

Variable generation times and Darwinian fitness measures

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Summary

Reproductive value (RV) and net reproductive output (R_0) are frequently used fitness measures. We argue that they are only appropriate when intervals between reproductive events are fixed, as they are dimensionless generation-to-generation scalings with units offspring per parent. A fitness measure should account for two different effects of a decrease in generation time: (1) increased survival due to shorter exposure to mortality agents and (2) increased frequency of reproduction. R_0 and RV deal with the first of these two effects, while a measure with a physical dimension *per time* [T^{-1}] is needed to account for the second. The Malthusian growth parameter, r , meets this requirement and in situations where time to reproduction is variable, we propose ρ , the instantaneous rate of spread of descendants (from an individual) be used instead of R_0 . As an alternative to RV , we suggest using the instantaneous difference $\Phi = \rho - r$, where r is the population rate of increase. While RV and R_0 are dimensionless ratios, Φ , and ρ are *per time* rates which are appropriate in accounting for alterations in generation time.

Keywords: life-history; phenotypical fitness; generation time; reproductive rate

Introduction

There has been long debate on the use of population growth rate parameters as fitness measurements (e.g. Charlesworth, 1980; Nur, 1984; Stenseth, 1984; Murray, 1985; Stearns, 1992). Fitness is hard enough to define, let alone measure. We will leave the measurement problems untouched and be satisfied with an intuitive understanding of phenotypical fitness: that natural selection has favoured those individuals who have reproduced successfully at a higher rate than the population as a whole, where successfully means that a premium is also put on offspring survival. Thus, a fitness measurement should consist of the rate of reproduction of an individual and the survival of its offspring, scaled according to the reproductive rate of the population. Much of the controversy arises from not stating explicit dimensions and units, especially quantities with one as their numeric value. This has no implications for the calculus, but prevents the discovery of dimensional inconsistencies and, inevitably, biased estimators. As such, R_0 is

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Table 1. Definition of symbols, dimensions and units

Symbol	Description	Dimension	Unit
λ	Finite increase	–	–
ρ	Individual instantaneous rate of increase	$[T^{-1}]$	Year ⁻¹
Φ	$= \rho - r$	$[T^{-1}]$	Year ⁻¹
b	Lifetime fecundity	$[I]$	Daughters
K	Relation between fecundity and generation time	$[T^{-1}]$	Daughters per mother per year
M	Instantaneous mortality rate	$[T^{-1}]$	Year ⁻¹
m	Mother	$[I]$	Female
N_t	Population size at time t	$[I]$	Females
R_o	Net reproductive output	–	Daughters per mother
RV	Reproductive value	–	Daughters per mother per population increase during T
r	Population instantaneous rate of increase	$[T^{-1}]$	Year ⁻¹
S	Survival probability over generation time	–	–
T	Generation time	$[T]$	Years
t	Time	$[T]$	Years
Δt	Basal time	$[T]$	Inverse unit of Φ , ρ and r
w	Finite dimensionless fitness	–	–

Dimensional symbols: I, individual; T, time.

frequently termed the net reproductive (or reproduction) *rate* (e.g. Keyfitz, 1968; Charlesworth, 1980; Caswell, 1989; Stearns, 1992). An inspection of the dimensions, however, gives no indication that this parameter is a rate, as the time dimension is not explicitly expressed. A biological variable has three attributes: a numerical value, a unit of measurement and a physical (or biological) dimension. Equations must be consistent with regard to each of these factors. To separate dimensions from units, dimensions are given in brackets []. All the symbols, their dimensions and the units that are used below are defined in Table 1.

Reproductive value (RV) and net reproductive output (R_o)

The fitness of a phenotype has been approximated by the reproductive value (RV) (Fisher, 1930; Charnov, 1990; Stearns, 1992). RV is a measure of two different phenomena: (1) the discrete reproduction of an individual, weighted against (2) the continuous reproduction of its population over the same time span. Stearns (1992, p. 223) defines RV more stringently as ‘the number of offspring that an average organism in a particular age class can expect to have over the rest of its life under the conditions prevailing, discounted back to the present by the current population growth rate’. Reproduction must account for both number and persistence of offspring before it can be assessed as the ratio between the numbers of individuals separated by one generation, that is, the adult offspring per mother as compared to population growth over the same interval.

