The evolution of fitness in life-history theory

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ABSTRACT

Theory concerning the evolution of life history (the schedule of reproduction and survival) focuses on describing the life history which maximises fitness. Although there is an intuitive link between life history and fitness, there are in fact several measures of the 'black box' concept of fitness. There has been a debate in the bio-mathematical literature on the predictive difference between the two most commonly used measures; intrinsic rate of increase r and net reproductive ratio R_0. Although both measures aim to describe fitness, models using one of the measures may predict the opposite of similar models using the other measure, which is clearly undesirable. Here, I review the evolution of these fitness measures over the last four decades, the predictive differences between these measures and the resulting shift of the fitness concept. I focus in particular on some recent developments, which have solved the dilemma of predictive differences between these fitness measures by explicitly acknowledging the game-theoretical nature of life-history evolution.

Key words: Life-history, fitness optimisation, density dependence, evolutionarily stable strategy (ESS).

CONTENTS

I. INTRODUCTION

Life history is the way an organism spreads its reproduction over its lifetime. It is commonly visualised as a Table with age-specific reproductive and survival rates (Table 1). Clearly, an organism's life history must form an adaptation to the environment it lives in (Bradshaw, 1965; Southwood, 1977). As such, theories on the evolution of life history focus on the notion that life histories observed have a maximal fitness and natural selection prunes away less optimal life histories. However, fitness presents an illusive 'black box'. There is no *a priori* rule on optimality and although the link between life history and fitness is conceptually clear, defining fitness is not intuitively straightforward. Traditionally, several fitness measures have been used. Firstly, the intrinsic rate of increase or the Malthusian parameter $r[=\ln(\lambda)]$, which is given by the Euler-Lotka equation

$$\sum_{x=1}^{\infty} \lambda^{-x} l_x m_x = 1, \qquad (1)$$

where, as in Table 1, l_x is the survival to age x and m_x the fecundity at age x. Here, λ is a demographic description of the growth rate of a population, but it can also be interpreted as the spread of a rare allele in a population (see Charlesworth, 1980, p. 196–7). Nevertheless, the underlying assumption is that the mortality and fecundity (l_x and m_x) schedules remain constant; thus, the environment is assumed to be constant. The population will then converge to a stable age distribution and will grow exponentially at rate r (see e.g. Stearns, 1992, p. 24 for demonstration). Thus, r is the *per capita* instantaneous rate of increase per time unit of a population in stable age distribution.

Another often-used fitness measure is the per generation ratio of multiplication

$$R_0 = \sum_{1}^{\infty} l_x m_x. \qquad (2)$$

This measure can be interpreted as the expected number of daughters that a female produces in her lifetime. Due to its straightforwardness, the measure R_0 has inspired many empirical studies on lifetime reproductive success (Clutton-Brock, 1988; Newton, 1989). In using R_0 as a fitness measure one assumes that variation in generation time makes no selectional difference. An individual can 'take its time' in reproducing, because only the total amount of offspring produced is counted. Earlier reproduction will generally be favoured by an increase in r, but will have a small impact on R_0 (e.g. Table 1); this example concisely illustrates some different properties of these two measures.

Reproductive value (Fisher, 1930) measures the relative contribution of different individuals to population growth and specifically incorporates a discounting effect of λ on reproduction. For discrete generations, reproductive value v of an individual of age z can be denoted as (Caswell, 1989)

$$v_z = \frac{\lambda^{z-1}}{l_z} \sum_{x=z}^{\infty} \lambda^{-x} l_x b_x, \qquad (3)$$

where b_x denotes the effective fecundity (number of

Table 1. *Hypothetical life-history table for two organisms*
(Presented for several age-classes as denoted by x, the survival probability p_x from age x to $x+1$, the fraction l_x of individuals which survive from birth to at least age x and the average number of female offspring m_x produced by a mother while being in ageclass x. Only the reproductive part of the population (most often females) is counted. The population of organism A is growing at rate $r = 0.13$ and has net reproductive ratio $R_0 = 1.4$, whereas organism B has the same r ($= 0.13$), but a lower R_0 ($= 1.17$).)

Organism A					Organism B				
x	p_x	l_x	m_x	$l_x m_x$	x	p_x	l_x	m_x	$l_x m_x$
0	0.55	1	0	0	0	0.32	1	0	0
1	0.43	0.55	0	0	1	0.16	0.32	3	0.96
2	0.27	0.24	4	0.96	2	0.08	0.05	4	0.2
3	0.18	0.065	6	0.39	3	0.02	0.004	3	0.012
4	0.08	0.012	4	0.048	4	0	8×10^{-5}	2	1.6×10^{-4}
5	0	0.001	1	0.001					
		$\Sigma l_x m_x = R_0 =$		1.40			$\Sigma l_x m_x = R_0 =$		1.17

offspring surviving to enter the population the next year, $b_x = m_x p_0$ in Table 1). Offspring production is discounted for the growth or decline of the population as a whole, as measured by λ in equation (3). In a growing population, where $\lambda > 1$, offspring produced earlier in the life of the parent is more valuable. Since the population is smaller at that point, offspring produced early presents a proportionately larger contribution to the population than offspring produced later in the parent's life. When $\lambda < 1$, the reverse holds and offspring produced later in the life of the parent are more valuable. Reproductive value weighs the contribution for population growth of different groups of individuals within a population and is, as such, a relative measure between groups. Usually, reproductive values are defined relative to a newborn's reproductive value (v_1) of 1. This measure of fitness has been used in some empirical studies (e.g. Daan, Dijkstra & Tinbergen, 1990) and is commonly used in verbal arguments on life history. It is also an important concept in many of the models discussed below.

Both R_0 and r are used in many life-history optimisation models, some of which will be discussed here. It has been suggested that the choice of fitness measure is a matter of taste (Kozłowski, 1993). However, these two different fitness measures generate different conclusions when investigating the same problem, which is clearly undesirable. Roff (1992, pp. 183–184) and Stearns (1992, pp. 31–33) accepted that these differences were incorporated in models which aimed to explain variation in life-history traits. They pointed out that one should pay 'considerable attention to the assumptions underlying the analysis' (Roff, 1992, p. 184) and that 'there is room for more work on how changing fitness definitions changes predictions about life-history evolution' (Stearns, 1992, p. 33).

Recently however, this problem of predictive differences between fitness measures has been solved using a conceptual framework, which explicitly recognises life-history evolution as a game-theoretical process (*sensu* Maynard Smith & Price, 1973). One of the main attractions of this evolutionary framework is the general base of the fitness concept. The aim of the present paper is to provide an overview of the increasing refinement of the concept of 'fitness' over the last four decades. As such, it starts by illustrating some relatively simple concepts, which are central to theories on life-history evolution, by examples from the literature.

The development of a common evolutionary framework is an important contribution to life-history theory, not only because a seemingly accepted problem in life-history theory has been solved, but perhaps mostly as a canalisation in visualising evolution.

II. SOLVING COLE'S PARADOX WITH REPRODUCTIVE EFFORT

This section deals with the 'roots' of the interest in life-history problems. I will focus on both Cole's (1954) and Williams' (1966) papers, which are amongst the most influential papers in life-history theory. Cole's (1954) paper is often considered the starting point of a long tradition in considering life-history problems, although this view diminishes the work of Fisher (1930). Williams's (1966) paper has influenced both theoretical and empirical inquiries by introducing the concept of reproductive effort and by partitioning reproductive value. The symbols used in reviewing the theory are summarised in Table 2.

(1) Cole's paradox

Cole's (1954) paper can be seen as the starting point for the interest in the *per capita* growth rate r as a measure of fitness. Cole demonstrated the sensitivity of r to changes in demographic parameters such as age at first reproduction. Furthermore, Cole described the relationship between the reproductive strategies of an annual and a perennial species, for which he coined the terms semelparous (reproduction occurring all at once) and iteroparous (spreading the reproduction over several seasons).

