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Measuring Fitness in Life-history Studies

Jan Kozłowski

BECAUSE NATURAL SELECTION changes the frequencies of genes, population genetics is the ultimate method to study evolution. However, optimization methods have proved more powerful than population genetics techniques for the study of complex adaptations such as life-history characteristics. All predictions of optimization problems are sensitive to the criterion of optimality, called the 'performance index' in control theory and 'fitness' in evolutionary biology. Stearns¹ is right in saying that fitness is only a problem-solving tool and that no general definition of fitness has been found; nevertheless choosing a fitness measure for a given evolutionary problem cannot be arbitrary.

The most widely used fitness measure in life-history theory is r , known as the intrinsic rate of natural increase or the Malthusian parameter; r is the root of the Euler–Lotka equation

$$1 = \int_0^{\omega} e^{-rx} l_x m_x dx \quad (1)$$

where x represents age, ω maximum longevity, l_x probability of surviving to age x , and m_x the number of offspring at age x .

For any age-dependent and constant-in-time l_x and m_x , population will increase or decrease exponentially after reaching a stable age distribution. The genotype with the highest r is the fittest: it will grow more rapidly than all other genotypes. However, exponential growth cannot last forever, so r as a fitness measure is limited to two cases: (1) when exponential population growth stops after a time, such as when the season ends and the probability of surviving to the next growth period is equal for all genotypes; and

(2) when maximum r equals 0, i.e. the population is in a steady state.

Another commonly used measure of fitness is lifetime offspring production, called net reproductive rate R and defined as

$$R = \int_0^{\omega} l_x m_x dx \quad (2)$$

This measure is convenient because Eqn 2 can be expressed as

$$R = \int_0^a l_x m_x dx + \int_a^{\omega} l_x m_x dx \quad (3)$$

where a is any given age. If the genotypes do not differ in l_x and m_x below age a , the one with the highest right side integral of Eqn 3 is the fittest. In other words, it is enough to compare life histories from the age at which the first difference in life-history parameters appears. Ignoring the early part of life is usually impossible when r is maximized, because r depends on mortality and fecundity during the entire life.

The net reproductive rate is a good fitness measure only for stationary populations. The models implicitly or explicitly assume that density dependence operates somewhere in the life cycle, usually before the first difference in life histories occurs.

R must equal one for a steady state, and it must be maximized. This apparent paradox is unraveled by an ESS (evolutionary stable strategy) argument: the genotype that cannot be invaded at equilibrium by any other genotype wins, i.e. when the best genotype has R equal to one, all the other genotypes have $R < 1$.

Using r or R as a fitness measure is a matter of taste for stationary populations. In all other cases the predictions may differ completely: for example, predicted optimal age at maturity is not affected by early juvenile mortality when lifetime off-

spring production is maximized², but is usually affected strongly when the Malthusian parameter is maximized³.

So what should we maximize in life-history optimization models? In a new paper, Kawecki and Stearns⁴ have solved the dilemma. They adopted Pulliam's idea of source-sink population structure^{5,6}. The classic Euler–Lotka equation defines r for a uniform environment in which offspring experience the same conditions as parents. But most populations inhabit heterogeneous environments, with patches where reproduction exceeds mortality (sources) and patches where reproduction does not compensate for death and the population thrives due to more immigration than emigration (sinks). It does not matter whether there is a continuous gradient between the various patches. Offspring migrate from better to poorer places and *vice versa*, but they do so asymmetrically, more from source to sink than from sink to source, because more are produced in the better patches. Source-sink population structure explains the common phenomenon that R often differs from zero in a locality, whereas population number seems more or less constant.

Kawecki and Stearns⁴ generalize the Euler–Lotka equation to populations living in such source-sink environments: not only will the population converge to a stable age distribution, but also the proportion of individuals in each habitat will remain constant through time. The number of individuals in the entire population and in any habitat will grow exponentially at the same rate r . This rate must be calculated across all habitats, both sources and sinks, and is dependent not only on l_x and m_x for all habitats, but also on the distribution of offspring among the habitats in each generation.

