

REVIEW ARTICLE

Defining fitness in evolutionary models

DEREK A. ROFF*

Department of Biology, University of California, Riverside, CA 92521, USA

Abstract

The analysis of evolutionary models requires an appropriate definition for fitness. In this paper, I review such definitions in relation to the five major dimensions by which models may be described, namely (i) finite versus infinite (or very large) population size, (ii) type of environment (constant, fixed length, temporally stochastic, temporally predictable, spatially stochastic, spatially predictable and social environment), (iii) density-independent or density-dependent, (iv) inherent population dynamics (equilibrium, cyclical and chaotic), and (v) frequency-dependent or independent. In simple models, the Malthusian parameter ' r ' or the net reproductive rate R_0 may be satisfactory, but once density-dependence or complex population dynamics is introduced the invasion exponent should be used. Defining fitness in a social environment or when there is frequency-dependence requires special consideration.

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Introduction

A central idea of Darwin's thesis is that organisms vary in their ability to leave descendents, a trait that is now generally called 'Darwinian fitness' or simply 'fitness'. In the simplest case, the term 'descendents' might refer to immediate offspring, but more generally the time horizon is longer than a single generation and takes into account the differential rate of increase of genotypes in a population. There is certainly no real issue with the basic concept of fitness, but it has proven a rich source of discussion when implementing operational definitions of fitness in evolutionary models (Brommer 2000; Brommer *et al.* 2002). Such models attempt to determine the equilibrium trait values and, in some cases, their evolutionary trajectory, under the influence of natural selection. Evolutionary models may be classified along five broad dimensions: (i) finite versus infinite (or very large) population size, (ii) type of environment (constant, fixed length, temporally stochastic, temporally predictable, spatially stochastic, spatially predictable and social environment), (iii) density-independent or density-dependent dynamics, (iv) inherent population dynamics (equilibrium, cyclical and chaotic), and (v) frequency-dependent or independent. Considerable theoretical attention has been given to a

subset of these combinations but it is probably possible to find models that include all combinations. In this review, I shall summarize what the current state is with respect to mathematically defining fitness in evolutionary models. I shall focus on those combinations of dimensions for which there is a relatively strong theoretical justification for the fitness criterion and, where possible, suggest the fitness criterion for other combinations.

It is appropriate to commence this review with the equation of fitness from which our mathematical ideas have developed, namely the demographic model introduced in an evolutionary context by Fisher (1930). Fisher (1930) took an actuarial approach, assuming a population at a stable age distribution in which case the rate of growth of the population, r , can be described by the age-specific schedules of reproduction and survival as brought together in the characteristic (or Euler) equation:

$$\int_0^{\infty} e^{-rx} l(x) m(x) dx = \int_0^{\infty} e^{-rx} V(x) dx = 1, \quad (1)$$

where $l(x)$ is the survival to age x and $m(x)$ is the number of female births at age x . The above equation can also be written in discrete form: which model is to be preferred will depend upon the details of the underlying biological model.

*E-mail: Derek.roff@ucr.edu.

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Qualitative results are not affected by this type of variation and I shall not explicitly distinguish between the two cases in this overview. For a homogeneous population at stable equilibrium, r equals zero and the characteristic equation reduces to,

$$\int_0^{\infty} l(x)m(x) dx = \int_0^{\infty} V(x) dx = 1. \quad (2)$$

In the absence of density-dependence, we have the net reproduction rate, R_0

$$R_0 = \int_0^{\infty} l(x)m(x) dx = \int_0^{\infty} V(x) dx > 1. \quad (3)$$

This parameter, R_0 , is one of the most widely used operational metrics of fitness (e.g., Clutton-Brock 1988; Roff 1992; Stearns 1992; Charnov 1993) but, as discussed in the section ‘constant environment, density-dependence with a stable equilibrium’, its use implies a particular definition of the biological scenario, which is often not explicitly acknowledged.

Fisher (1930) argued that selection will favour that life history which maximizes r , which he termed the Malthusian parameter (and actually used the symbol m) in honour of Thomas Malthus, who in his ‘*Essay on the principle of population*’ pointed out that populations increase geometrically. This parameter is also referred to as the intrinsic rate of increase or simply the rate of increase (hence the present use of the symbol r or sometimes specifically r_0 to distinguish it from rates of increase calculated with other factors included). The characteristic equation was derived earlier (see Lotka 1907; Sharpe and Lotka 1911), but Fisher was the first to see its importance as a measure of fitness; ‘The Malthusian parameter will in general be different for each different genotype, and will measure the fitness to survive of each’ (Fisher 1930, pp. 46). As pointed out by Charlesworth (1970), it is not really desirable to equate r with a genotype as segregation and recombination will be changing the frequency of genotypes in the population. However, it is true, as discussed below, that under the circumstances considered by Fisher (1930) the parameter r will increase until an equilibrium is reached. While, the operational definitions of fitness may vary under different scenarios, they all have the above equation as their basic root. That is, fitness is measured by the long-term growth rate of a population. Invasion by a mutant form is contingent on its long-term growth rate relative to that of the resident population.