Cole used a structurally simple model, where there was no age structure, unlike the definitions of r and R_0 given in the introduction here. Furthermore, his model did not include any mortality and various authors (e.g. Gadgil & Bossert, 1970; Bryant, 1971) have criticised this lack of realism and have since extended Cole's model. Charnov & Schaffer (1973) introduced both juvenile survival j and adult survival p and calculated the rate of increase of an annual λ_a ($\lambda = e^r$) as

$$\lambda_a = \frac{N(t+1)}{N(t)} = m_a j, \tag{4}$$

with $N(t)$ the number of individuals that reproduce

Table 2. *Symbols used in the text. Some symbols are combined using a subscript, which specifies the variable, e.g.* m_x *is the reproduction in age class* x *(see also Table 1)*

Symbol	Use
a	% of resources allocated into reproduction (reproductive effort).
b	Effective fecundity.
E	Parameter categorising the environment.
$\mathbf{E}$	Vector denoting the stage-specific environmental conditions.
j	Juvenile survival.
K	Carrying capacity.
k	Environmentally determined individual growth rate.
$\mathbf{L}$	Projection matrix.
l_x	The probability to survive to age x, $\left(= \prod_{i=0}^{x-1} p_i \right)$.
m	The average number of same sex offspring produced.
$\mathcal{N}$	Population size.
$\mathbf{N}$	Stage-structured population vector.
$\check{\mathcal{N}}$	Equilibrium population size.
p	Adult survival.
$\check{p}$	Extrinsic survival probability, independent of effort and density.
$\hat{p}$	Intrinsic survival probability, dependent on effort and density.
R_0	Net reproductive ratio (fitness measure).
r	Intrinsic rate of increase, $= \ln (\lambda)$ (fitness measure).
r_g	Global rate of increase of a heterogenous population as a whole.
r_l	Local rate of increase of a sub-population in a heterogenous population.
rv	Residual reproductive value.
s	Size.
t	Time.
T	Type of a trait under study (possibly multi-dimensional).
v	Reproductive value.
$\mathbf{X}, \mathbf{Y}$	Vector composed of the traits under study.
x, y, z	Age class.
α	Age at first reproduction.
β	Proportional increase in φ due to a certain action.
γ	Proportional decrease in φ due to a certain action.
δ	Fraction of a population in a habitat patch dispersing to other habitat patch(es).
κ	Costs in terms of a proportional decrease in rv due to a certain action.
$\tilde{\kappa}$	Barely justified costs, when positive change in v equals the negative change.
Λ	Dominant Lyapunov exponent.
λ	Intrinsic rate of increase, $= e^{-r}$ (fitness measure).
$\Lambda_{\mathbf{X}}(\mathbf{Y})$	Lyapunov exponent of invasion by $\mathbf{Y}$ in a population with trait(s) $\mathbf{X}$.
φ	Reproductive value currently at stake.
ω	Last stage class, e.g. age.

at time t and m_a the reproduction of an annual. Likewise, for a perennial

$$\lambda_p = \frac{\mathcal{N}(t)m_p j + \mathcal{N}(t)p}{\mathcal{N}(t)} = m_p j + p. \qquad (5)$$

The perennial and annual reproductive modes are equivalent in terms of the fitness measure λ when

$$\lambda_a = \lambda_p, \quad \text{if, and only if}$$
$$m_a j = m_p j + p. \qquad (6)$$

The annual thus has to achieve an increase of p/j in fecundity when changing to perennial reproductive mode. The dilemma raised by Cole's work was to explain why perennial species evolved, if 'the advantage gained by going from annual to perennial reproduction should be *less than or equal* to adding one individual to the effective litter size in an annual species' (Bryant, 1971, p. 76); this statement refers to the adult survival probability p in equation (6), since $0 \leqslant p \leqslant 1$.
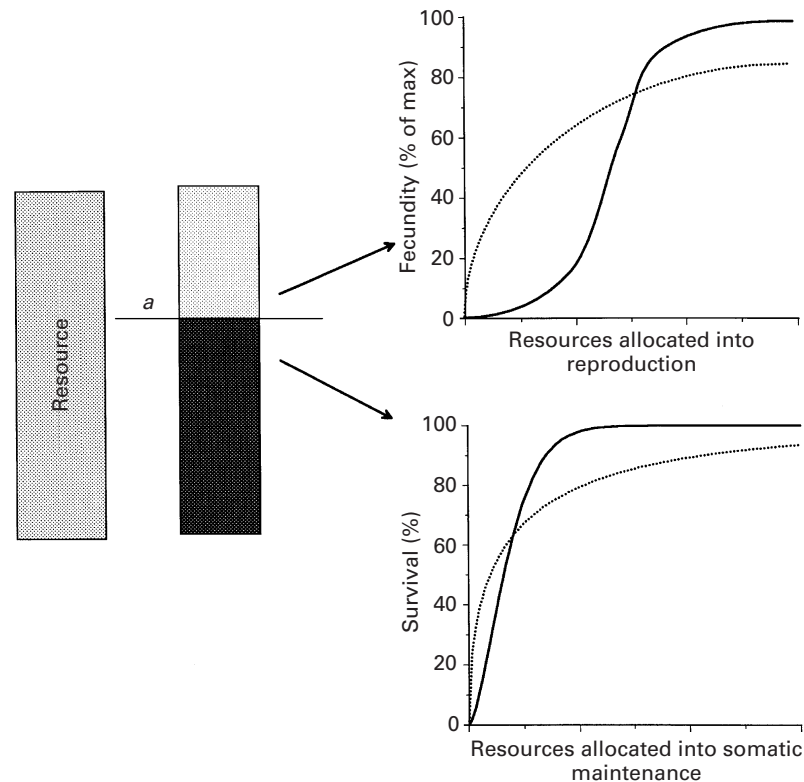
Fig. 1. Schematic representation of a possible intra-individual trade-off mediated by reproductive effort. An organism has a certain amount of resources and allocates a proportion a of this into reproduction, which is also termed the reproductive effort. Increasing reproductive effort will increase the amount of resources put into reproduction (grey area). Nevertheless, the amount of resource is finite and increasing reproductive effort will thus decrease the amount of resource remaining for the individual's own somatic maintenance (dark area), which may affect the individual's own survival. The realised fecundity and survival may depend (in various non-linear ways) on the amount of resources which are allocated into each fitness component. See also Fig. 2.

Intuitively, one understands that the challenge for a semelparous species is to replace itself and leave as many offspring as the iteroparous species. If juvenile survival is low, then only a high increase in fecundity can accomplish this. Charnov & Schaffer's (1973) result implies that semelparous species should always have a higher fecundity than iteroparous species, as $m_a > m_p$ when $p/j > 0$. Stearns (1992, p. 190) quoted several studies that have shown this both within species and between species.

(2) Models based on reproductive effort: Williams's approach

Cole's (1954) division into the two opposing life-history tactics, semelparity versus iteroparity, requested an explanation as to how an organism then should divide its reproduction over its lifetime. The extreme strategies are one 'bang' reproduction followed by death in contrast to a more balanced spread of reproduction over more seasons. This means that one has to incorporate an age-structure in order to study an optimal 'spread' of an organism's reproduction during its lifetime.

Williams (1966) put forward the idea of costs and benefits (Williams used interest) of the 'expenditures on reproductive processes' (p. 687). Central to Williams's approach is the concept of a trade-off, resulting from differential allocation of available energy between components of fitness. As each unit of available energy can be spent only once, increased allocation to one component of fitness implies allocating energy away from another component. This concept makes it possible to find the optimal life history over different ages, when cost and benefits of allocating energy into the fitness components are balanced against each other.

Williams used the Fisherian reproductive value [v; equation (3)] as the currency in the trade-off. He thereby distinguished between two types of action. One with a 'positive response', giving an increase of β in the reproductive value that is 'immediately at stake' (φ). This is coupled to a cost κ, measured for

the *remaining* reproductive value $(v - \varphi)$, which Williams called residual reproductive value (rv). Thus,

$$positive\ response = (1 + \beta)\,\varphi + (1 - \kappa)\,rv. \quad (7)$$

Secondly, there is a negative response that causes no decrease in residual reproductive value, only a decrease of γ in φ. Thus,

$$negative\ response = (1 - \gamma)\,\varphi + rv. \quad (8)$$

If the positive change in reproductive value equals the negative change, the 'barely justified' cost $\hat{\kappa}$ equals

$$\hat{\kappa} = \frac{(\beta + \gamma)\,\varphi}{rv}. \quad (9)$$

Thus, costs have to be justified not only in terms of their net gain in φ, the reproductive value at stake, but also in terms of the proportion between φ and the residual reproductive value rv. However, most authors (e.g. Lessels, 1991; Stearns, 1992; but see Pásztor & Loeschke, 1989), have interpreted equation (7) as the case where φ represents the total value of the current breeding season, so-called current reproductive value as opposed to residual reproductive value. Williams considered this a 'special case' (p. 689) and led the way by speculating how it could be tested. Interestingly, however, Williams originally formulated equations (7) and (8) on micro-scale decisions (e.g. do I forage one more time before going to sleep?)