R_o is defined as the number of female offspring a female is expected to produce over her lifetime, which, for the semelparous situation equals the number of adult female offspring an

adult female gives rise to. The number of descendants replacing the adult mother is the product of fecundity and juvenile survival, i.e.

$$R_o = (b/m)S \quad (1a)$$

where b/m is the individual fecundity (number of female offspring produced by and per a female) and S is the probability of offspring survival from egg to adult. Hence, from a numerical point of view, m could be omitted. From a dimensional viewpoint, however, it should not be neglected. As the 'individual' is not a dimension of the SI system, we define here the dimension [I] and the common units ind. (individuals) and females are assumed to be associated with this unit. The time dimension is not explicitly expressed in any of the variables on the right-hand side of Equation 1a. Although survival is obviously related to time, time is not commonly expressed in the unit of S . Survival is often expressed as $S = e^{-MT}$, where M is the instantaneous mortality rate [T^{-1}] and T is the generation time. Thus Equation 1a becomes

$$R_o = bm^{-1} e^{-MT} \quad (1b)$$

As the death of an individual is a discrete rather than a continuous process, e^{-MT} should be interpreted as the individual juvenile survival probability. Regardless of how survival is represented, S in Equation 1a must be dimensionless and, although R_o is frequently called the net reproductive rate, R_o represents a dimensionless ratio of the number of individuals in a parent-offspring line. RV scales expected individual performance (R_o) against the population's growth over the same time interval T and since in a continuous breeding population $N_T/N_o = e^{rT}$, we can write

$$RV_o = R_o e^{-rT} \quad (2)$$

where RV_o represents RV at age zero, i.e. lifetime reproductive value. By inspection of the dimensions, we see that RV is also dimensionless. Hence, both RV and R_o are ratios rather than rate measurements.

Instantaneous rate of increase

The instantaneous population growth parameter in Equation 2 is also commonly used to express fitness (e.g. Fisher, 1930; Cole, 1954; McLaren, 1963; Lewontin, 1965; Lande, 1982; Sibly and Calow, 1986). The dimension of r [T^{-1}], is obtained from its definition

$$r = \frac{1}{N} \frac{dN}{dt} \quad (3)$$

Thus, in contrast to R_o , r is a true rate. It was originally defined for population growth where N is the population size and t is time. Later, we will need both the current population rate of increase and the rate of spread of descendants from an individual and we therefore reserve r for the population and ρ for the individual. At the individual level, the instantaneous increase, ρ , is the instantaneous production of offspring minus the death rate. As commonly shown in textbooks, r and R_o (as defined at the population level) are closely related and for semelparous reproducers we have the following relationship between instantaneous growth rate (ρ), net reproductive output (R_o), generation time (T), fecundity (b) and mortality (M) at the individual level:

$$\rho = \ln R_o / T = \ln(bm^{-1} e^{-MT}) / T = [\ln(bm^{-1}) / T] - M \quad (4)$$

On the right-hand side of Equation 4 we see that the instantaneous growth rate is the difference between the instantaneous birth and death rates, which is another way of defining r (e.g. Lotka, 1925).

By comparing Equations 1b and 4 we see that generation time has a different impact on R_0 compared to ρ . R_0 is actually independent of generation time *per se*, as will be illustrated in the next section, but it does depend on the generation time for juvenile survival.

Influence of generation time

Stearns (1992, p. 31) has stated that 'In using R_0 , one makes the implicit assumption that variation in generation length makes no difference to the outcome of selection. The only thing that counts is the number of offspring produced per lifetime, no matter how long it takes to produce them.' This, however, is not entirely true, as the numerical value (although not the dimension) of R_0 does depend on generation length (unless mortality is zero). By inserting different generation times in Equation 1b and keeping the others constant, it may be asserted that reproductive output increases with reductions in generation time and therefore it might seem that R_0 is a *per time* rate that rewards early reproduction. This reward is, however, only a consequence of the definition of survival as being dependent on time ($S = e^{-TM}$). Hence, the increased R_0 is due to a shorter exposure to mortality risk and not to a decreased generation time *per se* (which is the argument of Stearns (1992)). This can easily be seen when mortality is zero ($M = 0$ and $S = 1$), as a reduction in generation time therefore has no influence on the value of R_0 , assuming that there is the same number of offspring. From Equation 4 we see that the value of ρ is affected by alterations in generation time also when mortality is zero.

Fitness

As stated in the Introduction, we assume that fitness increases with an increase in both reproduction *rate* and juvenile survival. As shown above, generation time affects both. Hence, generation time should be appropriately represented in the rate of reproduction and in survival. As is also shown above, R_0 *may* respond indirectly to alterations in generation time if such changes also affect survival. It does not respond, however, to the decreased turnover time associated with reduced generation time and this is reflected in ρ .

