed distribution: piece-wise continuous on  $[0, \omega(w))$  but discrete at  $X = \omega(w)$ . For notational convenience, let  $R_{X|w}(x|w)$  be understood to be zero for  $X \notin [0, \omega(w))$ .

Consider function  $R_{X|w}$  on the interval  $I_j$  for  $j = 1, 2, \dots, J$ . Since the components of set  $\mathcal{F} = \{c^{(1)}, c^{(2)}, \dots, c^{(j-1)}\}$  have failed and are not operating on  $I_j$ , their removal from the system at birth would not affect the system reliability on  $I_j$ . Refer to this hypothetical system with the  $\mathcal{F}$  components removed as the  $j$ -*protosystem*, which is

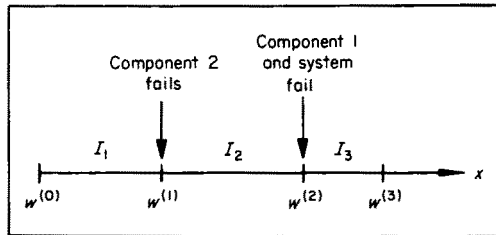


FIG. 2. Description of wearout failure events at a point  $w = (w_1, w_2, w_3)$  for the order-3 system in Fig. 1. For illustration, let  $w_2 < w_1 < w_3$ . Then  $w^{(1)} = w_2$ ,  $w^{(2)} = w_1$ ,  $w^{(3)} = w_3$  and  $c^{(1)} = 2$ ,  $c^{(2)} = 1$ ,  $c^{(3)} = 3$ . By inspection of the structure,  $J = 2$  and  $w^{(J)} = \omega(w) = w^{(2)}$ . Thus, random variable  $X$  is restricted to the interval  $[0, w^{(2)})$ . Note that at another point  $w$  where  $w_1 < w_3 < w_2$  (or  $w_1 < w_2 < w_3$ ),  $J = 1$  and  $X \in [0, w^{(1)})$ .

a definite, fixed structure containing the  $n-j+1$  components of the set  $\mathcal{G} = \{c^{(j)}, c^{(j+1)}, \dots, c^{(n)}\}$ . By assumption 2, the reliability on  $I_j$  is

$$R_{X|W}(x|w) = P(X_r > x | W = w)P(X_w > x | W = w), \quad x \in I_j, \quad j = 1, 2, \dots, J \quad (4)$$

where  $X_r$  is the age of random failure and  $X_w$  is the age of wearout failure of the  $j$ -protosystem. However, by assumption 5,

$$P(X_w > x | W = w) = \begin{cases} 1 & \text{if } x \in [0, w^{(j)}) \\ 0 & \text{elsewhere} \end{cases} \quad (5)$$

and therefore

$$R_{X|W}(x|w) = P(X_r > x | W = w), \quad x \in I_j, \quad j = 1, 2, \dots, J. \quad (6)$$

Thus, from eqn (6) and assumption 3, the system reliability on  $I_j$  is determined completely by the structure of the  $j$ -protosystem, composed of components  $\mathcal{G}$ , and the component failure rate  $\lambda$ . We will derive explicit formulas for  $R_{X|W}$  for two important classes of structures:  $k$ -out-of- $n$  and series-parallel systems.

A  $k$ -out-of- $n$  system is operational as long as any  $k$  of its  $n$  components are operational. (When  $k = n$ , we have a series structure; when  $k = 1$ , a parallel structure.) From the reliability expression for  $k$ -out-of- $n$  systems (Barlow & Proschan, 1981) and the fact that the  $j$ -protosystem is a  $k$ -out-of- $(n-j+1)$  system, the reliability at a point for  $k$ -out-of- $n$  systems is

$$R_{X|W}(x|w) = \sum_{l=k}^{n-j+1} \binom{n-j+1}{l} e^{-l\lambda x} (1 - e^{-\lambda x})^{n-j+1-l}, \quad x \in I_j, \quad j = 1, 2, \dots, J. \quad (7)$$

Immediately prior to failure,  $n-k$  components have failed; at failure, one additional component fails, and hence,  $J = n - k + 1$ .

A series-parallel system consists of  $k$  series modules,  $\mathcal{M}_1, \mathcal{M}_2, \dots, \mathcal{M}_k$ , each of which is a parallel unit. (Parameter  $k=2$  for the order-3 structure shown in Fig. 1.) Let  $n_{jm}, n_{1m} \geq 1$ , be the number of components in module  $m$  ( $m = 1, 2, \dots, k$ ) of the  $j$ -protosystem. Quantity  $n_{jm}$  can be determined *a priori* for a system at  $w$  from its structure and ordered wearout failures  $\mathcal{F}$ . Define the indicator function

$$I_{lm} = \begin{cases} 1 & \text{if } c^{(l)} \in \mathcal{M}_m \\ 0 & \text{if } c^{(l)} \notin \mathcal{M}_m \end{cases}, \quad l = 1, 2, \dots, J-1, \quad m = 1, 2, \dots, k. \quad (8)$$

Then the number of components in module  $m$  on  $I_j$  is

$$n_{jm} = n_{1m} - \sum_{l=1}^{j-1} I_{lm}, \quad j = 1, 2, \dots, J, \quad m = 1, 2, \dots, k \quad (9)$$

and the reliability at a point for series-parallel systems is

$$R_{X|W}(x|w) = \prod_{m=1}^k [1 - (1 - e^{-\lambda x})^{n_{jm}}], \quad x \in I_j, \quad j = 1, 2, \dots, J. \quad (10)$$

For general series-parallel systems,  $J$  does not have a simple formula (because  $J$  depends on how  $c^{(j)}, j = 1, 2, \dots, n$ , are distributed among the modules); however, it is defined as the smallest integer  $J$  satisfying the equation  $n_{j+1, m} = 0$  for some  $m$ .

(C) THE WEAROUT EQUATION

The derivation of the multiple-integral equation starts from an expression for the density, denoted  $\pi$ , of  $\mathbf{W}$  on the subpopulation of progeny born at any evolutionary time  $t$ . Let  $g$  be the joint density of random scalar  $Y$ , age in the total population, and random vector  $\mathbf{W}$ . Then, since the density of births is the normalized mass on  $y=0$ , it is by definition true that

$$\pi(\mathbf{w}) = \frac{g(0, \mathbf{w})}{\int_{\mathcal{W}} g(0, \mathbf{w}) d\mathbf{w}}, \quad \mathbf{w} \in \mathcal{W}$$

$$= 0 \quad \text{elsewhere}^\dagger \tag{11}$$

where  $d\mathbf{w} = dw_1 dw_2 \dots dw_n$  and the denominator is the normalizing constant. By the definition of conditional density,

$$g(y, \mathbf{w}) = g_{Y|\mathbf{W}}(y|\mathbf{w})f(\mathbf{w}), \quad 0 \leq y < \omega(\mathbf{w}) \tag{12}$$

and hence from eqns (11) and (12) (with  $y = 0$ )

$$f(\mathbf{w}) = \frac{\int_{\mathcal{W}} g_{Y|\mathbf{W}}(0|\mathbf{w})f(\mathbf{w}) d\mathbf{w} \pi(\mathbf{w})}{g_{Y|\mathbf{W}}(0|\mathbf{w})}. \tag{13}$$

Functions  $g_{Y|\mathbf{W}}$  and  $\pi$  are presently unknowns; however, we can derive expressions for them in terms of  $R_{X|\mathbf{W}}$  and  $f$  and thereby have an integral equation with  $f$  as the only unknown.