Williams (1966) partitioned reproductive value into a change in current reproductive value and a change in future reproductive value and suggested that natural selection would mould species such that the sum of both current and future change is maximised. The key point lies in realising that such fitness components as reproduction and survival, which make up an individual's life history, are not fixed values as in Cole's approach. Instead, these fitness components are dependent on each other and a trade-off situation underlies them. For example, an iteroparous species can allocate a certain amount of energy to its reproduction each year, using the rest for its own somatic maintenance. If the degree of somatic maintenance affects the parent's survival, there will be a trade-off between reproduction and survival (Fig. 1). The fraction of available energy used for reproduction is referred to as reproductive effort.

(3) The equivalence of maximising fitness to maximising reproductive value

After its formulation by Fisher (1930), reproductive value has been an important concept in life-history theory. Many empirical researchers have argued in terms of reproductive value when discussing optimality of a specific life history (e.g. Daan *et al.* 1990; Tinbergen & Daan, 1990). The popularity of reproductive value is based on the equivalence of maximising fitness, as measured by r, to maximising reproductive value (Schaffer, 1974).

Reproductive value can be used as a powerful visualisation of the essence of life-history optimisation. This is best illustrated by Schaffer's (1974) pioneering analysis of life-history optimisation in age-structured populations. Schaffer (1974) specifically addressed the question of age and reproductive effort in populations with indeterminate growth. For simplicity, I will here exclude growth as a factor, as the argumentation follows similar logic.

Firstly, one assumes that the effective fecundity at age x, b_x, is both dependent on the allocation into reproduction (reproductive effort) made at age x, a_x, and the allocations made previously, but does not depend on future reproductive effort. Effective fecundity b_x therefore corresponds to the number of offspring that actually enter the reproductive population the following year and is equivalent to $m_x p_0$ according to the definitions of Table 1. Similarly, the survival to age class x, l_x, depends on all the reproductive efforts prior to age x. Thus,

$$b_x = b_x(a_1, a_2, \ldots, a_x) \qquad x = 1, 2, \ldots ; \quad (10)$$

$$l_x = l_x(a_1, a_2, \ldots, a_{x-1}) \quad x = 1, 2, \ldots .$$

For a population with a stable age composition, the Euler-Lotka equation (1) is

$$1 = b_1/\lambda + b_2 p_1/\lambda^2 + b_3 p_1 p_2/\lambda^3 + \ldots ,$$

and

$$\lambda = b_1 + p_1(b_2/\lambda + b_3 p_2/\lambda^2 + \ldots). \quad (11)$$

The term between brackets denotes the reproductive value of a two-year-old, v_2. Thus

$$\lambda = b_1 + p_1 v_2. \quad (12)$$

Because the reproductive effort of a newborn a_1 underlies b_1 and p_1 as the outcome of the trade-off between reproduction and survival [equation (10), Fig. 1], the a_1 which maximises the right-hand term
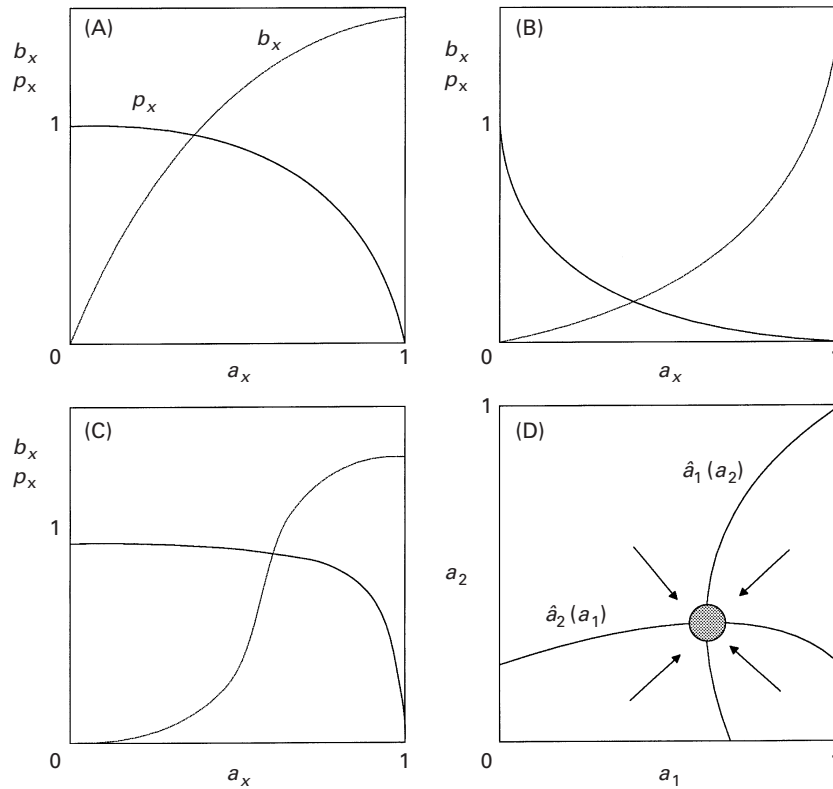
Fig. 2. Diagrams showing some possible relationships between allocation (a_x), survival (p_x) and reproduction (b_x). Possible relations of survival and reproduction with higher allocation, are in (A) decreasing marginal returns for fecundity and increasing marginal returns in survival (concave up) and the reverse in (B) with increasing marginal returns for fecundity and decreasing marginal returns for survival (concave down). In (C), survival shows decreasing marginal returns, whereas reproduction increases non-linearly (sigmoidal) to a physiological maximum in allocation. Shown in (D) is a stability analysis (see text for details) for optimal reproductive effort for the situation sketched in (A) for a life history with three age classes; the population converges to an optimal reproductive effort (a_1^*, a_2^*) where $0 < a_x^* < 1$ (iteroparity). Similar analyses for (B) show that $a_x^* = 0$ or $a_x^* = 1$ (semelparity) and for (C) that $a_x^* = 0$ or $a_x^* = 1$ or $0 < a_x^* < 1$. Figures drawn after Schaffer (1974).

of equation (12) also maximises λ. For any age class x, Schaffer (1974) showed that

$$\max\{b_x + p_x v_{x+1}\} = \max\{\lambda\}. \qquad (13)$$

Here, fecundity b_x and survival p_x are subjected to a trade-off and the precise relationship is specified by the assumed shape of their dependence on reproductive effort (Fig. 1). Schaffer (1974) considered analytical optimisation of a life history with three age classes. As the life history is truncated, there is no residual reproductive value for the last age class and the effort in the last age class a_3 simply maximises b_3 and is thus in this case independent of the effort made at other ages. The optimality of the effort in the first two age classes can then be examined in a two-dimensional (a_1, a_2) plane (Fig. 2D) by specifying the relationship between a_1 and a_2. As an example, consider fertility b_x and survival p_x as concave functions of effort (Fig. 2A). For the effort made at the first two age classes, reproductive effort

at one age class affects the optimality (in terms of the fitness measure λ) of the effort made at the other age; the optimal life history has to evolve as a package. The maximum of the bracketed expression on the left-hand side of equation (13) is attained by setting its first-order derivative to zero [i.e. $d(b_x + p_x v_{x+1})/da_x = 0$]. Thus, for age class 1 and 2,

$$\frac{db_1}{da_1} = -\frac{d(v_2 p_1)}{da_1} \qquad (14)$$

$$\frac{db_2}{da_2} = -\frac{d(v_3 p_2)}{da_2}$$

To find the allocation values (a_1^*, a_2^*) that satisfy equation (13), consider a_1 as a function of a_2, written as $\hat{a}_1(a_2)$ and *vice versa*. Equation (14) can then be used to specify the shape of these functions and the stability of the optimal reproductive effort values

(a_1^*, a_2^*). Any deviation from a_2^* reduces the reproductive value v_2 and thus $\hat{a}_1(a_2)$ will increase. Likewise, $\hat{a}_2(a_1)$ will decrease with a perturbation from a_1^*, as this will decrease the value of λ and hence increase v_3, since the reproduction b_3 is then discounted for with a lower λ (see Fig. 2D).