Phenotypical fitness is reproducing at a higher rate than other members of the population. An individual may have a high fitness even when $bS < 1$ and $\rho < 0$, as long as the rest of the population suffers even more. This aspect of fitness is included in R_0 by the weighing factor e^{-rT} , but R_0 is biased due to R_0 . As a better measure of phenotypical fitness we suggest the instantaneous difference in increase with dimension $[T^{-1}]$

$$\Phi = \rho - r \quad (5a)$$

where r represents instantaneous change in population size during T (Equation 3). While one or both of ρ and r may be negative, Φ is positive only when the increase rate of the individual is higher than that of the population, as would be expected for a phenotypical fitness measurement. It may be desirable to express fitness as a ratio of individual versus population performance. For this use, the finite term w corresponds to Φ :

$$w = e^{\Phi\Delta t} = e^{\rho\Delta t}/e^{r\Delta t} = \lambda_p/\lambda_r \quad (5b)$$

where Δt is basal time (i.e. numeric value one and inverse unit of Φ , ρ and r). Contrary to R_0 and R_0 , the instantaneous Φ and the finite w account correctly for the generation time.

Consequences for optimal habitat and risk-taking

Recently, life history theory has been used to explain and predict animal distributions (e.g. Werner and Gilliam, 1984; Clark and Levy, 1988; Aksnes and Giske, 1990). In all these papers, predictions were based on the maximization of R_o . In the following analysis we show that R_o will not predict the optimal risk-taking associated with an optionally reduced generation time.

Marginally acceptable changes in mortality risk associated with an environmental change in generation time can be studied by considering two (or n) habitats, one having a higher fitness value than the other ($R_{o1} > R_{o2}$, $\rho_1 > \rho_2$). We assume that the optimal habitat choice of the individual is independent of population growth rate (r), so that the measurements of individual performance (Equations 1b and 4) will describe the individual relative fitness as well as the comparative measurements do (Equations 2 and 5). Thus, the optimal habitat is where R_o or ρ , respectively, is maximized:

$$\max(R_o) = \max(bm^{-1}e^{-MT}) \text{ (total reproduction)} \quad (6)$$

or

$$\max(\rho) = \max[\ln(bm^{-1})/T - M] \text{ (reproductive rate)} \quad (7)$$

(Of course, time scales other than the generation time are important and short-time trade-offs may differ widely from those derived here (Stephens, 1981; Mangel and Clark, 1988). As already emphasized, in these very simplistic models, b , T and M have different impacts on the fitness measurements and thus on the predicted optimal habitats. Also, in most habitats, b , M and T will be interdependent. We will assume that lifetime fecundity is the same in habitats 1 and 2, i.e. $b_1 = b_2 = b$. If habitat 1 should provide a higher fitness value (measured as R_o), the following inequality should be satisfied:

$$R_{o1} > R_{o2} \Rightarrow T_1/T_2 < M_2/M_1 \quad (8)$$

Hence, a reduction in generation time is favourable as long as it is linked to a less than equal relative increase in mortality rate. Using the instantaneous rate as a fitness measurement, we end up with a very different inequality that has to be satisfied in order to achieve higher fitness in habitat 1:

$$\rho_1 > \rho_2 \Rightarrow T_1/T_2 < 1 + (M_2 - M_1)T_1/\ln(bm^{-1}) \quad (9)$$

Here, we see that fecundity has not been eliminated and the optimal T versus M trade-off depends on the actual fecundity. Following Werner and Gilliam (1984) and Gilliam and Fraser (1987), there have been several studies showing that juvenile animals trade-off growth rate (g) versus mortality risk by minimizing M/g . These results are based on maximization of R_o and the assumption that generation time is inversely proportional to growth rate. Unfortunately, Inequality 9 shows that this simple rule does not account appropriately for the generation time.