There has been discussion in the literature as to whether evolutionary models must necessarily be based on genotypic differences (e.g. Waxman and Gavrillets 2005). A rich theory called adaptive dynamics (Dieckmann and Doebeli 2005) has developed, largely ignoring the genetical basis of the life-histories examined (Dieckmann 1997; Ernande *et al.* 2004). In fact, Fisher, who was clearly concerned about the geneti-

cal basis of evolution, never provided a rigorous mathematical argument for r as the appropriate measure of fitness in genetical models. This lacuna was filled only relatively, recently, by the work of Charlesworth (1994, , for the collected analyses) and Lande (1982).

Constant environment, density-independent, stable-age distribution

This is the situation modelled by Fisher (1930), for which the characteristic equation provides the appropriate fitness criterion, although, as noted above, he did not provide a formal mathematical proof of this. Charlesworth (1994) showed that in a population genetical framework, a mutant allele will spread in a resident population if the mutation increases the intrinsic rate of increase of the genotype possessing the mutation. Lande (1982) showed that for a quantitative genetic model with weak selection and a nearly stable age-distribution ‘life-history evolution continually increases the intrinsic rate of increase of the population, until an equilibrium is reached’ (Lande 1982, pp. 611; see also Charlesworth 1993). The general discrete mathematical model for this situation is the Leslie matrix, which comprises the age-specific fecundities and survival probabilities. The finite rate of increase, $\lambda (= e^r)$ is given by the dominant eigenvalue of the Leslie matrix. For the continuous case, as given in equation (1), either an analytical solution can be found from the functional form of $V(x)$ or numerical methods can be employed. Coding in MATLAB and R is available for the general analysis of projection matrix models in Caswell (2001), Morris and Doak (2002), and Stubben and Milligan (2007).

Demographic stochasticity

As noted above, implicit in the characteristic equation is the assumption of a constant environment, a stable age-distribution and an infinite (or very large) population, so that variation due to demographic stochasticity can be ignored. The question of the spread of a mutant allele in a finite population has been considered in great detail in the population genetics literature (Wright 1931, 1969; Crow and Kimura 1970; Hedrick 2000; Gillespie 2006). In such models, fitness is mathematically defined with respect to a genotype: thus, for the single locus, two-allele case, we have w_{AA} , w_{Aa} and w_{aa} , where the subscripts refer to the genotypes. Relative fitness is then obtained by setting the largest w to 1 and the others as proportions of the largest value. This characterization of fitness is typical of population genetic models. An important implicit assumption of most of these models is that generation length is fixed, which greatly simplifies analytical approaches.

The potential effect of demographic stochasticity on the validity of r as an appropriate definition of fitness has not been well studied. Lewontin (1965) examined how variation in development time versus the age-schedule of reproduction would affect r and, hence, which would be under stronger se-

lection (for a critique of this work, see Roff 1992). However, this analysis pertains more to selection acting on components of the life-history rather than demographic stochasticity *per se*. Demetrius and Ziehe (2007) related the Malthusian parameter to population size through the demographic variance, defined as,

$$\sigma^2 = \frac{\int_0^{\infty} e^{-rx} V(x) (-x[r - H] + \ln(V(x))) dx}{\int_0^{\infty} x e^{-rx} V(x) dx}, \quad (4)$$

where,

$$H = \frac{\int_0^{\infty} e^{-rx} V(x) \ln[e^{-rx} V(x)] dx}{\int_0^{\infty} x e^{-rx} V(x) dx}. \quad (5)$$

H is called the evolutionary entropy: it characterizes the robustness of the population, i.e., the ability of the population to retain its phenotypic characteristics in the face of random perturbations in its phenotypic state. H is negatively correlated with the coefficient of variation in population size. A mutant can be characterized by its effect on r and σ^2 ;

$$\begin{aligned} \Delta &= r^* - r \\ \Delta\sigma^2 &= \sigma^{*2} - \sigma^2, \end{aligned} \quad (6)$$

where $*$ denotes the mutant and the selective advantage of the mutant, s , is given by

$$s = \Delta r - \frac{1}{N} \Delta\sigma^2, \quad (7)$$

where N is the population size. Note that as population size approaches infinity, the selective advantage converges to the Fisherian model. The present analysis takes into an account that populations are of finite size, whereas the usual, unstated, assumption is that the population is very large. Predicted outcomes can be determined given the signs of Δr and $\Delta\sigma^2$ and are shown in table 1.