An organism thus has a series of choices and can be considered as trying to maximise equation (13) each year, thereby balancing the cost of breeding at age x with the subsequent reproductive success (of next year), as incorporated in the residual reproductive value; a similar conclusion was reached by Goodman (1974). Schaffer (1974) also showed that equation (13) is equivalent to maximising an organism's current reproductive value v_x. A simple proof for this as suggested by Goodman (quoted in Gleeson, 1987) is to rewrite the Euler-Lotka equation [equation (1)] using the formula for reproductive value [equation (3)] to obtain

$$1 = \sum_{x=1}^{z-1} \lambda^{-x} l_x m_x + \frac{l_z}{p_0 \lambda^{(z-1)}} v_z. \qquad (15)$$

For a set of life histories identical to age z only λ and v_z are free to vary; they must vary in the same direction to maintain identity. Therefore, the life history with the highest λ will have the highest reproductive value v_z at each age z.

(4) Models of reproductive effort: extension of Williams

Schaffer (1974) developed an analytical model for three age classes and studied the effect between growth, fertility and survival on life history, using graphical representations of fertility and survival as functions of reproductive effort (Fig. 2). If these functions are concave (Fig. 2A) then the organism in question would be iteroparous; if they are convex (concave down, Fig. 2B) then semelparity should take place. However, Schaffer (1974) also noted that there may be 'alternative reproductive strategies' that are evolutionary stable, when these gain curves are less regular and have several bumps. Schaffer & Rosenzweig (1977) suggested that these multiple equilibria in the life history may apply to related species with different life histories that were 'trapped' on different adaptive peaks.

Pianka & Parker (1975) concluded similarly that iteroparity makes sense when the allocation functions are concave functions of reproductive effort. Following Williams (1966), Pianka & Parker (1975) argued that there is a trade-off between an
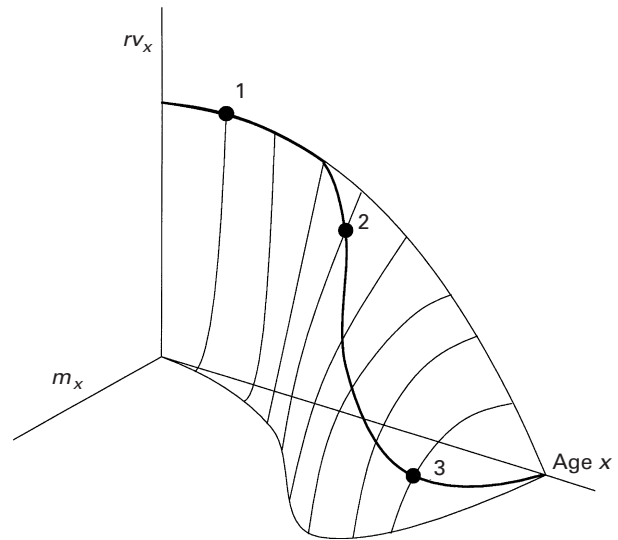

Fig. 3. Schematic representation of the three-dimensional relationship between age x, current fecundity m_x and residual reproductive value (rv_x). The thick line shows the life history that maximises the reproductive value $v_x = m_x + p_x v_{x+1} = m_x + rv_x$, where p_x is survival probability. The curves that delineate the three-dimensional body correspond to the situations drawn in Fig. 1; point 1 selects for postponing reproduction (concave down, Fig. 1B), whereas optimisation allows sub-maximal reproduction in points 2 and 3 (concave up, Fig. 1A). Figure drawn after Pianka & Parker (1975).

organism's residual reproductive value (rv_x) and its reproduction at age x (m_x). There is then a three-dimensional relation between the possible current reproduction of a species at age x, and the effect of that reproduction on its residual reproductive value. The life history of a species can thus be visualised by the trajectory of its life history through a three-dimensional body describing this relationship (Fig. 3). Intersection of this body at different ages can give a convex or concave relation. This can then be used to describe the age-specific reproduction for a species (as in Fig. 2).

Pianka & Parker (1975) and Hirschfield & Tinkle (1975) were among the first to specifically point out the consequences of individual variation on the life-history patterns observed. In terms of Fig. 3, this individual variation could be reflected in different relationships between individuals; for example, the trajectory of mortality with age is probably not the same for each individual. Pianka & Parker (1975) postulated that individuals should allocate their resources in response to the consequences this has for their residual reproductive value (Fig. 3). The problem with testing this notion lies in the difficulty of describing the relationship between age, possible

current reproduction and subsequent residual reproductive value for any species. Physiologically, an organism may be able to produce any amount of offspring that ranges from none to a certain maximum. Associated with producing a certain amount of offspring are, as in equations (6) and (7), both positive and negative consequences in terms of parental fitness (Fig. 3). For verification of such a balancing of costs and benefits, one cannot study natural variation in current reproduction, because this does not measure the possible reproduction of an individual. Experiments have therefore focused on the manipulation of offspring number in groups of individuals producing the same amount of offspring to test the optimality of a clutch produced with respect to the residual reproductive value. In terms of Fig. 3, one thus creates (artificial) variation along the m_x axis. In birds, it has been shown that costs are paid in terms of residual reproductive value, due to either a decrease in future reproduction (e.g. Gustafsson & Sutherland, 1988) or a decrease in survival (e.g. Daan, Deerenberg & Dijkstra, 1996), although this does not always hold (for review see Lessels, 1991).

III. REPRODUCTIVE EFFORT AND DENSITY DEPENDENCE

(1) The ESS concept

Charlesworth & Léon (1976) and Charlesworth (1980) incorporated the notion of an evolutionarily stable strategy (ESS; Maynard Smith & Price, 1973; Maynard Smith, 1982) in fitness maximisation. A population is at an ESS with respect to some phenotype (or set of phenotypes) when the introduction of a rare mutant type with a different phenotype only leads to elimination of that (mutant) phenotype. Charlesworth & Léon (1976) interpreted the ESS logic as a maximisation of a fitness measure (r or R_0); the maximum in the fitness measure with respect to the trait under investigation should therefore represent an ESS, since alternative life histories present a decrease in the chosen fitness measure, and hence are selected against. Charlesworth & Léon (1976) extended Schaffer's (1974) model and discussed the optimal reproductive effort as the trait under investigation in both density-independent and density-dependent populations that were structured in age classes. For density-independent populations they assumed that r was maximised, while for density-dependent populations R_0 was maximised. They assumed that survival in

age class x, p_x and its fertility b_x are functions of both population density N and allocation made at age x, a_x. Between different genotypes only the parameters of this functional dependence differ. Thus, $p_x = p_x(N, a_x)$ and $b_x = b_x(N, a_x)$. For a fixed value of N, p_x is a concave, decreasing function of a_x, whereas b_x is increasing (similar reasoning as in section II.3, Fig. 2A). In a density-dependent population where all members possess the same life-history parameters, the population equilibrium density $\check{N}$ is given by

$$R_0(\check{N}) = \sum_{x=0}^{\omega} l_x(\check{N}) \, b_x(\check{N}) = 1, \qquad (16)$$

where ω denotes the last age class.

Since b_x is an increasing function of a_x, one can dispense with a_x and express p_x as a function of b_x for mathematical convenience. The maximum in R_0 is then given by the first- and second-order partial derivatives of R_0 with respect to b_x only, since we are concerned with comparing individuals (the ESS argument works at the individual level). Thus,

$$\frac{\partial R_0}{\partial b_x} = 1 + \frac{\partial p_x}{\partial b_x} v_{x+1} = 0, \qquad (17a)$$

$$\frac{\partial^2 R_0}{\partial b_x^2} = \frac{\partial^2 p_x}{\partial b_x^2} v_{x+1} < 0, \qquad (17b)$$

$$\frac{\partial^2 R_0}{\partial b_x \partial b_y} = 0, x \neq y, \qquad (17c)$$

where v_{x+1} is the reproductive value at age $x+1$. By setting the first partial derivative to zero [equation (17a)], one obtains the conditions for the extreme values (both minimal and maximal) of R_0 with respect to b_x. The maximum is then further specified by setting the second-order partial derivative smaller than zero [equation (17b)]. The last condition specifies that changes in reproductive output b_y at any age y other than age x should not cause a change in R_0 with respect to b_x; thus, reproductive effort in any age class should only affect the reproduction in that age class and not in another age class. This is the mathematical convenience of using R_0 instead of λ (compare with section II.3, equation (13)).