Since  $f$  is stationary, it is possible for  $g_{Y|\mathbf{W}}$  to be stationary, and we will derive a formula for the stationary density. Consider age  $Y$  at point  $\mathbf{w}$ , where it is restricted to the interval  $[0, \omega(\mathbf{w})]$ . Let  $y$  be any point on this interval, and partition  $[0, y]$  into  $M + 1$  points  $\{y_0, y_1, \dots, y_M\}$  such that each subinterval  $L_k = [y_k, y_{k+1})$ ,  $k = 0, 1, \dots, M - 1$ , has the same length  $\Delta y = y_{k+1} - y_k$ . In  $y_k$  time units, the subpopulation (or event or state within the total population  $P$ ) for which  $X > y_k \cap Y \in L_0$  at time  $t$  will pass through state  $Y \in L_k$  at  $t + y_k$  (see Fig. 3). These individuals must pass through state  $y \in L_k$  in order to die beyond age  $y_k$  (i.e. in order for  $X > y_k$ ). Clearly, only individuals in the subpopulation  $Y \in L_0$  (birth) at time  $t$  can occupy the subpopulation  $Y \in L_k$  at  $t + y_k$ . Hence, since all individuals not in  $X > y_k$  die before  $Y \in L_k$  is reached, the individuals in  $X > y_k \cap Y \in L_0$  are the sole occupants of  $Y \in L_k$ . Therefore,

$$P(Y \in L_k) = P(X > y_k \cap Y \in L_0) \tag{14}$$

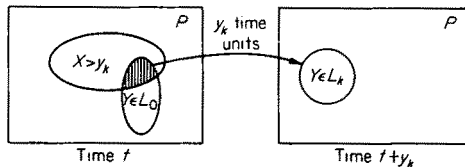


FIG. 3. Transformation of a subset of the births ( $Y \in L_0$ ) at time  $t$  to the age class  $Y \in L_k$  at time  $t + y_k$ .

† For brevity, let all functions of  $\mathbf{w}$  be hereafter understood to be defined for all  $\mathbf{w} \in \mathcal{W}$  and to be identically zero elsewhere.

where conditioning on  $W = w$  is understood, and the distribution function is given by

$$P(Y \leq y) = \lim_{\Delta y \rightarrow 0} \sum_{k=1}^M P(X > y_k \cap Y \in L_0). \tag{15}$$

We can rewrite eqn (15) in terms of a known conditional probability  $P(X > y | Y \in L_0)$ , the reliability at a point; the reliability is a conditional probability (in addition to  $W = w$ ) because it is the survival function for a cohort, a subset of the population. Thus,  $P(X > y | Y \in L_0)P(Y \in L_0) \cong R_{X|w}(y|w)\Delta yP(Y \in L_0)$ , and in the limit  $\Delta y \rightarrow 0$ ,

$$P(Y \leq y) = \int_0^y R_{X|w}(y|w) \lim_{\Delta y \rightarrow 0} P(Y \in L_0) dy. \tag{16}$$

Letting the upper integration limit in eqn (16) be  $y = \omega(w)$ , solution for the constant limit  $P(Y \in L_0)$ , and resubstitution of the latter into eqn (16) gives

$$P(Y \leq y) = \int_0^y \frac{R_{X|w}(y|w)}{\int_0^{\omega(w)} R_{X|w}(x|w) dx} dy \tag{17}$$

as the distribution function. Differentiation of eqn (17) then gives

$$g_{Y|w}(y|w) = \frac{R_{X|w}(y|w)}{\int_0^{\omega(w)} R_{X|w}(x|w) dx} \tag{18}$$

as the desired general expression for the conditional density.

For brevity of notation for the special value  $g_{Y|w}(0|w)$ , the birth rate as required in eqn (13), let

$$\Phi(w) = g_{Y|w}(0|w). \tag{19}$$

From eqn (18) and the fact that  $R_{X|w}(0|w) = 1$ ,

$$\Phi(w) = \frac{1}{\int_0^{\omega(w)} R_{X|w}(x|w) dx} \tag{20}$$

where  $R_{X|w}$  is given by eqns (7) and (10) for  $k$ -out-of- $n$  and series-parallel structures, respectively. Since the denominator of eqn (20) is  $E(X)$  at  $w$  (or since  $f$  is stationary and therefore the failure rate equals the birth rate),  $\Phi$  is also the failure rate at  $w$ .

Prior to deriving a formula for density  $\pi$ , consider (at time  $t$ ) the probability of progeny arising in any fixed region  $\mathcal{U} \subseteq \mathcal{W}$ . Let random vector  $W$  (dropping the primes used in assumptions 9 and 10) represent the progeny and  $V$  represent parents on wearout space  $\mathcal{W}$ . Since parents ( $Y \geq r$ ) must have a wearout failure age at least as great as  $r$ , point  $V$  is restricted to the subspace

$$\mathcal{V} = \{v: \omega(v) \geq r\} \tag{21}$$

where  $\mathcal{V} \subseteq \mathcal{W}$ . (Hereafter it is understood that  $V$  is restricted to this subspace.) Let  $\phi$  be the density of  $V$  and  $P(v, \mathcal{U})$  be the probability that a given parent at  $v$  gives

rise to progeny in  $\mathcal{U}$ . Then the probability of progeny arising in  $\mathcal{U}$  from all points  $\mathbf{v} \in \mathcal{V}$  is

$$P(\mathbf{W} \in \mathcal{U}) = \int_{\mathcal{V}} P(\mathbf{v}, \mathcal{U}) \phi(\mathbf{v}) \, d\mathbf{v}. \quad (22)$$