Environments of fixed length (e.g. deterministic seasonal environments)

An example of this type of environment is a univoltine life cycle in a seasonal environment that shows no interannual

variation. One fitness metric in this instance is the number of offspring produced by a female at the end of the season that survive to reproduce (Roff 1980). If multiple generations are possible, then the fitness criterion becomes the reproductive success of the descendents of a female that originated at the start of the season, passing into the next season of offspring. By adding the mathematical constraints of a cut-off, these definitions can be subsumed under the more general fitness criterion of invasibility, discussed below.

Constant environment, density dependence with a stable equilibrium

This case was studied extensively by Charlesworth (1972), who showed that the focus of selection is the age-group or age-groups in which the density-dependent regulation occurs, called the critical age group: selection will favour the strategy that maximizes the number of individuals in the critical age-group. If the population model is written as a projection matrix, the maximum fitness is given by the dominant Lyapunov exponent (van Dooren and Metz 1998). Metz *et al.* (1992), and later Ferriere and Gatto (1995), asserted that the dominant (also called the leading) Lyapunov exponent is an appropriate general criterion of invasibility. Rand *et al.* (1994) called this parameter the invasion exponent. As this criterion measures the long-term growth rate of a population (Ferriere and Gatto 1995), it relates directly to the Malthusian parameter. At least in the model examined by van Dooren and Metz (1998), an equivalent fitness measure that is easier to calculate is the net reproduction rate (= expected offspring production by a female: see equation error! reference source not found.)

The question of the relationship between equilibrium population size and relative fitness has risen repeatedly commencing with the concept of r -selection and K -selection (see review in Roff 1992). It is clear from the definition of the critical age-group that fitness cannot, in general, be equated to population size, nor would we expect that relative selection pressures could be evaluated from total population size. Caswell *et al.* (2004) explored this problem and produced a general theorem on density-dependent sensitivity in matrix population models:

Table 1. Predicted outcome of a mutant with specified effects on r and σ^2

Δr	$\Delta\sigma^2$	N	Invasion	Extinction
Positive	Negative	Does not matter	Highly likely	
Negative	Positive	Does not matter		Highly likely
Positive	Positive	$> \Delta\sigma^2/\Delta r$	Highly likely	
Positive	Positive	$> \Delta\sigma^2/\Delta r$		Decreasing with N
Negative	Negative	$> \Delta\sigma^2/\Delta r$		Highly likely
Negative	Negative	$> \Delta\sigma^2/\Delta r$	Decreasing with N	

Let $A(\theta, f_1(n), \dots, f_m(n))$ be a density-dependent population projection matrix depending on a parameter θ and on m functions of population density (e.g. m critical age-groups) f_1, \dots, f_m . Let \hat{n} be an equilibrium population vector satisfying $\hat{n} = A(\theta_0, f_1(\hat{n}), \dots, f_m(\hat{n}))\hat{n}$ (thus \hat{n} is a right eigenvector of $A[\theta_0, f_1(\hat{n}) \dots f_m(\hat{n})]$ corresponding to the dominant eigenvalue $\lambda = 1$) and the functions $f_i(n)$ have Taylor series expansions in the neighbourhood of \hat{n} . Now,

$$\left. \frac{\partial \lambda}{\partial \theta} \right|_{\theta_0, \hat{n}} = \frac{\partial g^T \hat{n}}{\partial \theta}, \quad (8)$$

where,

$$g_i = \left(- \sum_{j=1}^m \frac{\partial \lambda}{\partial f_j} \frac{\partial f_j}{\partial n_i} \right) \Big|_{\theta_0, \hat{n}}. \quad (9)$$

This theorem makes clear that the effective equilibrium density \tilde{N} is not the census number but rather a weighted value of a life-stage (e.g. age-group) as determined by its effect on λ (measured by $\partial \lambda / \partial f_i$) and its contribution to the density-dependence (measured by $\partial f_i / \partial n_i$). The elasticity of λ to θ is proportional to the elasticity of \tilde{N} to θ

$$\frac{\theta}{\lambda} \frac{\partial \lambda}{\partial \theta} \Big|_{\theta_0, \hat{n}} = \frac{\theta}{\lambda} \frac{\partial \tilde{N}}{\partial \theta} = \tilde{N} \frac{\theta}{\tilde{N}} \frac{\partial \tilde{N}}{\partial \theta}. \quad (10)$$