Charlesworth & Léon (1976) were the first to note the importance of density dependence when they stated that the conclusions 'depend on the precise model of population regulation which is envisaged' (p. 454). They further distinguished between two types of density dependence affecting either each age class equally or only the juvenile age class(es). Density dependence in all age classes would select for a decrease of effort with age. However, if density dependence acted on the juvenile age class(es), the

opposite would be selected for, i.e. an increase in reproductive effort with age.

Charlesworth (1980, p. 232) noted that for completeness, all life histories corresponding to local maxima should be enumerated, not just the global maximum and that, strictly speaking, the ESS analysis ought to be conducted by calculating the survival probabilities of mutant genes in the population. However, the approach of Charlesworth & Léon (1976) was still based on total maximisation of r. R_0 was set at 1 for the density-dependent models [equation (16)], but no specification was made for r, although it is implicit in the use of equation (17) that r is constant, because otherwise the reproductive values could not be treated as constants. The underlying view was that r describes the rate at which a rare gene spreads in a population and a mutant with a less than maximal r will be selected against. Hence, for a life history to be evolutionary stable, any perturbation of the life-history parameters will cause a decrease in r (Taylor, Gourley & Lawrence, 1974).

(2) Density dependence

One shortcoming of the modelling approach of Charlesworth & Léon (1976) is that in density-dependent populations, the fitness measure R_0 is assumed to depend only on the trait under investigation, the reproductive effort. Michod (1979) provided an important extension of this model, where he used the framework provided in section III.1, but noted explicitly the separate effect of both reproductive effort and density in determining R_0. Mutants with allocation strategy a_{mut} must be at a selective disadvantage compared to the evolutionarily stable strategy a^*. Since a mutant is rare with respect to the population as a whole, Michod (1979) assumed that the impact of the mutant on the density-dependent regulation of the population was negligible. In the context of equations (15) and (16), the ESS can thus be specified as

$$R_0(a_{mut}, \check{N}) < R_0(a^*, \check{N}) = 1 \qquad (18)$$

where the equilibrium density of the predominant population $\check{N}$ is affecting the mutant with reproductive effort a_{mut} and in the ESS, any mutant's growth rate $R_0(a_{mut}, \check{N})$, is lower than the growth rate of the predominant population [equations (18)]. Michod (1979) derived a general description for the change in life history relative to the change in extrinsic survival probability (e.g. a change in predation) in a certain age class. The probability of

surviving in age class x is given by $p_x(a_x, N) = \check{p}_x \hat{p}_x(a_x, N)$, where $\check{p}_x$ denotes the extrinsic survival which is independent of allocation and density and $\hat{p}_x$ the survival probability resulting from the allocation and density. Michod (1979) obtained general expressions for the change in the b_x^* and $\check{N}$ relative to the change in extrinsic survival probability in a certain age class [$db_x^*/d\check{p}_x$ and $d\check{N}/d\check{p}_x$]. He immediately noted that $d\check{N}/d\check{p}_x > 0$, which means that a decrease in external survival probability in age-class x will also result in a decrease in the population equilibrium density. Hence, changes in life history (in this case, externally caused mortality) are coupled to density effects within the population as a whole. These results underline that optimisation of a life history only with respect to a single trait while completely ignoring density dependence may be a rather limited approach.

IV. PREDICTIVE DIFFERENCES BETWEEN r AND R_0

(1) Individual optimisation using r as the fitness measure

Stearns & Koella (1986) shifted the focus in life history away from the reproductive effort concept and drew attention to the interaction between individual life-history traits and the environment. They argued that much of the variation in life-history traits was phenotypically plastic (as opposed to genetically determined). A trait is said to be phenotypically plastic if genetically identical organisms can produce different phenotypic responses in different environments. For example, in plants, clones of one individual may produce very different structural types when grown in different environments (e.g. Bradshaw, 1965). Similar reasoning applies to life-history traits as, for example, offspring production or size at maturity. Such phenotypic plasticity is adaptive when producing a certain phenotypic response under a certain environmental condition gives a fitness advantage. There is then a set of optimal solutions over a range of environmental conditions whereby an individual's fitness is maximised. Such a set of optimal actions is called a reaction norm (Woltereck, 1909; Bradshaw, 1965; Stearns 1976).

Stearns & Koella (1986) considered an organism with a size-fecundity relation where age and size are related due to growth. The dilemma such an organism faces is at what age to mature, given a certain environmentally determined growth rate.

good environment

poor environment

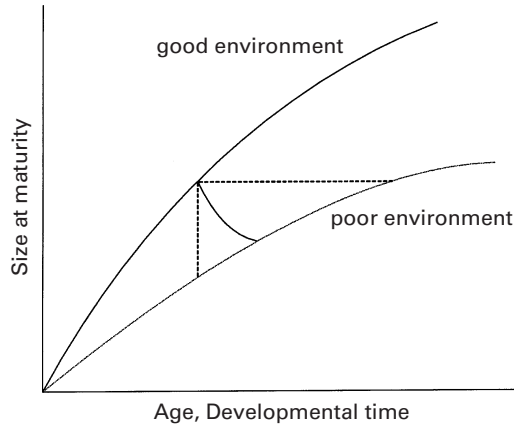Size at maturity

Age, Developmental time

Fig. 4. The dilemma of maturation with respect to age and size in two qualitatively different environments, characterised by, for example, growth rate. Three possible tactics are displayed. Always mature at the same age (dashed vertical line) will lead to a smaller size at maturity in poorer environments, which may be detrimental, e.g. in terms of fecundity. Always mature at the same size (horizontal dashed line), however, will only allow maturation at a later age in the poorer environment, which may also be detrimental, e.g. in terms of the remaining lifespan. The reaction norm (solid curve) describes the optimal action (age and size at maturity) over a range of environments. Drawn after Stearns (1992).

What should be the norm of reaction in age at maturity as a function of growth rate along an environmental axis (Fig. 4)? Clearly, by maturing at a fixed age, the size at maturation will be smaller for slower growth and thus the fecundity will be less. Maturing at a fixed size will take a longer time in environments with slower growth rates, resulting in a higher risk of mortality or will result in much shorter remaining reproductive lifespan.

Assuming an organism in a single, stationary population, Stearns & Koella (1986) described the reaction norm for age at maturity to a change in the organism's environment. When x denotes age, s the size of the individual, α the age at first reproduction and the fecundity m can be written for each environment, which is specified by the growth rate k, as

$$m(x, k) = 0 \quad for \ x < \alpha, \qquad (19a)$$

since there is, by definition, no reproduction before the age at first reproduction. After the start of reproduction, fecundity is determined by an individual's size, which depends on both its age and the environment, such that

$$m(x, k) = m[s(x, k)] \quad for \ x \geqslant \alpha. \qquad (19b)$$

(after Stearns, 1992). The mortality $l(\alpha, x, k)$ is then dependent on juvenile mortality j before an individual starts reproducing and adult mortality p for a reproducing individual and is assumed to be exponentially decreasing.

$$l(\alpha, x, k) = e^{-j(\alpha,k)x} \quad for \ x < \alpha, \qquad (20)$$
$$= e^{-j(\alpha,k)\alpha} e^{-p(k)(x-\alpha)} \quad for \ x \geqslant \alpha.$$

The Euler–Lotka equation is then

$$\int_{\alpha}^{\omega} m(x, k) \cdot l(\alpha, x, k) \, e^{-rx} dx = 1, \qquad (21)$$

which is equivalent to equation (1), but formulated in continuous time. Stearns & Koella (1986) used the maximisation principle, discussed in section III.1 and given by equation (17), in this case $\partial r / \partial \alpha = 0$ and $\partial^2 r / \partial \alpha^2 < 0$, to find the values of r that satisfy these conditions and equation (21). This results in a mathematical description of the age/size for which it is optimal to mature, given a certain environment (Fig. 4).

(2) Reaction norms using R_0 as the fitness measure

The approaches of Kozłowski & Wiegert (1987) and Kozłowski & Uchmanski (1987) are similar to the approach sketched in the previous section. The main difference is their use of R_0 as the fitness quantity to be maximised, which conforms with the assumptions that population growth has no influence on fitness (see Introduction). I will here briefly discuss the ideas of Kozłowski & Wiegert (1987) and Kozłowski (1992), based on a graphical representation (Fig. 5).