Consequences for optimal age at maturity

R_o may not only misjudge the correct trade-off, but may also invoke incorrect variables in a life history optimization. To demonstrate this, assume that fecundity is a function of body size, linearly increasing with age at maturity ($b/m = KT$). Let the mortality rate be constant over generation time, so that survival $S = e^{-MT}$. With these two simplistic assumptions optimal age at reproduction can be investigated by solving Equations 6 and 7 for all values of T . First, we see from Equation 7 that age-independent mortality risk will give a constant reduction in ρ and will not influence optimal age at maturity. By using ρ , the trade-off depends on the steepness of the

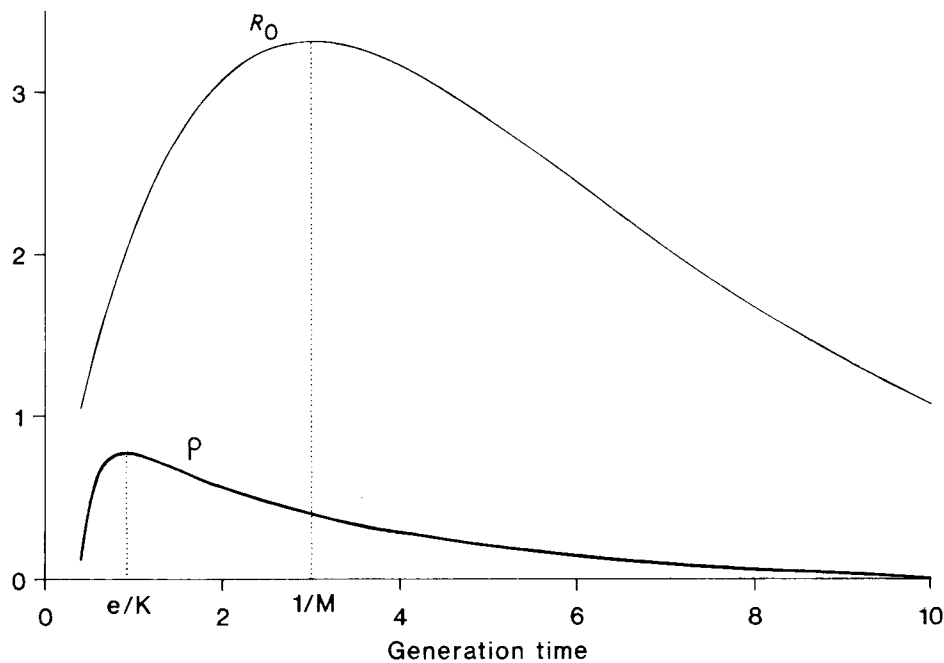


Figure 1. Dependency of R_0 and ρ on generation time (T). Under the assumptions that survival can be expressed as $S = e^{-TM}$ and fecundity as $b/m = KT$, the global maximum is at $T_{R_0} = 1/M$ and at $T_\rho = e/K$. In this example $K = 3$ and $M = 1/3$.

age-dependent fecundity function (K) and generation time. The opposite applies by using R_0 ($= KT e^{-MT}$) and Equation 6: optimal age is independent of the age-dependent fecundity, but cannot be separated from the mortality rate. By differentiation of R_0 and ρ with respect to generation time, it is easy to show (Fig. 1 and Appendix) that R_0 has a global maximum at $T_{R_0} = 1/M$, while the global maximum of ρ is at $T_\rho = e/K$ (where e is the base of the natural logarithm).

The above expressions for optimum generation time show that when conditions worsen, so that M increases and K decreases, the optimum generation time predicted from R_0 will decrease, while ρ predicts an increase. By rearranging Equation 1b to $T_{R_0} = -\ln(R_0 m/b)/M$ and Equation 4 to $T_\rho = \ln R_0 / \rho$ and solving for $T_{R_0} > T_\rho$, we find that the predicted optimum generation time is lower by using R_0 than by using ρ when $R_0 < 1$ and $\rho < 0$. Thus, when breeding earlier is not worthwhile (cf. Sibly and Calow, 1986), R_0 underestimates the optimum generation time. Again it is shown that conclusions based on R_0 may be misleading, but nevertheless common.

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Appendix

Let $bm^{-1} = KT$

Proof that ρ is at maximum at $T = e/K$:

$$\begin{aligned}\rho &= \ln(KT)/T - M \\ d\rho/dT &= (1/T^2) (1 - \ln(KT)) \\ d\rho/dT = 0 &\Rightarrow \ln(KT) = 1 \Rightarrow T = e/K\end{aligned}$$

which is a maximum because $d^2\rho/dT^2 = -T^{-3}(1 + 2\ln(KT)) < 0$ at $T = e/K$.

Proof that R_0 is at maximum at $T = 1/M$:

$$\begin{aligned}R_0 &= Ke^{-MT} \\ dR_0/dT &= -Me^{-MT} (1 - MT) \\ dR_0/dT = 0 &\Rightarrow T = 1/M\end{aligned}$$

which is a maximum because $d^2R_0/dT^2 = -M^2e^{-MT}(MT - 2) < 0$ at $T = 1/M$.