By assumptions 9 and 10, the transition probability

$$P(\mathbf{v}, \mathcal{U}) = \int_{\mathcal{U}} \tau_{\mathbf{w}}(\mathbf{w}, \mathbf{v}) \, d\mathbf{w} \quad (23)$$

where density function  $\tau_{\mathbf{w}}$  is

$$\tau_{\mathbf{w}}(\mathbf{w}, \mathbf{v}) = \tau_{\mathbf{w}}(w_1, v_1) \tau_{\mathbf{w}}(w_2, v_2) \dots \tau_{\mathbf{w}}(w_n, v_n), \mathbf{w} \in \mathcal{W}, \mathbf{v} \in \mathcal{V} \quad (24)$$

and  $\tau_{\mathbf{w}}$  is assumed given. Since the condition for parents being at point  $\mathbf{v}$  is that  $Y \geq r$ , the density of parents is given by the expression

$$\phi(\mathbf{v}) = \frac{\int_r^{\omega(\mathbf{v})} g(\mathbf{y}, \mathbf{v}) \, d\mathbf{y}}{\int_{\mathcal{V}} \int_r^{\omega(\mathbf{v})} g(\mathbf{y}, \mathbf{v}) \, d\mathbf{y} \, d\mathbf{v}} \quad (25)$$

and the denominator, the normalizing constant, is generally less than unity since  $\mathcal{V} \subseteq \mathcal{W}$ . Equations (22), (23) and (25) then give

$$P(\mathbf{W} \in \mathcal{U}) = \frac{\int_{\mathcal{V}} \int_{\mathcal{U}} \tau_{\mathbf{w}}(\mathbf{w}, \mathbf{v}) \, d\mathbf{w} \int_r^{\omega(\mathbf{v})} g(\mathbf{y}, \mathbf{v}) \, d\mathbf{y} \, d\mathbf{v}}{\int_{\mathcal{V}} \int_r^{\omega(\mathbf{v})} g(\mathbf{y}, \mathbf{v}) \, d\mathbf{y} \, d\mathbf{v}} \quad (26)$$

as the desired expression.

For brevity of notation, let

$$\Gamma(\mathbf{v}) = \int_r^{\omega(\mathbf{v})} g_{\mathcal{V}|\mathbf{W}}(\mathbf{y}|\mathbf{v}) \, d\mathbf{y} \quad (27)$$

which is the conditional probability of being a parent at point  $\mathbf{v}$ . Since  $f(\mathbf{v})$  is a constant (assumption 6), we see from eqn (12) that the integral in eqn (26) is

$$\int_r^{\omega(\mathbf{v})} g(\mathbf{y}, \mathbf{v}) \, d\mathbf{y} = \Gamma(\mathbf{v}) f(\mathbf{v}). \quad (28)$$

From eqns (18) and (20), we can evaluate  $\Gamma(\mathbf{v})$  as

$$\Gamma(\mathbf{v}) = \Phi(\mathbf{v}) \int_r^{\omega(\mathbf{v})} R_{\mathcal{X}|\mathbf{W}}(\mathbf{y}|\mathbf{v}) \, d\mathbf{y} \quad (29)$$

where  $R_{\mathcal{X}|\mathbf{W}}$  is given by eqns (7) and (10) for  $k$ -out-of- $n$  and series-parallel structures, respectively.

Density  $\pi$  is obtained by differentiation of its distribution function. Because  $\mathcal{U}$  can be any region, consider  $\mathcal{U} = \mathcal{U}^*$ , where

$$\mathcal{U}^* = \{\mathbf{w}: \mathbf{W}_1 \leq w_1, \mathbf{W}_2 \leq w_2, \dots, \mathbf{W}_n \leq w_n\} \quad (30)$$

and where  $\mathbf{W}$  represents progeny on  $\mathcal{W}$ . By substituting  $\mathcal{U}^*$  for  $\mathcal{U}$  in eqn (26) and using relation (28), we have the distribution function for progeny as

$$P(\mathbf{W} \in \mathcal{U}^*) = \frac{\int_{\mathcal{V}} \int_{\mathcal{U}^*} \tau_{\mathbf{W}}(\mathbf{w}, \mathbf{v}) \, d\mathbf{w} \Gamma(\mathbf{v}) f(\mathbf{v}) \, d\mathbf{v}}{\int_{\mathcal{V}} \Gamma(\mathbf{v}) f(\mathbf{v}) \, d\mathbf{v}}. \tag{31}$$

Differentiation of this with respect to  $\mathbf{w}$  then gives

$$\pi(\mathbf{w}) = \frac{\int_{\mathcal{V}} \tau_{\mathbf{W}}(\mathbf{w}, \mathbf{v}) \Gamma(\mathbf{v}) f(\mathbf{v}) \, d\mathbf{v}}{\int_{\mathcal{V}} \Gamma(\mathbf{v}) f(\mathbf{v}) \, d\mathbf{v}} \tag{32}$$

as the desired progeny density. The denominator is the density's normalizing constant, as can be seen by substituting  $\mathcal{W}$  for  $\mathcal{U}$  in eqn (26).

To complete the derivation of the wearout equation, substitution of eqns (19) and (32) into eqn (13) gives the desired function as the multiple-integral equation

$$f(\mathbf{w}) = \frac{\int_{\mathcal{W}} \Phi(\mathbf{w}) f(\mathbf{w}) \, d\mathbf{w} \int_{\mathcal{V}} \tau_{\mathbf{W}}(\mathbf{w}, \mathbf{v}) \Gamma(\mathbf{v}) f(\mathbf{v}) \, d\mathbf{v}}{\Phi(\mathbf{w}) \int_{\mathcal{V}} \Gamma(\mathbf{v}) f(\mathbf{v}) \, d\mathbf{v}} \tag{33}$$

where definite integrals  $\Phi(\mathbf{w})$  and  $\Gamma(\mathbf{v})$  are defined by eqns (20) and (29), respectively,  $n$ -dimensional density function  $\tau_{\mathbf{W}}$  is defined by eqn (24), and Euclidean  $n$ -spaces  $\mathcal{W}$  and  $\mathcal{V}$  are defined by eqns (1) and (21), respectively.