There exists a trade-off between growth and reproduction. An organism will therefore grow until it reaches a certain age and size at which point it will start reproducing with a fixed fecundity. The size of the organism and thus the fecundity it achieves will depend on the timing of maturation and there is therefore a non-linear increase in potential fecundity with age (Fig. 5). On the other hand, survival decreases non-linearly with age but is independent of reproduction. Fitness, as measured by R_0, can be calculated as $R_0 = \int_{\alpha}^{\omega} m(\alpha) \, l(x) \, dx$, which is equivalent to equation (2), but formulated in continuous time. Graphically, R_0 is represented by the volume of the solid in Fig. 5 and is affected by varying the age of first reproduction (x_1, x_2 and x_3 in Fig. 5).

In a similar fashion to equations (19) and (20), one can specify a function for how the environment
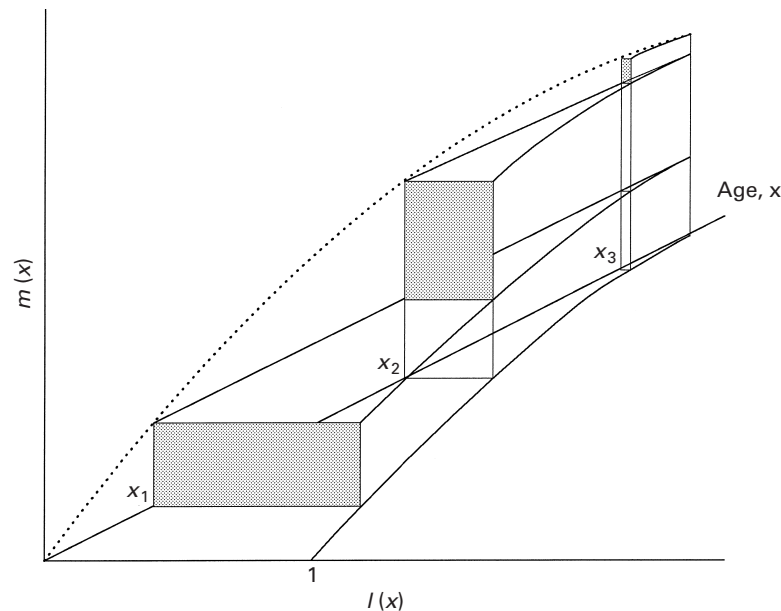
Fig. 5. Graphical representation of the dilemma of age at maturation. The age-dependent survival $[l(x)]$, decreases monotonically with age. The solid line in the $[m(x), x]$ plane depicts the potential fecundity which depends on the age (or likewise, size) at maturation. Thus, fitness R_0 can be described as a three-dimensional solid $\int m(\alpha) \, l(x) \, dx$, defined by these dimensions and where α is the age at first reproduction. Shown in the figure are several intersections, representing different ages at maturation (x_1, x_2 and x_3) and the fitnessvolumes resulting from these. Clearly, early maturation, in this case, gives a higher fitness (larger volume). Figure drawn after Kozłowski (1992).

underlies the fecundity and survival functions. Kozłowski (1992) discussed several alternative models that can be incorporated in this scenario. The optimal age/size at first reproduction α^* is given by maximising the fitness measure, thus $dR_0/d\alpha^* = 0$. This results in a curve connecting the points at which the organism should switch from growing to reproducing, depending on the environment. This so-called switching curve describes the reaction norm for a population as a function of the assumed relationships between growth and fecundity.

(3) Differences in model predictions using r and R_0; the problem

The models used by Kozłowski & Wiegert (1987) and by Stearns & Koella (1986) essentially studied the same question. They also tried to solve the same question (optimal age/size at first reproduction) with a similar approach. Nevertheless, there are different predictions, which are due to the maximisation of different fitness measures, r versus R_0. Stearns (1992, p. 148) noted that when using r, age at maturity is delayed when the environmental growth rate is decreased; if using R_0, age at maturity

is delayed when the growth rate is increased. Kozłowski (1993) noted that the predictions also differed between the models when there was a change in juvenile survival rate; the optimum was not affected when R_0 was maximised, but was affected when r was used.

Roff (1992, pp. 183–184) presented an example which clearly showed the predictive difference between these two fitness measures. Roff then argued that the choice of which fitness measure to use should be made with considerable attention to the underlying assumptions. I will give Roff's (1992) example here, as also discussed by Pásztor, Meszéna & Kisdi (1996). Consider a semelparous organism that produces offspring at age α, after which it dies. The fecundity is then given by $m(\alpha)$. The probability of mortality through birth j is instantaneous, after which the mortality rate is p. Thus, survival to α is an exponentially decreasing function $[l_\alpha = je^{-p\alpha}]$. Furthermore, in this simplified example, there is no environmental variation incorporated, as in sections IV.1 and IV.2. For such an organism, it follows [see also equations (1) and (2)] that

$$r = \frac{\ln[m(\alpha) je^{-p\alpha}]}{\alpha} = \frac{\ln m(\alpha) + \ln j}{\alpha} - p, \quad (22a)$$

$$R_0 = m(\alpha) je^{-p\alpha}. \quad (22b)$$

Under the assumption that r, or R_0 is the quantity maximised by evolution, the optimal age of reproduction is thus given by (for rationale behind this see section III.1)

$$\frac{dr}{d\alpha} = \frac{1}{\alpha}\left(\frac{m'(\alpha)}{m(\alpha)} - \frac{\ln m(\alpha)}{\alpha} - \frac{\ln j}{\alpha}\right) = 0, \quad (23\,a)$$

$$\frac{dR_0}{d\alpha} = je^{-p\alpha}(m'(\alpha) - m(\alpha)\,p) = 0, \qquad (23\,b)$$

where m' denotes the first derivative $dm(\alpha)/d\alpha$. Roff (1992, p. 184) now concludes from equation (23) that when r is the right fitness measure the optimal α does not depend on 'adult' survival p, only on survival through birth, j, since in equation $(23\,a)$ only the term between brackets can equal zero and j but not p is present in this term. Following a similar reasoning, it becomes obvious that when R_0 is the fitness measure, the opposite is true. This is a very clear example where changing the fitness measure changes the prediction of the model in a similar fashion as was also noted by Stearns (1992) and Kozłowski (1993).

(4) Spatial heterogeneity; the solution to the problem?

Stearns & Koella (1986) calculated a reaction norm as the optimal solution in terms of fitness, where fitness was measured by r for each environmental 'point' (from here on referred to as habitat). The model's formulation [equations (19)–(20)] implies that all the offspring produced actually stay in the same habitat as the parents. It is hard to understand how in such a situation phenotypically plastic traits can evolve, since one expects that the population will adapt to the local environmental circumstances (Houston & McNamara, 1992; Kawecki & Stearns, 1993). For reaction norms to evolve, there should be a wide variation in environmental conditions which the offspring should be able to encounter (Fig. 6). Kawecki & Stearns (1993) extended the approach of Stearns & Koella (1986) and allowed the offspring to encounter different habitats from their parents. It should be noted however, that Houston & McNamara (1992) earlier reached the same conclusion using a structurally different method.

Kawecki & Stearns (1993) incorporated the idea of a source-sink habitat, where there are differences in habitat quality. There are some habitats where the local r, r_l, is less than null (sink) or larger than null (source). Juvenile individuals (e.g. seeds, pollen, fledged young) distribute themselves over these
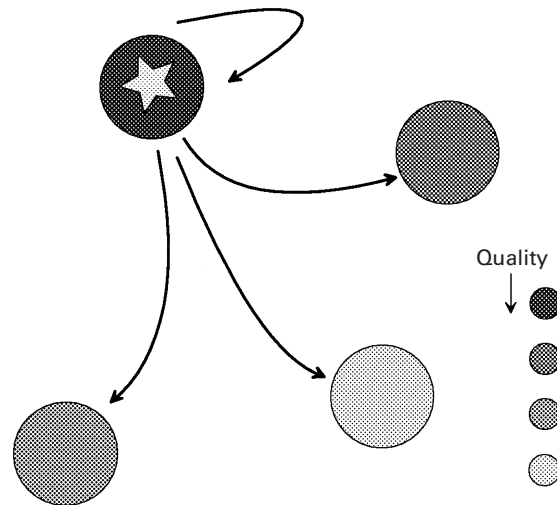

Fig. 6. Schematic presentation of the spatio-temporal connection between local conditions. The environmental variation an organism encounters is represented by variation in the local habitat quality. However, the future conditions for offspring and possibly for parents do not necessarily remain the same. For example, some offspring will disperse to habitats of different quality than the focal patch (indicated by a star). Alternatively, habitat quality may vary temporally and the future local quality may differ from the current one. A reaction norm presents the collection of optimal actions depending on the local quality and should therefore incorporate the possibility of an individual encountering all these different local conditions.

habitats and stay there for the rest of their lives (Fig. 6). By definition, more individuals will be born in the source habitats than in the sink habitats; hence, dispersal from source to sink will be greater than from sink to source. Caswell (1989) and McNamara (1991) showed that such a population will converge to a stable distribution in which the proportions of the individuals living in each of the habitats will be constant and the population will grow exponentially at rate r_g (global r). For determining a reaction norm, r_g must be maximised. This in contrast to the former approach (section IV.1), where the local r_l was maximised. Kawecki & Stearns (1993) calculated r_g using the Euler-Lotka equation (1) over all habitats; thus, r_g does not only depend on the survival and fecundity schedules in each local site, which is determined by the habitat type, but is also dependent on the distribution of the offspring over the different habitats in each generation.