Any change that increases λ will increase the effective equilibrium density but not necessarily the total census population. The sensitivity of the invasion exponent to a change in the parameter θ , is given by the elasticity of λ to θ :

$$\frac{1}{\lambda} \frac{\partial \lambda}{\partial \theta} \Big|_{\theta_0, \hat{n}}, \quad (11)$$

from which it is evident that invasion of a mutant will increase the effective equilibrium density and the ESS (evolutionarily stable strategy, which is that strategy that cannot be invaded) will maximize the effective equilibrium density.

As noted earlier, for a homogeneous population at stable equilibrium, r equals zero and the characteristic equation reduces to equation (2) and, thus, ignoring the density-dependent effect, we have the net reproduction rate, R_0 (equation (3)). The use of R_0 as an operational metric of fitness implies a particular definition of the biological scenario, which is often not explicitly acknowledged. In order for R_0 to be an appropriate definition of fitness, either the density-dependence should be selectively neutral or the density-dependence should be neutral with respect to the trait under study. For example, population size might be controlled by density-dependent mortality in the larval stage, while the object of study is the evolution of female age at maturity. In this case, we can examine the relationship between the age at maturity and fitness under the working assumption that genotypes do not differ in the characteristics of their larvae. Since population size is stable, the expected

lifetime fecundity, R_0 , is then the appropriate measure of fitness (Roff 1992, pp. 39). Determination of the optimal life-history using r may give a different answer to that obtained using R_0 (Roff 1992, pp. 183–184; Stearns 1992, pp. 31–33): both answers cannot be right and the correct one (if either is correct) depends upon the population dynamical assumptions. If the population is assumed to be at equilibrium and the above assumption(s) of density-dependence hold, then R_0 is appropriate. On the other hand, if the population is in a growing phase and again the above assumption(s) of density-dependence hold, then r is appropriate. If density-dependence is not selectively neutral then neither metric is appropriate, and the analysis must take the selective effects of the density-dependence into account, as described earlier in this section. For further discussion see Mylius and Diekmann (1995), and Brommer (2000).

Constant environment, variable population dynamics

Even in a constant environment, a population may still show fluctuations as a result of the deterministic properties of the population model. A general and much used example of such a model is the Ricker function:

$$N(t+1) = \lambda N(t) e^{-MN(t)}, \quad (12)$$

where $N(t)$ is the population size at time t , λ is the finite rate of increase at low population numbers and M is a parameter that could be the mortality of juveniles resulting from competition or cannibalism by the parents. Depending on the value of λ , the population is either stable ($1 < \lambda \leq 2$), oscillates with a period of 2^n (where n is a positive integer, the value of n depending on the value of λ , with $e^2 < \lambda < e^{2.6924}$) or displays chaotic fluctuations ($\lambda > e^{2.6924}$).

What we would like to know is whether a mutant can invade such a population, which is generally termed the resident population. To find this out, we consider the situation at the beginning of the process when the mutant is so rare that it cannot have a significant effect on the dynamics of the system. If under these circumstances the mutant can increase in frequency then we presume that it will increase to fixation in the population. Note that this assumption presupposes no frequency-dependence. Nor does it suppose that there is necessarily a unique parameter set that is resistant to invasion by all other mutants (see below for further discussion). We can write the trace for the resident population as,

$$\begin{aligned} N_R(t) &= \lambda_R e^{-M_R N_R(t-1)} N_R(t-1) \\ N_R(t-1) &= \lambda_R e^{-M_R N_R(t-2)} N_R(t-2), \\ N_R(t) &= N_R(0) \lambda_R^t \prod_{x=0}^{t-1} e^{-M_R N_R(x)}, \end{aligned} \quad (13)$$

where the subscript R designates the parameters of the resident population. Taking logarithms yields,

$$\ln N_R - \ln N_R(0) = t \ln \lambda_R - M_R \sum_{x=0}^{t-1} N_R(x). \quad (14)$$