### 3. Application

#### (A) SOLUTION OF THE WEAROUT EQUATION

Since life tables are discrete and because solution of the wearout equation is computationally intensive, a discrete analog of the continuous equation is used in this application. This avoids the cost of accurate numerical integration while giving (up to the convergence criterion) an exact solution: the discrete probability density function  $\tilde{f}$  that is the heterogeneous wearout distribution for a species. Let wearout space be the finite, discrete  $n$ -space of integer lattice points

$$\tilde{\mathcal{W}} = \{\mathbf{w}: 1 \leq w_1 \leq b, 1 \leq w_2 \leq b, \dots, 1 \leq w_n \leq b\} \tag{34}$$

where  $\mathbf{w} = (w_1, w_2, \dots, w_n)$  has only integer components,  $n$  is the order of the system, and  $b$  is the integer maximum of each co-ordinate of the finite space. Likewise, let the subspace of points at which system lifetime is sufficient for reproduction be  $\tilde{\mathcal{V}}$ , given by eqn (21) with integer co-ordinates of  $\mathbf{v}$  and integer  $r$ . The discrete analog of the wearout equation is then

$$\begin{aligned} \tilde{f}(\mathbf{w}) &= \frac{\sum_{\tilde{\mathcal{W}}} \Phi(\mathbf{w}) \tilde{f}(\mathbf{w}) \sum_{\tilde{\mathcal{V}}} \tilde{\tau}_{\mathbf{W}}(\mathbf{w}, \mathbf{v}) \Gamma(\mathbf{v}) \tilde{f}(\mathbf{v})}{\Phi(\mathbf{w}) \sum_{\tilde{\mathcal{V}}} \Gamma(\mathbf{v}) \tilde{f}(\mathbf{v})}, & \mathbf{w} \in \tilde{\mathcal{W}}, \mathbf{v} \in \tilde{\mathcal{V}} \\ &= 0 \quad \text{elsewhere} \end{aligned} \tag{35}$$

where  $\tilde{\tau}_{\mathbf{W}}$ , a discrete probability density function, and  $\Phi$  and  $\Gamma$ , continuous functions with lattice-point arguments, are described below.

$\tilde{\tau}_w$  is the discrete analog of multidimensional density  $\tau_w$ , the product of  $n$  continuous component densities  $\tau_w$  that govern the distribution of progeny component lifetimes. Although it is assumed given in the theory, nothing is actually known about continuous density  $\tau_w$ , and for the present work I assume the following *ad hoc*: (1)  $\tau_w(w_i, v_i)$  ( $i = 1, 2, \dots, n$ ) is independent of parent lifetime  $v_i$  up to a translation; (2) it is unimodal; and (3) the mode occurs at  $w_i = v_i$ . We will use two simple two-parameter models that satisfy these assumptions—a piecewise cosine density (Raab & Green, 1961) and a triangular density—and estimate their parameters empirically. Once estimated, the parameters are assumed constant for all species. Let continuous random variable  $\Delta$  be defined as  $\Delta = W_i - v_i$ , where random variable  $W_i$  (real) is the lifetime of component  $i$  for an offspring and  $v_i$  (real) is that for the parent. The cosine density is then given by the formula

$$\hat{\tau}_w(\delta) = \begin{cases} \frac{a_1 a_2}{\pi(a_1 + a_2)} (\cos a_1 \delta + 1), & -\frac{\pi}{a_1} \leq \delta \leq 0 \\ \frac{a_1 a_2}{\pi(a_1 + a_2)} (\cos a_2 \delta + 1), & 0 < \delta \leq \frac{\pi}{a_2} \end{cases} \quad (36)$$

where  $\delta$  is a value of the random variable  $\Delta$ ,  $a_1$  is the single real parameter of the left branch ( $\delta \leq 0$ ), and  $a_2$  is the parameter of the right branch. It is more meaningful to express the density in terms of its first two moments,  $E(\Delta)$  and  $Var(\Delta)$ , rather than  $a_1$  and  $a_2$ . Letting  $E = E(\Delta)$  and  $V = Var(\Delta)$ , we have accordingly

$$a_2 = \frac{-c_1 + \sqrt{c_1^2 - 4c_0c_2}}{2c_2} \quad (37)$$

$$a_1 = \frac{(\pi^2 - 4)a_2}{(\pi^2 - 4) - 2\pi a_2 E} \quad (38)$$

where  $c_0 = -4\pi^2(\pi^2 - 4)^2(\pi^2 - 6)$ ,  $c_1 = 8\pi^3(\pi^2 - 4)(\pi^2 - 6)E$ , and  $c_2 = 4\pi^2[3(\pi^2 - 4)^2V - (\pi^4 - 48)E^2]$ . The triangular component density is given by formulas analogous to (but simpler than) eqns (36)-(38). For either case, the *discrete* component density is defined by

$$\begin{aligned} \tilde{\tau}_w(w_i, v_i) &= \int_{w_i - v_i - 1/2}^{w_i - v_i + 1/2} \hat{\tau}_w(\delta) d\delta, & 1 \leq w_i \leq b, \quad r \leq v_i \leq b \\ &= 0 \quad \text{elsewhere} \end{aligned} \quad (39)$$

where  $w_i$  and  $v_i$  ( $i = 1, 2, \dots, n$ ) are integers and  $\delta$  is real. The discrete multi-dimensional density is then

$$\begin{aligned} \tilde{\tau}_w(w, v) &= \tilde{\tau}_w(w_1, v_1) \tilde{\tau}_w(w_2, v_2) \dots \tilde{\tau}_w(w_n, v_n), & w \in \tilde{W}, \quad v \in \tilde{V} \\ &= 0 \quad \text{elsewhere.} \end{aligned} \quad (40)$$

Because of the large amount of computer time required to solve eqn (35), the species in this application are modeled as order-2 or order-3 series systems. Since

they are series systems, the structure function  $\omega$  is  $\omega(\mathbf{w}) = \min(w_1, w_2, \dots, w_n)$  and functions  $\Phi$  and  $\Gamma$  have the simple formulas

$$\begin{aligned} \Phi(\mathbf{w}) &= \frac{-\ln p}{1 - p^{\omega(\mathbf{w})}}, & \mathbf{w} \in \tilde{\mathcal{W}} \\ &= 0 & \text{elsewhere} \end{aligned} \tag{41}$$

and

$$\begin{aligned} \Gamma(\mathbf{v}) &= \frac{p^r - p^{\omega(\mathbf{v})}}{1 - p^{\omega(\mathbf{v})}}, & \mathbf{v} \in \tilde{\mathcal{V}} \\ &= 0 & \text{elsewhere} \end{aligned} \tag{42}$$

where  $p = e^{-n\lambda}$  and  $n = k$  in eqn (10) for a series system. Equations (41) and (42) imply that  $X$ , age of system failure from either random or wearout failure, and  $Y$ , age of a system, are continuous at each point  $\mathbf{w}$  of discrete space  $\tilde{\mathcal{W}}$ .

Given the parameters estimated below for each species, eqn (35) is solved by a numerical version of the method of successive approximations (Jerri, 1985). The 0th approximation,  $\tilde{f}_0$ , is taken as the discrete uniform distribution on  $\tilde{\mathcal{W}}$ . Convergence is accepted when

$$|\tilde{f}_j - \tilde{f}_{j-1}| < C \tag{43}$$

where  $\tilde{f}_j$  is the  $j$ th approximation of  $\tilde{f}$  and  $C$  is the convergence criterion. An example of solution  $\tilde{f}$  for a series system is shown in Figs 4 and 5, and although not used in the life-table studies, the solution for the same organism modeled as a parallel system is shown in Figs 6 and 7. The constant-probability contours, Figs 5 and 7, are analogous to molecular orbitals.