The key point in describing a reaction norm lies in appreciating the connectivity between the habitats of different qualities. The offspring of a parent living in a poor quality habitat have a chance of ending up

in a better quality habitat and 'doing better' than their parent and the opposite holds for offspring of parents in high quality habitats. Thus, maximisation of fitness in each environmental 'point' of local (parental) condition (*sensu* Stearns & Koella, 1986) is not sufficient. Houston & McNamara (1992) and Kawecki & Stearns (1993) assumed that offspring are distributed randomly among the habitat patches and showed that maximisation of r_g becomes equivalent to maximisation of the reproductive value at birth, v_0 in the local habitat. To see this, consider that the production of an adult for the next time step is the sum of itself (if it survives) and the number of descendants it leaves. If a fraction δ of the offspring disperses from the natal habitat and there are two qualitatively different habitats then the future success of the offspring will depend on the quality of the habitat in which they start reproducing. The future success of offspring is incorporated in their reproductive value. In applying Schaffer's (1974) general result [equation (13)], the reproduction has to be weighted by the reproductive value to get the optimal strategies for habitat 1 as

$$\max\{pv_1^1 + b(1-\delta)\,v_0^1 + b\delta v_0^2\} = \max\{r_g\}, \quad (24)$$

where survival p and reproduction b are subjected to a trade-off and v_i^j represent the reproductive value in habitat j, of an individual characterised by i as adult ($i = 1$) or juvenile ($i = 0$). A similar argument works for habitat 2. In Stearns & Koella's (1986) approach, equation (13) itself was used for each environmental condition separately and all offspring thus stayed in the same habitat. In comparing equations (13) and (24), reproduction b either increases in importance if a parent is in a poor habitat, but its offspring have a good chance of reaching better places or decreases in importance if the opposite holds. McNamara (1993) gives a more general account of the methods and discussion for this kind of optimisation approach.

Kozłowski (1993) advocated the use of R_0 as a fitness measure. Because the world has not been taken over by any species, Kozłowski (1993) thought that an equilibrium in population size is a reasonable assumption (i.e. $r_g = 0$) and reproductive value then reduces to R_0. Kawecki & Stearns (1993, p. 168) explicitly mentioned that their model generated the same predictions as those models that used R_0 as the fitness measure. Thus, by explicitly taking into account the spatial heterogeneity of the environment, the use of R_0 and r will generate the same results. Kozłowski (1993) concluded that such a fitness measure was 'good news for field ecologists' and should provide a link between theoretical and empirical biologists. One can partition reproductive value into two parts where the first one is identical for all life histories up till age z and the second incorporates the difference that occurs after age z. This is similar to Williams's (1966) partitioning of reproductive value into current and residual reproductive value (section II.2). Kozłowski (1993) stated that data on life-history preceding age z are not relevant to optimisation of life-history following z. This has obvious benefits, since it is usually difficult to obtain any measures on life history for an organism at early developmental stages in the field. For example, there may be a period of 'invisibility' between offspring leaving their natal sites and the recapture of offspring, since it is rarely possible to follow non-reproducing organisms. Field ecologists would thus be pleased with a demonstration that they could dispense with this period of 'invisibility' in considering life-history adaptations. Nevertheless, this assertion has since received severe criticisms, as will be discussed in the following section.

V. THE ESS CONCEPT REVISITED; SOLVING THE PROBLEM

In all approaches discussed so far, optimality of a life history referred to maximisation of the fitness measure chosen. However, maximisation of r *per se* is problematic (Yodzis, 1981), since r is defined as a measure of demographic growth through the Euler-Lotka equation [equation (1)]. Solutions where r is maximal and greater than 1 imply continuous exponential growth; an unlikely evolutionary outcome. Therefore, the next step was an approach that attempted to incorporate population regulation. However, for mathematical convenience, in density-dependent populations R_0 was considered the fitness measure to be maximised (e.g. Charlesworth & Léon, 1976; Michod, 1979), leaving r unspecified. As discussed, maximisation of one of the two fitness measures cannot be assumed to be equivalent. Hence, the link between these fitness measures is of special importance.

(1) Density dependence

Density dependence was ignored in the models of reaction norms previously described (section IV). However, the interplay of allocation strategies and density dependence underlying population dynamics (Michod, 1979; Charlesworth, 1980) means that the predictions of these models concern the optimal

reaction norm at a fixed density. Moreover, underlying these models are certain assumptions on individual state; state is a term borrowed from system theory and, when applied to an individual, refers to structuring of a population into groups characterised by their age, size, physical condition, habitat quality or other relevant measurement (Caswell *et al.*, 1972; Metz & Diekmann, 1986). In general, R_0 can be used in models where the state of an individual is fixed for its lifetime, although in certain cases it can be calculated for dynamic states as well (e.g. Diekmann, Heesterbeek & Metz, 1990). On the other hand, r can be used when the state changes randomly from year to year and the state distribution of parents and their offspring is the same (Houston & McNamara, 1992; Kisdi, Meszéna & Pásztor, 1998). When describing a reaction norm over a range of states (e.g. habitats, section III.4), the state distribution between offspring and parent probably differs from one another (Fig. 6). For example, the parent stays in one habitat, but the offspring will encounter several habitats (Houston & McNamara, 1992; Kawecki & Stearns, 1993). When the overall population density is fixed, density dependence can be ignored in making predictions of a reaction norm (e.g. Stearns & Koella, 1986; Daan *et al.*, 1990), although this is a rather limiting setting. Furthermore, when making a comparison of the reaction norm between two stationary populations of the same species, density dependence should be involved and in this case the maximisation of r and R_0 should lead to the same result (see also Charlesworth, 1980).

Mylius & Diekmann (1995) pointed out that the parameters r and R_0 are linked in 'ecological equilibrium', when $r = 0$ and $R_0 = 1$ by definition. In the context of the example from Roff (1992) given above, Pásztor *et al.* (1996) argued that when $r = 0$ and $R_0 = 1$, equation (22) [either (22*a*) or (22*b*)] reduces to

$$\frac{\ln[m(\alpha)j]}{\alpha} = p. \qquad (25)$$

Thus, in equilibrium, the adult survival rate p is linked to the age at maturity α, the fecundity $m(\alpha)$ and the fraction j surviving the juvenile stage. Therefore, any change in one of these parameters leads to a change in the other parameters in obtaining the next equilibrium. It is thus not reasonable to accept that maximisation of r leads to different results than maximisation of R_0, since these two measures are linked. One merely has to

acknowledge that changes in any life-history parameter are coupled to changes in equilibrium population density. When the additional assumption of population-dynamical equilibrium is not made, the location of the optima of the two fitness measures can be different (Mylius & Diekmann, 1995).

The most likely reason that populations attain equilibrium is density regulation. In discussing the reaction norm models of section IV, Kozłowski (1993) even stated that 'the models implicitly or explicitly assume that density dependence operates somewhere in the life cycle, usually before the first difference in life histories occurs'. In fact, as Michod (1979, III.3) showed, any change in the environment that affects the mortality or fertility in one age class will lead to a change in population density. Fitness therefore not only depends on the strategy (in this case the α), but also on the environment (E) and the density (N); thus $r(\alpha, E, N)$ and $R_0(\alpha, E, N)$.

In the example given in section IV.3 [equation (22) and (23)], optimisation will lead to the same result when acknowledging that r and R_0 are linked in equilibrium. To see this for the example discussed above, consider that when all variables are linked in ecological equilibrium as in equation (25), inserting equation (25) in equations (23*b*) and writing m for $m(\alpha)$, gives

$$\frac{dR_0}{d\alpha} = \frac{m'}{m} - \frac{\ln mj}{\alpha} = 0, \qquad (26)$$

which is equivalent to equation (23*a*).