Taking limits then gives,

$$\ln \lambda_R - M_R \frac{\sum_{x=0}^t N_R(x)}{t} = \lim_{t \rightarrow \infty} \frac{1}{t} E [\ln N_R(t) - \ln N_R(0)] \quad (15)$$

which is the dominant Lyapunov exponent, given the symbol s by Ferriere and Gatto (1995). Because a mutant will be in insignificant numbers in the initial invasion, the growth trajectory of a population is given by the growth trajectory of the resident population, i.e. $\sum_{x=0}^t N_R(x)$. Thus, the invasion (Lyapunov) exponent of a mutant, s_m , is given by,

$$s_m = \ln \lambda_m - M_m \frac{\sum_{x=0}^t N_R(x)}{t}, \quad (16)$$

and the condition for the mutant to invade is:

$$\frac{\ln \lambda_m}{M_m} > \frac{\ln \lambda_R}{M_R}. \quad (17)$$

In the above example, it is possible to derive an exact expression for the invasion (Lyapunov) exponent: this will frequently not be the case and numerical methods will have to be employed (Metz *et al.* 1992). Greenman *et al.* (2005) provide an example in which exact solutions can be obtained. Nothing in the above theory precludes the existence of a polymorphism, and indeed the origin of the theory for temporal variation, discussed below, was initiated by the presence of dimorphism for dormancy in plants (Cohen 1966).

Temporally stochastic environments

Environments are rarely, if ever, temporally stable and such variation is likely to be reflected in variation in vital rates. (Cohen 1966) considered the problem of fitness under such circumstances, focussing specifically upon the issue of delayed germination in plants. In general, a population growth rate converges to a fixed quantity, which Tuljapurkar (1982) labelled a to distinguish it from the Malthusian parameter. In a constant environment, a is equivalent to the Malthusian parameter. Population size at some time t can be represented by,

$$\begin{aligned} N(t) &= \lambda(t-1)N(t-1) \\ N(t-1) &= \lambda(t-2)N(t-2) \\ N(t) &= N(0) \prod_{x=0}^t \lambda(x). \end{aligned} \quad (18)$$

Taking logarithms yields,

$$\ln N(t) = \ln N(0) + \sum_{x=0}^t \ln[\lambda(x)]. \quad (19)$$

As noted above, under relatively unrestrictive conditions—namely (i) demographic weak ergodicity, (ii) the random process generating vital rates is stationary and ergodic, and

(iii) the logarithmic moment of vital rates is bounded (Tuljapurkar 1989, see Tuljapurkar 1990 for a definition of demographic weak ergodicity)—the value of $N(t)$ becomes independent of the initial condition, $N(0)$, and the long-run growth rate and, hence, the fitness of a particular life-history is given (Tuljapurkar and Orzack 1980; Caswell 2002) by,

$$\ln \lambda = \lim_{t \rightarrow \infty} \frac{1}{t} E[\ln N(t) - \ln N(0)]. \quad (20)$$

Fitness is measured by the geometric mean of the finite rate of increase, which Tuljapurkar and Orzack (1980) denote by the symbol ' a ' and Tuljapurkar *et al.* (2003) by ' $\ln \lambda_s$ '. In a population without age-structure, the expected value of $\ln \lambda$, is a function of the arithmetic mean finite rate of increase, $\bar{\lambda}$, and its variance, σ_{λ}^2 . Using a Taylor series expansion, and assuming third order moments can be neglected, an approximate formula (Lewontin and Cohen 1969) is:

$$E(\ln \lambda) \approx \ln \bar{\lambda} - \frac{\sigma_{\lambda}^2}{2\bar{\lambda}^2}. \quad (21)$$

The important point is that increases in the variance in the rate of increase—decrease fitness. Thus, selection will favour strategies that both increase the arithmetic rate of increase and decrease its variance. One way in which the latter can be achieved is by producing variation in offspring phenotypes. This concept appears to have been put forward at least three times since 1966. It is implicit in Cohen's (1966) analysis of the optimal germination rate in a randomly varying environment, was explicitly advanced verbally by Den Boer (Den Boer 1968), who referred to it by the term 'spreading the risk', and finally discussed by Gillespie (1974, 1977) in the context of variation in offspring number. Slatkin (1974), in reviewing Gillespie's work, labelled the phenomenon as 'bet-hedging', a term that has stuck. The foregoing arguments apply to populations of infinite size, but we might expect from the analysis of Demetrius and Ziehe (2007) that this fitness measure may break down at low population sizes. Indeed, for a particular scenario in which there is a common and a rare environment King and Masel (2007) showed that bet-hedging would not be favoured when,

$$N < \sqrt{2(s+1)/(s\theta)}, \quad (22)$$

where N is population size, s is the selective advantage associated with switching in the rare environment, and θ is the rate of encountering the rare environment.