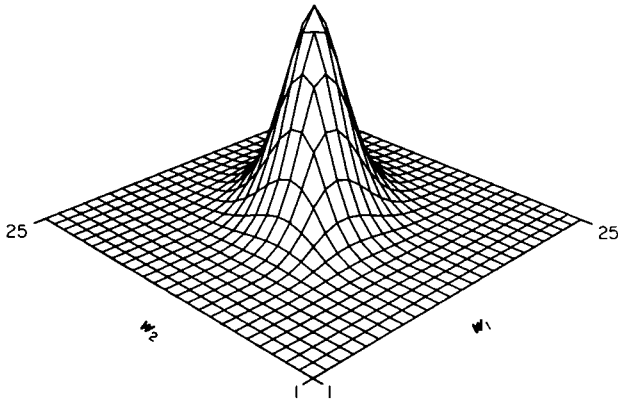


FIG. 4. The heterogeneous wearout distribution  $\tilde{f}$  for the African buffalo modeled as a series system.

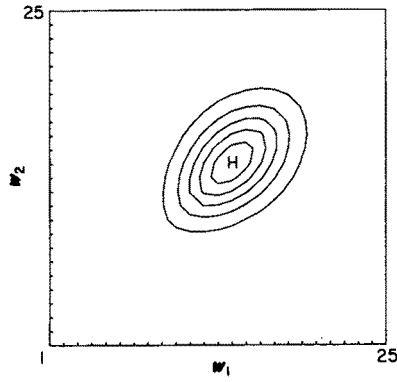


FIG. 5. Contour plot of  $\tilde{f}$  for the buffalo as a series system. (The symbol H marks the maximum point.)

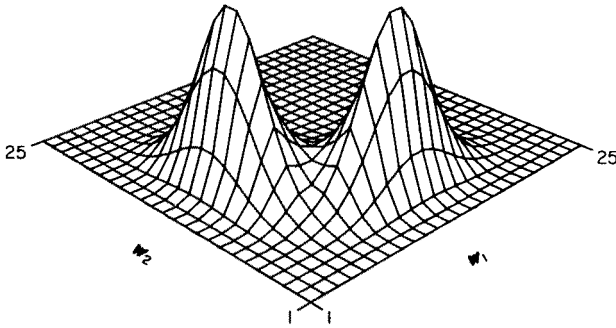


FIG. 6. The heterogeneous wearout distribution  $\tilde{f}$  for the African buffalo modeled as a parallel system.

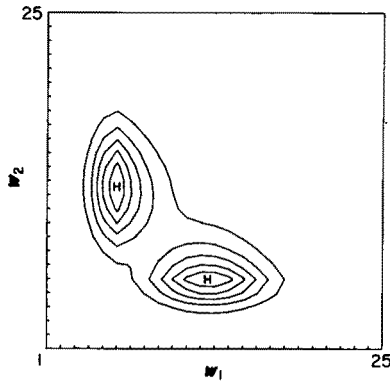


FIG. 7. Contour plot of  $\tilde{f}$  for the buffalo as a parallel system.

## (B) ESTIMATION OF PARAMETERS

With  $n$  implied by a given  $\omega$ , we need parameters  $r$ ,  $\lambda$ ,  $b$ ,  $E$ , and  $V$  for each of the four ungulates—wild boar, Dall sheep, African buffalo, and hippopotamus—whose life tables we will predict, and  $r$ ,  $\lambda$ , and  $b$  for a fifth, domestic sheep, whose life table will be used to estimate  $E$  and  $V$  empirically for the other four. Estimates of the parameters are displayed in Tables 1 and 2.

Parameter  $r$ , the earliest age of reproduction, is estimated as the species' observed mean age of first reproduction rounded to the nearest integer. For wild boar, Dall sheep, and hippopotamus, I accept the values tabulated by Millar & Zammuto (1983), based on the references they cite, except that for Dall sheep, for which see Bunnell & Olsen (1981). However, as is clear from the work of Sinclair (1977) and references therein, their tabulated value for buffalo ( $r=4$ ) is not correct, and the value  $r=5$  is more accurate. For domestic sheep, an age-at-first-breeding of 1.5 years (Hickey, 1960) plus a gestation period of five months (Singh, 1966) gives the estimate  $r=2$ .

Rather than  $\lambda$ , we estimate a function of  $\lambda$ ,  $q=1-e^{-n\lambda}$ , where  $p=1-q$  is the parameter in eqns (41) and (42). Since the species are modeled as series systems, the reliability at a point is the exponential survival function

$$R_{X|W}(x|w) = e^{-n\lambda x} = p^x, \quad 0 \leq x < \omega(w) \quad (44)$$

and the constant  $p = e^{-n\lambda}$  is the probability of not dying of *random* causes on any unit interval of age. Hence,  $q = 1 - p$  is estimated as the annual mortality rate of the species at the earliest age of maturity (before aging has become significant), or  $q = \hat{q}(r)$ , where  $\hat{q}$  is the mortality-rate regression function for the species (Miller, 1988).

TABLE 1  
*Parameters  $r$ ,  $q$ , and  $b$*

Species	$r$ (yr)	$q$	$b$ (yr)			$K\beta$
			$M=4$	$M=8$	$M=12$	
domestic sheep	2	0.036	17	28	38	38
wild boar	2	0.46	8	13	18	25
Dall sheep	4	0.047	18	28	38	41
buffalo	5	0.035	25	39	54	60
hippopotamus	10	0.012	65	103	141	139

TABLE 2  
*Parameters  $E$  and  $V$  (common to all species)*

Experiment	$E$ (yr)	$V$ (yr <sup>2</sup> )
E1	-0.592	0.618
E2	-0.596	0.404
E3, E4	-0.600	0.364
E5	-0.514	0.919
E6	-0.61	0.65

Ideally, we would like  $b = \infty$ . Although there is very little mass on the boundary of  $\mathcal{W}$  with the computationally practical values that we do use (e.g. see Fig. 4), finite  $b$  still has an effect on the location, and to a lesser extent the shape, of stationary  $\tilde{f}$ . Because a value large enough to make this effect negligible for the hippopotamus is impractical for the laborious estimation of  $E$  and  $V$  (using the domestic sheep life table below), parameter  $b$  is prorated for each species: The size of  $b$  is proportional to the location and dispersion of the species' empirical distribution of  $X$ . This causes the error resulting from finite  $b$  to be shared approximately equally by all computed life tables. We therefore compute  $b$  as a function of the first two sample moments of  $X$

$$b = \max [\text{nint} (m_\alpha + Ms_\alpha), \beta] \quad (45)$$

where function  $\text{nint}$  gives the nearest integer to a real argument,  $m_\alpha$  is the species' sample mean of  $X$  (conditioned on  $X \geq \alpha$ , where  $\alpha$  is the smallest value of  $x$  in the empirical table),  $M$  is an integer constant,  $s_\alpha$  is the sample standard deviation of  $X$ , and  $\beta$  is the largest value of  $x$  in the table; see Miller (1988) for  $m_\alpha$ ,  $s_\alpha$ , and  $\beta$ . We also compute  $b$  more simply as a function of the sample maximum of  $X$

$$b = K\beta \quad (46)$$

where  $K = 19/6$ , which gives the value  $b = 38$  for domestic sheep, the value corresponding to  $M = 12$  in eqn (45).