When a population has a source-sink structure, there are patches

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with high, moderate, low and negative r . In the classic model, life history traits evolve independently in each habitat: local r should be maximized in the model. Kawecki and Stearns⁴ disprove this, and recently the same result has been obtained independently by Houston and McNamara⁷: global r should be maximized and it is likely to be close to zero. This broadens the applicability of lifetime offspring production (R) as a fitness measure, not only for closed populations at equilibrium but also for spatially structured populations with an average growth rate equal to zero.

Maximization of global r is equivalent to maximization of reproductive value at birth (the right side of the Euler-Lotka equation) in every local patch. Reproductive value at birth differs from lifetime offspring production by the discount factor $\exp(-rx)$ for offspring born to a mother of age x . In this discount term, r is not the Malthusian parameter resulting from l_x and m_x in a given locality but rather the rate of increase of the entire population. This means that, in source-sink populations, offspring production is discounted by the same number in all patches. On the other hand, local r 's are also local discount factors in isolated patches.

Both new papers^{4,7} use their generalized fitness measure to analyse the evolution of optimal norms of reaction. The traditional approach was to calculate the value of a trait that maximized local r for each habitat. Calculations were repeated for different habitats, and the dependence of that trait value on environmental characteristics was called the 'optimal reaction norm'. This procedure implicitly assumed that the offspring encountered the same environmental conditions as their parents. However, under this assumption, optimal reaction norms, i.e. adaptive phenotypic plasticity, cannot evolve! For an optimal reaction norm to be selected for, the ancestors must have lived in a range of environmental conditions. Reaction norms are adaptations to the partial unpredictability of conditions for the offspring.

The calculation of optimal reaction norms must allow for the distribution of environmental conditions that siblings can encounter^{4,7}. How does this difference in procedure affect reaction norms for life-history traits? Consider the reaction norm for age at maturity in a set of habitats differing in juvenile survival. If juvenile mortality gradually

increases, corresponding local r 's gradually decrease. A high rate of population increase strongly selects for early maturation. When banks pay high interest (high r), money should be put into the account (reproduction) as soon as possible. When banks do not pay interest at all (steady state) only the balance (offspring number) counts, not the date of deposit. With all other parameters kept constant, traditional calculations predict later maturation in habitats with high juvenile mortality. A proper calculation uses the same r for all habitats. Thus, we should not expect delayed maturation in habitats with a high juvenile mortality rate.

Other examples of differences in predictions are given by Kawecki and Stearns and by Houston and McNamara. Optimal age at maturity depends on age-independent mortality when global r is maximized, and does not depend on it if local r 's are maximized⁴. Similarly, the reaction norm for optimal clutch size is insensitive to juvenile mortality if adult survival depends on clutch size^{4,7}. Traditional calculations predicted an increase of clutch size under increased juvenile mortality.

How will the findings of these four authors^{4,7} change life-history theory? Neither the advocates of the Malthusian parameter nor the advocates of lifetime offspring production are right. Reproductive value at birth is the proper measure of fitness, and r occurring in it is usually external to the model; life history is optimized under any assumed r . Some authors⁸ intuitively adopted this measure of fitness years ago. We must remember that it is often reasonable to assume global $r = 0$, and R will be maximized in such a case.

Models that maximize discounted offspring production (reproductive value at birth) are structurally similar to those that maximize lifetime offspring production. The important difference is that the average population growth rate comes into play, affecting optimization results for $r \neq 0$. Such a fitness measure is good news for field ecologists. Often it is difficult to estimate all the parameters for r , especially those for early life. When offspring production discounted by an assumed r is maximized, data on life history preceding age a are not relevant to optimization of life history following a . For example, data on adult life may be sufficient to test predictions about size and age

at maturity or post-maturity allocation of resources to growth and maturity. Thus, the contributions of Kawecki, Stearns, Houston and McNamara should strengthen the link between life history theory and field ecology.

Acknowledgements

I thank M. Cichon, M. Jacobs, T. Kawecki, A. Lomnicki, P. Olejniczak, J. Radwan and J. Weiner for critically reviewing the manuscript. This work was supported partly by KBN grant No. PB 1100/P2/92/02 and partly by Swiss Nationalfonds grant No. 70PP-029565.

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