With age-structure, the long-term population growth rate in relation to the arithmetic average can be written (Orzack and Tuljapurkar 1989) as,

$$a \approx \ln \lambda - \frac{\mathbf{S}^T \mathbf{V} \mathbf{S}}{2}, \quad (23)$$

where $\ln \lambda$ is the dominant eigenvalue of the average Leslie matrix, \mathbf{S} is a column vector of the sensitivities of λ to a fluctuation in the matrix elements (i.e., $S_{ij} = \delta \ln \lambda / \delta x_{ij}$, where

x_{ij} is the ij element), S^T is its transpose and V is a variance-covariance matrix of the elements (x_{ij}). Equation (23) can be illustrated with a simple two age-class model described by Tuljapurkar (1989). Population change is described by the equation,

$$N(t + 1) = A(t)N(t), \quad (24)$$

where

$$N(t) = \begin{pmatrix} N_1(t) \\ N_2(t) \end{pmatrix} \quad A(t) = \begin{pmatrix} \frac{m_1}{x} & \frac{m_2}{x} \\ S & 0 \end{pmatrix}. \quad (25)$$

Fecundity at age i equals m_i and survival from age class 1 to age class 2 equals S . Uncorrelated temporal variability is described by the parameter x which follows a gamma distribution with probability density function;

$$P(x) = \frac{v^v}{(v-1)!} x^{v-1} e^{-vx}. \quad (26)$$

The parameter v measures the variance, with the variance increasing as v approaches zero, and x approaching 1 as v approaches infinity. If the parameters are fixed at their average values, the ratio $m_2N(t)/m_1N(t)$ converges to a stable value, say R^* . The growth rate of the population is then given by,

$$r = \ln \bar{\lambda} = \ln \left(\left[\frac{m_2 S}{m_1} \right] R^* \right). \quad (27)$$

The long-run average growth rate of the population with temporal variability, a , is approximately

$$a \approx r - \left(\frac{1}{2x\lambda^2 C^2} \right) \left(m_1 + \frac{m_2}{\lambda} \right)^2, \quad (28)$$

where $C = 2 - (m_1 x / [(x-1)\lambda])$. As in the case of (21), the average growth rate is diminished by variability in the vital rates. Thus, it is insufficient to determine the most fit life-history using the growth rate from the averaged values of the life history.

Temporally variable, density-dependent environments

From the proceeding discussions the most appropriate measure of fitness is the invasion exponent. Given the complexity of the interactions, it is likely that analytical solutions will not be typically available and one will have to resort to simulation analysis. Benton and Grant (2000) investigated the reliability of alternate measures of fitness for models in which there was both density-dependence and temporally uncorrelated variation. Four models of density-dependence were investigated: Beverton and Holt-type, Ricker-type, Usher-type with gradual onset of density-dependence, and Usher-type with sudden onset of density-dependence. Beverton and Holt-type models produce a stable equilibrium, whereas the Usher-type with sudden onset of density-dependence generally produce chaotic behaviour. The dynamical behaviour

of the other two depends on parameter values, though Benton and Grant (2000, pp. 773) state that “the vast majority of other combinations of density-dependence. . . resulted in equilibrium dynamics”. Given the predicted differences between models with equilibrium versus nonequilibrium dynamics, it is unfortunate that the analysis did not divide the results both according to the four model types and the two dynamical behaviors. Benton and Grant (2000) considered the following ‘surrogate’ measures of fitness: r , R_0 and a , estimated both with and without density-dependent effects and the average (both arithmetic and geometric) population size, K .

First, Benton and Grant (2000) simulated constant environments and found, as expected, that for the chaotic models none of the fitness criteria performed well. On the other hand, the $DI-R_0$ (density-independent R_0) and K performed well for the Beverton–Holt model, which does not exhibit chaotic behaviour. In a stochastic environment, the best predictor of the invasion exponent was K , although it has to be remembered that the density-dependence in the models was a direct function of total population size. The general message from these analyses is that if the population is expected to show variable dynamics, due to either environmental fluctuation or intrinsic population dynamical properties, and density-dependence is not a consequence of a response to total population number, the only viable measure of fitness is the invasion exponent. In populations showing more or less stable equilibria, the density-independent R_0 appeared to be a reasonable measure, which is reassuring, given the considerable number of analyses based on this fitness measure.