Parameters  $E$  and  $V$ , assumed common to all species, are empirically estimated as the values that give the best fit of the theoretical to the empirical survival curve for domestic sheep. The sheep life table is one of the best available (Miller, 1988). For a fixed  $r$  and  $\lambda$  (or  $q$ ), each choice of  $\omega$  and  $b$  requires a specific calibration of  $\hat{\tau}_w$ . Using the two choices of  $\omega$  corresponding to  $n = 2$  and  $n = 3$ , the parameters of Table 1, and the method of computing an *ab initio* life table below, ( $E, V$ )-parameter space was searched for the minimum of the least-squares criterion  $S_e$  (standard error of estimate)

$$S_e = \sqrt{\sum_{x=x_1}^{x_2} \frac{(l_x - l_x^*)^2}{x_2 - x_1 + 1}} \quad (47)$$

where  $l_x$  is the empirical survival function,  $l_x^*$  is the theoretical,  $x_1$  is the smallest value of  $x$  in common for the two life tables, and  $x_2$  is the largest.

### (C) COMPUTATION OF *AB INITIO* LIFE TABLES

By the definition of conditional probability

$$R_{X|W}(x|w) = \frac{P(X > x, W = w)}{\tilde{f}(w)} \quad (48)$$

where  $X$  is continuous at each discrete point  $w \in \mathcal{W}$ . Since  $X$  is continuous, the equality  $P(X > x) = P(X \geq x)$  holds, and the life-table survival function as conventionally defined,  $P(X \geq x)$ , has the formula

$$l_x^* = \sum_{w \in \mathcal{W}} \tilde{f}(w) R_{X|W}(x|w) \quad (49)$$

where we allow  $x$  to assume only integer values. From eqn (44) and since  $R_{x|w}(x|w) = 0$  for  $w \notin \{w: \omega(w) \geq x\}$ , eqn (49) gives (for series systems)

$$l_x^* = p^x \sum_{\{w: \omega(w) \geq x\}} \tilde{f}(w), \quad \alpha \leq x \leq \beta \quad (50)$$

where  $\alpha = r/2$  and  $\beta = b$ . The remaining conventional life-table functions are computed from  $l_x^*$  by standard methods.

To test the realism of the method, we have conducted six numerical experiments, designated E1–E6, each of which computes the life tables of the ungulate test species and which together allow examination of the effects of parameters  $b$  and  $n$  and function  $\hat{\tau}_w$  on the accuracy of the tables. This approach is necessary because  $b$ ,  $n$ , and  $\hat{\tau}_w$ —due either to computational or data limitations—are themselves, to varying degrees, unrealistic. The conditions for each experiment are summarized in the following list (the two conditions not indicated for each of E2–E6 are unchanged from E1):

E1:  $M = 4, n = 2$ , cosine  $\hat{\tau}_w$

E2:  $M = 8$

E3:  $M = 12$

E4:  $b = K\beta$

E5:  $n = 3$

E6: triangular  $\hat{\tau}_w$

The agreement between the theoretical and empirical life tables for domestic sheep, shown in Table 3, is the best that is possible with this method and the available data. This is because wearout eqn (35) is treated as a regression function having two adjustable parameters, E and V. The best fit slightly worsens as  $b$  is increased to more realistic values in the sequence E1–E3 but changes relatively little

TABLE 3  
Goodness-of-fit measures  $S_e$  (after multiplication by  $10^2$ ) for five ungulates†

Experiment	$S_e \times 10^2$					row sum
	Domestic sheep	wild boar	Dall sheep	buffalo	hippopotamus‡	
E1	1.29	8.55	2.48	2.96	10.1	25.4
E2	1.44	8.58	2.73	2.69	7.23	22.7
E3	1.46	8.58	3.02	3.49	8.00	24.6
E4	1.46	8.58	2.37	2.22	8.17	22.8
E5	1.21	8.33	2.53	4.24	—	—
E6	1.30	8.48	2.58	2.92	10.1	25.4

† Comparison limits  $x_1, x_2$ : 1, 12 (domestic sheep); 1, 8 (wild boar); 2, 13 (Dall sheep); 3, 19 (buffalo); 5, 44 (hippopotamus). Convergence criterion  $C = 10^{-7}$  and  $C = 10^{-8}$  for the  $n = 2$  and  $n = 3$  computations, respectively.

‡ The wearout equation was not solved for the  $n = 3$  (E5) hippopotamus case because of very large computer-time requirements.

beyond eight standard deviations (E2). In an opposite manner, the best fit improves as the system order is increased from  $n=2$  (E1) to the more realistic  $n=3$  (E5). There is little effect on the best fit whether the cosine (E1) or triangular (E6) density  $\hat{f}_w$  is used in eqn (35).

With the parameters in Tables 1 and 2, we can *predict* the life tables of the other four ungulates. This is not regression and does not involve any adjustable parameters. Table 3 and Fig. 8 compare the fit of  $l_x^*$  to  $l_x$  for all four. Fig. 9 compares the survival curves for the buffalo as a function of  $b$ , and Fig. 10 similarly compares the curves as a function of  $n$ . The main results are these: (a) Figure 8 illustrates (for the E2 conditions) that the predicted shapes of  $l_x^*$ , both convex and concave, are good. The largest deviations in shape, and consistently the largest  $S_e$  values for each of E1–E6, are for the species, wild boar and hippopotamus, that have the least reliable empirical life tables (Miller, 1988). The predicted shapes are excellent for the two species, Dall sheep and buffalo, that have the most reliable tables. (b) Figure 9, based on E1–E3 for the buffalo, shows that  $l_x^*$  changes very little as  $b$  is increased beyond eight standard deviations ( $M=8$ ). As  $b$  is increased, the mean of the

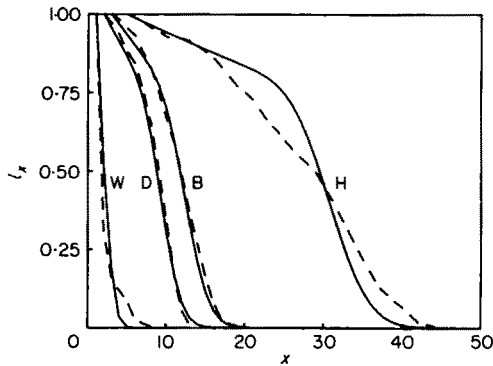


FIG. 8. Comparison of predicted (solid curves) and empirical  $l_x$  curves for four ungulates: wild boar (W), Dall sheep (D), African buffalo (B), and hippopotamus (H).

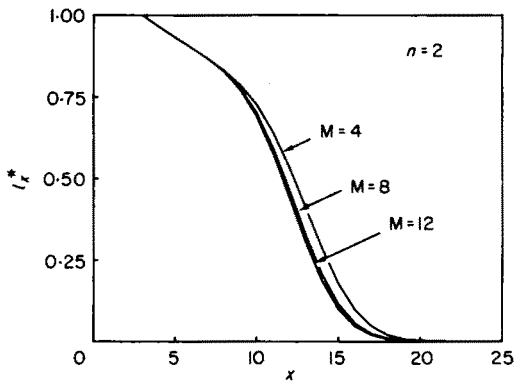


FIG. 9. Buffalo  $l_x^*$  as a function of  $b$  (with  $n=2$ ).

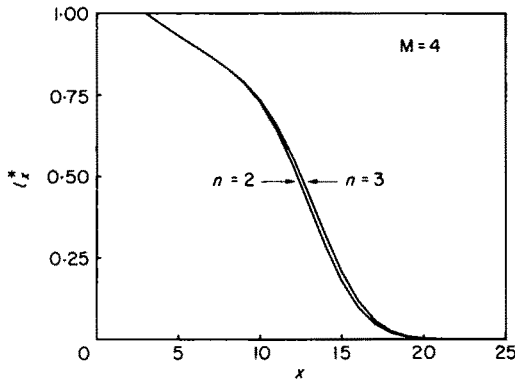


FIG. 10. Buffalo  $l_x^*$  as a function of  $n$  (with  $M = 4$ ).

TABLE 4

*Theoretical vs. observed life expectancies for four ungulates*

Method	Life expectancy (yr)			
	wild boar	Dall sheep	buffalo	hippopotamus
Observed	1.72	8.11	11.0	26.5
Theoretical	1.74	7.94	10.7	26.9
Relative error (%)	-1.2	2.1	2.7	-1.5

distribution decreases. (c) The row sums of  $S_e$  for E3 and E4 indicate that determining  $b$  from the sample maximum of  $X$ , eqn (46), gives comparable results (actually better in this instance) to determining it from two moments of  $X$ , eqn (45). (d) Figure 10, based on E1 and E5 for the buffalo, illustrates that both the shape and location of  $l_x^*$  are only slightly affected as  $n$  is increased from  $n = 2$  to  $n = 3$ . As  $n$  is increased, the mean of the distribution increases. (e) E1 and E6 for all four ungulates demonstrate that the results are insensitive to the exact shape of  $\hat{\tau}_w$  (but they are very sensitive to its moments  $E$  and  $V$ ).

Table 4 compares the theoretical and observed life expectancies  $E(X|X \geq \alpha)$ , where  $\alpha = r/2$ , as computed from the *ab initio* (under the E2 conditions) and empirical life tables, respectively. (The values  $x_1$  in the footnote of Table 3 are the same as  $\alpha$ , the smallest  $x$  in the theoretical tables.) The table displays the two values of life expectancy and reports the relative errors  $(m - \mu)100\%/m$ , where  $m$  is the observed and  $\mu$  is the theoretical life expectancy, both in units of years. The agreement in all cases is excellent.

#### 4. Discussion

There is little doubt from its ability to compute *ab initio* life tables that the wearout equation is basically realistic. As a validation study, this is a rigorous test because

the equation must predict the correct shape and location of an entire function, the life table of a species. Although parameters  $q$  and  $b$  are derived from the empirical life table for each species, this input of empirical data is not significantly influencing the predicted table. Estimation of  $q$  requires only a single value,  $q_r$ , from the table or a single point from its mortality-rate regression function. Basing  $b$  on eqn (45), which requires two moments from the life table, is possibly more significant. However, experiments E1–E3 (Table 3 and Fig. 9), showing that very similar results are produced whether we place  $b$  at 4, 8 or 12 standard deviations beyond the mean, suggest that  $b$  cannot significantly be influencing the computed table. Moreover, the alternative method of basing  $b$  on eqn (46) requires only a single value from the table, the sample maximum  $\beta$ , and E3 and E4 clearly show that this works about as well. The predicted and empirical survival functions  $l_x$  (Fig. 8 and Table 3) are in good agreement, both in shape and location, for all four test species, which represent a broad range of survival characteristics. Since the agreement is consistently better for the species, Dall sheep and buffalo, that have the more reliable empirical data, the poorer fit for wild boar and hippopotamus is probably due more to poor data than to deficiency of eqn (33) or eqn (35). If the equation is realistic, the accuracy of its predictions should improve, or at least not worsen, as  $n$  increases, since the ungulates obviously have a very high order. However, a conclusion in this regard is partially obscured by the contrary effects of finite  $b$ : In the results for domestic sheep (Table 3), larger  $n$  did improve the best fit, but larger  $b$  worsened it; in the prediction experiments for the buffalo (Figs 9 and 10), larger  $n$  shifted  $l_x^*$  to the right, but larger  $b$  shifted it to the left. Thus, in the important limit of very large  $n$  and  $b \rightarrow \infty$ , I believe the predictions, if not improved, will at least not be fundamentally different from those observed here. For all four species, the predicted and observed life expectancies (Table 4), which range from less than two years to more than 26, are in excellent agreement, the maximum relative error being less than 3%.

Since wearout eqn (33) has been derived exactly, its scope of applicability is determined by the scope of the assumptions. The reliability-theoretic assumptions do not apply to organisms that are not fixed systems in their terminal stage of life. The equation would not apply, for example, to trees, which continue to grow throughout life, or to bacteria, which divide. By the assumption of only two modes of death, the theory applies only to a terminal adult form. It does not apply, for example, to the juvenile period of life for mammals or to the more extensive early developmental stages of insects. The assumption that  $\lambda$  is the same for all components can be made valid for series-parallel systems, which approximate the structure of organisms at the highest level of organization, by grouping components into modules (Birnbaum & Esary, 1965) such that failure rate  $\lambda$  is approximately the same for each. Since  $f$  is assumed stationary, the equation applies only to species that are evolving slowly, i.e., via classical Darwinian evolution. There is no explicit assumption of a type of selection or of even natural selection itself (although the ingredients of individual selection are assumed) or of a particular genetic apparatus—the theory could apply to self-replicating machines having genetic apparatuses very different from those of biological organisms. Since all individuals can give birth, the model

includes hermaphroditic and asexual forms. For bisexual forms, we can simply ignore males, a common approach, but apply the conclusions of the theory to males if sexual dimorphism is small and, in particular, both sexes have similar reliability properties. Although most vertebrate populations use discrete rather than continuous reproduction, the latter is probably a satisfactory approximation for the discrete case; however, the theory does not apply to semelparous species. In summary, while the assumptions undoubtedly include many more species, they are satisfactory approximations for mammalian species.