Spatially variable environments

Starting with Levene (1953), there have been a considerable number of population and quantitative genetic analyses of the conditions required for the maintenance of genetic variation (reviewed in Roff 1997). So far as I am aware, these analyses have assumed nonoverlapping generations (i.e. no age-structure). The solution to defining fitness when the environment is spatially variable and there is a stable age-distribution was enunciated independently by Houston and McNamara (1992) and Kawecki and Stearns (1993). The critical realization in deriving the solution was that fitness must be measured over the entire environment simultaneously, and not patch-by-patch. Thus, if we take r as the appropriate fitness measure (meaning that we assume an equilibrium population) the measure that selection will maximize is the rate of growth of the population as a whole,

$$\int P(h) \int V(x, h) e^{-r_{pop} x} dx = 1, \quad (29)$$

where r_{pop} is the rate of growth of the entire population (as opposed to the rates of growth within each patch), $P(h)$ is the probability of patch of type h occurring and $V(x, h)$ is the value of $l(x)m(x)$ for patch of type h . One would expect that in a spatially variable world, a reaction norm would evolve

to modify the life-history patterns in response to the habitat parameters, the evolutionary change obviously being dependent on the presence and predictability of cues that indicate habitat type. Nevertheless, the maximization of fitness within each patch is subject to the constraint imposed by equation (29).

For density-dependent populations in which equilibrium is attained, and for which density-dependence is assumed to be selectively neutral, the appropriate criterion is the net reproduction rate, R , and the fitness criterion becomes,

$$R_{Pop} = \int P(h) \int V(x, h) dx, \quad (30)$$

meaning that selection will favour the life-history that maximizes R for the population as a whole. If density-dependence is not selectively neutral, then the above equation must include those effects.

Social environment

In the environments discussed so far, the relationship between individuals is of no consequence because social interactions are absent. When survival or reproduction depends upon interactions between individuals that might be related, it is necessary to take into account the increment of fitness accruing to the individual by virtue of such interactions. Two particular foci of studies of evolution in a social environment is the evolution of altruistic behaviour (Koenig 1988; Dugatkin and Reeve 1994, 1998; Thorne 1997; Ratnieks and Wenseleers 2008) and explaining the observation of individuals aiding in the rearing of the offspring of other individuals (Koenig *et al.* 1992; Bshary and Bergmueller 2008; Carranza *et al.* 2008).

The overall fitness, inclusive of interactions among relatives, was termed inclusive fitness by Hamilton (1964), though, because of the obscurity of his definition, it was, at least initially, frequently interpreted incorrectly (Grafen 1982). Operationally, inclusive fitness can be defined, or replaced by, Hamilton's rule, which states that organisms are selected to perform actions for which,

$$r^*b - c > 0, \quad (31)$$

where r^* is relatedness, and b , c refer to the effects of an allele on offspring production: bearers of this allele behave in such a manner that each has c fewer offspring, and the bearer's sib has b more offspring (Grafen 1984). Queller (1996) noted that it is phenotypes that interact, not genotypes, and suggested replacing r^* with $\frac{Cov(G_A, P_O)}{Cov(G_A, P_A)}$, where G_A is the genetic value of the 'actor' or focal individual, P_A is its phenotypic value and P_O is the phenotypic value of the average phenotype (for other formulations of the relatedness coefficient, see Pepper 2000). Taylor *et al.* (2006) expanded Hamilton's rule to a class-structured model, while Gardner *et al.* (2007) provide a multilocus version of the rule. Oli (2002) provides a method of estimating inclusive fitness in

an age-structured population using a Leslie matrix formulation. For other modifications of Hamilton's rule that have been advanced to account for such things as nonadditivity of fitnesses, the reader is referred to Fletcher and Zwick (2006).

More generally, b and c in equation (31) are referred to as the benefits and costs, respectively. A potential problem with using Hamilton's rule is in operationally defining these costs and benefits, leading some to attempt to use a more direct definition of inclusive fitness, which in turn has led to discussion over how to correctly calculate this quantity. The issue lies in the verbal description given by Hamilton (1964) that inclusive fitness is the sum of the fitness that would be obtained in the absence of the social environment (e.g. helpers at the nest) and the added increment due to the presence of the social environment. The problem is in calculating the former quantity. Creel (1990) pointed out that a potential paradox can arise if the social environment is essential for successful reproduction, as is almost the case for the dwarf mongoose, *Helogale parvula*. Stripping away the social environment leaves the reproductive individual with zero fitness, all the fitness being attributed to the helpers. Thus, there should be a contest to be helpers and not reproductives, which is clearly not the case and makes no sense genetically. Creel's solution to this paradox was shown by Queller (1996) to be inappropriate, and the solution resides in recognizing that Hamilton's rule applies strictly only when fitnesses are additive, which in the mongoose case they are not. The paradox is removed when nonadditive versions of Hamilton's rule are used (Queller 1996; Pepper 2000; West *et al.* 2002).

Frequency-dependence

A reasonably general definition of frequency-dependent selection is that given by Ayala and Campbell (1974, pp. 116): "The selective value of a genotype is frequency-dependent when its contribution to the following generation relative to alternative genotypes varies with the frequency of the genotype in the population". There are, however, other definitions, which though similar, can be subtly different, or more restrictive in the sense that stable coexistence is required (Heino *et al.* 1998). There is no reason why a stable equilibrium frequency of genotypes should be a requirement of frequency-dependent selection and some very simple games such as 'rock-paper-scissors' which are clearly frequency-dependent do not have a stable equilibrium (Maynard Smith 1998). Most models of frequency-dependent selection assume either competition between clones or Mendelian inheritance with a fixed generation time. In either case, fitness is defined in terms of the contribution of types (genotype or phenotype) to the subsequent generation.

An example of frequency-dependence is the occurrence of two types of males in several fish species, particularly salmon: one type of male is territorial, whereas the other is typically smaller, matures earlier, cannot maintain a territory, and attempts to sneak fertilizations (Gross 1982, 1985;

Hutchings and Myers 1988). The analysis of the equilibrium combination of the two types in the population has used either R_0 (Gross and Charnov 1980) or r (Hutchings and Myers 1994) as the fitness measure. A more frequently used approach is that of game theory in which the relative fitness of each type when interacting either with another of its type or another type is represented by a payoff matrix. The classic example of this approach is the hawk–dove game (Maynard Smith 1982): in this scenario there is a 2×2 payoff matrix indicating the payoff to a hawk when it interacts with either another hawk or a dove, and the payoff to a dove when it interacts with either a hawk or a dove. The game is frequency-dependent because, although a hawk interacting with a dove has a higher fitness than the dove, a hawk interacting with another hawk suffers a decrement in fitness. The equilibrium frequency of hawks and doves in the population depends upon the relative values in the payoff matrix and is called an evolutionarily stable strategy (ESS). It is obtained simply by equating the payoff to hawks with the payoff to doves: at equilibrium the two must be equal. In simple terms, an ESS is one that cannot be invaded by a mutant playing an alternate strategy (see Hammerstein 1998 for a more formal definition).

Recently, game theory and adaptive dynamics have coalesced, with fitness being defined as anything from the per capita rate of increase (i.e. r) to the invasion exponent (McGill and Brown 2007). While frequency-dependence may lead to either the preservation of multiple types in a population or a continuous cycling of types, the definition of fitness does not fundamentally change from what has previously been discussed.

Discussion

To say that fitness is invasibility is tautological: the tautology is eliminated when an operational method of predicting invasibility is given. Fisher (1930) was the first to give a precise mathematical definition of fitness, namely the Malthusian parameter, r . Given a life-table, this parameter is readily estimated and the influence of alterations in trade-offs or life-history components such as the age of first reproduction readily examined. As with any model, the characteristic equation makes certain assumptions regarding the biology and demography of the organism: density-independence, a constant environment, a stable age distribution. Importantly, the genetic mode of transmission does not appear to be important (Lande 1982; Charlesworth 1994). It should come as no surprise that the Malthusian parameter is not the appropriate measure of fitness under other assumptions.

A general, operational definition of fitness is the invasion exponent, of which r and R , two of the most widely used metrics, are special cases. The most appropriate method of calculation will depend upon the set of biological assumptions, though the mathematical definition remains the same. This parameter is suitable except where there is the influence of

the social environment or frequency-dependence. In a social environment, Hamilton's rule, or a suitable extension, can be used to establish fitness. With frequency-dependence, there may be no single optimum and either multiple types may be preserved in a population and/or there may be a cycling of types.

In many cases it may not be possible to mathematically define the invasion exponent. Under such circumstances it will be necessary to turn to a numerical analysis. One approach is to simulate a particular life-history and then examine the ability of an alternate life-history to invade the population, either assuming clonal reproduction or employing a genetic mode of transmission. In these models, the most fit strategy is that which can invade. However, as noted at the beginning of this discussion, such a definition is tautological though one can still define fitness, since this determines the number of any type at any given time (e.g. in a model of fixed generation length, fitness would be the number of descendants at the end of each generation).

While it can be shown theoretically that simple measures of fitness such as R fail under many circumstances, it has yet to be shown that these conditions are so biologically pervasive that the simple metrics should be abandoned. This remains a challenge for both theorists and empiricists.

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