Because the wearout equation describes the distribution of wearout over evolved reliability structures, it is as important to understanding the evolution of aging as the wave equation is to understanding chemistry. By statistically governing all component wearout of the system (up to the assumption that  $s_i = 0$ ), the equation governs the system wearout properties arising from the wearout of components—it would thus govern all system wearout except that systems containing parallel units can exhibit wearout even when the components do not (Birnbaum *et al.*, 1966). The seemingly enigmatic fact that organisms that have evolved the capacity for self-repair have also evolved components that age is equivalent to the condition that they have (essentially) stationary densities  $f$  and hence have evolved finite-valued random variables  $W_i$  ( $i = 1, 2, \dots, n$ ). Since wearout eqn (33) presumably has a solution only if  $f$  is stationary, the question “Why do organisms age?” can be asked mathematically as “Why (or under what conditions) does the wearout equation have a solution?”. The maintainability of the system once it has evolved aging depends on dispersion properties of solution  $f$ . Intuitively, the number of component repairs necessary to extend the system life by a given increment depends on the correlation of random variables  $W_i$ ; the more correlated they are, the more costly extension of the lifespan will be. It is clear from Figs 5 and 7 that this depends profoundly on the structure of the evolutionary system: The component lifetimes are positively correlated in the series system but not in the parallel system. Thus, insight into the question of whether the human lifespan can be significantly extended by repairing or replacing components can be gained by analysis of the wearout equation (Miller, 1987). As we have seen, because the equation governs the aging component of mortality, the shape of the survival curve and the value of the life expectancy for a species are determined largely by the system reliability structure and the shape and location of  $f$ . A possible practical application of the wearout equation is the computation of *ab initio* life tables for species, such as rare or extinct species, whose tables are too difficult or even impossible to construct empirically.

The significance of wearout eqn (33) is that it is the first theoretical advance in the evolution of aging at the level of detail—at the level of reliability structure—that is necessary to address the questions and applications above. To neglect reliability structure limits understanding of the evolution of aging in the same way that neglecting chemical structure, by having knowledge only of empirical formulas, would limit the understanding of organic chemistry. There has of course been prior theoretical work on the evolution of aging (see Rose (1983) and Miller (1987) for references), as well as applications of reliability theory to biological aging (see, e.g. Abernethy (1979), Kol'tover (1981), and Witten (1984)). However, none of the

previous work is a comprehensive theory at the fundamental level of reliability structure, and no other work to my knowledge is capable of computing realistic theoretical life tables (see Johnson (1963) and Forbes *et al.* (1970) for previous efforts). This equation is analogous to the wave equation of chemistry in that its solution gives virtually all information of interest about the evolution of wearout in complex systems. However, the information is necessarily more approximate than that obtained from solution of the wave equation because our assumptions are more approximate (and more complex) than those of quantum mechanics; also tempering the comparison is the fact that the wearout equation has undergone much less experimental testing than has the wave equation. In any case, I believe this equation, if it does withstand further experimental testing, can provide insight into fundamental questions in the biology of aging.

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#### REFERENCES

- ABERNETHY, J. D. (1979). The exponential increase in mortality rate with age attributed to wearing-out of biological components. *J. theor. Biol.* **80**, 333-354.
- BARLOW, R. E. & PROSCHAN, F. (1981). *Statistical Theory of Reliability and Life Testing: Probability Models*. Silver Spring, Maryland: To Begin With.
- BIRNBAUM, Z. W. & ESARY, J. D. (1965). Modules of coherent binary systems. *J. Soc. Indust. Appl. Math.* **13**, 444-462.
- BIRNBAUM, Z. W., ESARY, J. D. & MARSHALL, A. W. (1966). A stochastic characterization of wear-out for components and systems. *Ann. Math. Statist.* **37**, 816-825.
- BUNNELL, F. L. & OLSEN, N. A. (1981). Age-specific natality in Dall's sheep. *J. Mammal.* **62**, 379-380.
- FORBES, W. F., SPROTT, D. A., FELDSTEIN, M. & DOUNCE, A. L. (1970). A model to account for mortality curves of various species. *J. theor. Biol.* **29**, 293-299.
- HICKEY, F. (1960). Death and reproductive rates of sheep in relation to flock culling and selection. *N.Z.J. Agric. Res.* **3**, 332-344.
- JERRI, A. J. (1985). *Introduction to Integral Equations with Applications*. New York: Marcel Dekker.
- JOHNSON, H. A. (1963). Redundancy and biological aging. *Science, N.Y.* **141**, 910-912.
- KOL'TOVER, V. K. (1981). Reliability of the enzymatic defense of a cell against superoxide radicals and aging. *Dokl. Akad. Nauk SSSR (Biophys.)* **256**, 199-202.
- MILLAR, J. S. & ZAMMUTO, R. M. (1983). Life histories of mammals: an analysis of life tables. *Ecology* **64**, 631-635.
- MILLER, A. R. (1987). Evolutionary reliability theory. In: *Evolution of Longevity in Animals* (Woodhead, A. D. & Thompson, K. H., eds.). New York: Plenum Press.
- MILLER, A. R. (1988). A set of test life tables for theoretical gerontology. *J. Gerontol.* **43**, B43-49.
- RAAB, D. H. & GREEN, E. H. (1961). A cosine approximation to the normal distribution. *Psychometrika* **26**, 447-450.
- ROSE, M. R. (1983). Evolution of Aging. *Rev. Biol. Res. Aging* **1**, 19-24.
- SINCLAIR, A. R. E. (1977). *The African Buffalo: A Study of Resource Limitation of Populations*. Chicago: University of Chicago Press.
- SINGH, H. (1966). *Domestic Animals*. New Delhi: National Book Trust.
- SMITH, C. O. (1983). *Introduction to Reliability in Design*. Malabar, Florida: Robert E. Krieger.
- WITTEN, M. (1984). A return to time, cells, systems and aging: II. Relational and reliability theoretic approaches to the study of senescence in living systems. *Mech. Ageing Dev.* **27**, 323-340.