The problem of different predictions between fitness measures is solved when one models the effect of the environment explicitly (Mylius & Diekmann, 1995; Pásztor *et al.*, 1996). In addition to the evolutionary equilibrium, as given by the maximisation of the fitness measure ($\partial r/\partial \alpha = 0$), one has to consider the ecological equilibrium. As argued by Pásztor *et al.* (1996), incorporating r as a function of the life-history trait α, population density N and the environment E, the ecological equilibrium ($r = 0$) specifies that the directional change ($\partial r/\partial \alpha$, $\partial r/\partial N$, $\partial r/\partial E$) linked to a change in α, N and E ($d\alpha$, dN, dE) will ensure that the population stays in equilibrium if perturbed. Thus,

$$dr = \frac{\partial r}{\partial \alpha} d\alpha + \frac{\partial r}{\partial N} dN + \frac{\partial r}{\partial E} dE = 0. \qquad (27a)$$

Furthermore, the evolutionary equilibrium

$$d\frac{\partial r}{\partial \alpha} = \frac{\partial^2 r}{\partial \alpha^2} d\alpha + \frac{\partial^2 r}{\partial \alpha \partial N} dN + \frac{\partial^2 r}{\partial \alpha \partial E} dE = 0 \quad (27b)$$

follows similar argumentation. In the optimal life history $\partial r/\partial \alpha = 0$, equation $(27a)$ can then be reduced to

$$-dN = \frac{\partial r/\partial E}{\partial r/\partial N}dE = cdE, \qquad (28)$$

when writing c for $(\partial r/\partial E)/(\partial r/\partial N)$. Because E can be said to measure the environmental harshness, $\partial r/\partial E$ is negative (a harsher environments is characterised by a lower r). Increasing the harshness of the environment thus induces a decline in density, as was also shown by Michod (1979, III.3), which is balanced by the effect of density on r, thus ensuring that a new equilibrium is attained by the population.

It should be noted that the above holds for any life-history variable and not just the age at maturity, α may therefore be interpreted as any life history trait. Equation (28) can be substituted into equation $(27b)$ to find a general condition for maximisation of α over a change in the environmental condition. We are dealing with an evolutionary optimum and thus $\partial^2 r/\partial \alpha^2 < 0$ [equation (17)]. An optimal life history is delayed (i.e. $d\alpha^*/dE > 0$), if

$$\frac{\partial^2 r}{\partial \alpha \partial N}c < \frac{\partial^2 r}{\partial \alpha \partial E}. \qquad (29)$$

This clearly demonstrates that in general the optimal value for a life-history trait depends on both environment and density. This led Pásztor *et al.* (1996) to conclude that 'one must in general consider and test all the effects of the environment on the demographic variables, including the coupled density effects, in order to predict the change in the optimal strategy with the age-schedule of mortality (*contra* Kozłowski, 1993)'. Data gathered past age z (see section IV.4) is then not adequate enough for a correct evaluation, since the effect on mortality before age z may influence optimality considerations by changing the population density.

(2) Which fitness measure to use and when; the ESS argument revisited

The extension of the ESS framework, presented in section III, by Mylius & Diekmann (1995) clarifies the framework underlying these general solutions *in concreto*. Since a steady state is assumed (i.e. $r = 0$ and $R_0 = 1$), one essentially maximises a quantity that is assumed to have a fixed number (Maynard Smith, 1993). Kozłowski (1993) used an ESS argument to unravel the 'apparent paradox' in which he stated

that 'when the best genotype has $R_0 = 1$, all the other genotypes have $R_0 < 1$'. However, the condition that both $R_0 = 1$ and $r = 0$ was not incorporated in previous approaches.

Mylius & Diekmann (1995) studied the factors to consider when deciding which fitness measure to use, using the concept of invasibility, as discussed in Metz, Nisbet & Geritz (1992). In this concept, the quantity to be maximised is a function of two variables. As in Michod (1979), the ESS condition is specified by the growth rate of a mutant, now termed invader, in the environment set by the predominant population, which is termed the resident population. Thus, the type of the trait that is studied is denoted by the (possibly multi-dimensional) variable T. The environment is fully characterised by the condition E. Both variables T and E determine the population growth rate; i.e. $R_0(T, E)$ and $r(T, E)$. A population of type T will grow in this environment such that the equilibrium E will be a function of T, say $f(T)$. By definition, the growth rate of this resident will be

$$R_0(T_{res}, f(T_{res})) - 1 = r(T_{res}, f(T_{res})) = 0. \quad (30)$$

As also assumed by Michod (1979; see section III.3), the environment is set by the resident and a mutant with invading type T_{inv} will initially be rare with a negligible impact on the population dynamics. Thus, the mutant will be able to invade if $R_0(T_{inv}, f(T_{res})) > 1$ (or $r(T_{inv}, f(T_{res})) > 0$). This is equivalent to equation (18), only now the link between r and R_0 is stated explicitly in equation (30). At ESS, no mutant can invade (Maynard Smith & Price, 1973; Maynard Smith, 1982) and the growth rate of the invading type in the environment set by the resident will determine whether the resident is of an ESS type. The ESS environmental equilibrium is given by the type T^*, which is played at the ESS, thus $E^* = f(T^*)$. The function $R_0(T, f(T^*))$ is maximal if $T = T^*$ (equivalent for r) (see also Caswell, 1989, pp. 256–258). An ESS is then found by calculating the local maximum in the function $R_0(T, f(T^*))$ or $r(T, f(T^*))$. The maximisation can be visualised by the function $T \to R_0(T, E)$, which indicates that $R_0(T, E)$ is considered as a function of the variable T with fixed E (likewise for r; Mylius & Diekmann, 1995).

Using this concept Mylius & Diekmann (1995) analysed three general situations where maximisation of only one of the quantities is correct when ignoring density dependence. The general approach would be to find the point where the ecological equilibrium $R_0(T, E) - 1 = r(T, E) = 0$ and the evo-

lutionary equilibrium $T \rightarrow R_0(T, E)$ and $T \rightarrow r(T, E)$ are maximal. However, the maxima in R_0 and r are dependent on the way density dependence acts and therefore the form of density dependence becomes important. Mylius & Diekmann (1995) proved that

(1) If density acts in such a way that lifetime offspring production is reduced by an E dependent multiplication factor, then T^* is an ESS if and only if $T \rightarrow R_0(T, E)$ is maximal for $T = T^*$.

(2) If density dependence causes a uniform increase in mortality for all members of the population, then T^* is an ESS if and only if $T \rightarrow r(T, E)$ is maximal for $T = T^*$.

The maximisation of both r and R_0 is useful, but in different contexts. Different and more complex situations can occur where other quantities might be maximised (see Metz *et al.*, 1992; Heino, Metz & Kaitala, 1998).

In the case where E is one-dimensional (e.g. food density) and the function $R_0(T, E)$ is monotonic, the environmental condition is determined by the function $f(T)$ (see above).

(3) In the case of a one-dimensional environment and the function $E \rightarrow R_0(T, E)$ increasing (or decreasing), then T^* is an ESS if and only if $f(T)$ is minimal (or maximal) for $T = T^*$.

This last proof is consistent with the use of the carrying capacity K by Charlesworth (1971) and density dependence as discussed by Hastings (1978); the type that can hold on in the worst environmental conditions is the fittest, a form of pessimisation strategy. However, Mylius & Diekmann (1995) pointed out that population size can be measured in several ways (e.g. biomass, weight, numbers) and that these different measures are not necessarily all maximal at the same point.

One can attribute several ways in which density dependence acts in a population to these general results. For example, if adult mortality increases with increasing density the lifetime offspring production reduces, so result (1) applies. In the case where density affects the juvenile mortality by adding an E-dependent term, result (3) applies. When density tunes the juvenile and adult mortality to the same degree, result (2) applies.

To illustrate this with an explicitly formulated model, we may again consider equation (22) (Fig. 7). If density dependence scales the reproduction m, Mylius & Diekmann's (1995) result (1) applies where R_0 should be the correct fitness measure to be maximised. Clearly, R_0 and r respond differently to variation in α and E (Fig. 7). At the optimal age at

maturity, there should be an ecological equilibrium, i.e. $R_0(\alpha, E) - 1 = r(\alpha, E) = 0$ which is represented by the dashed curves in the contour plots (Fig. 7 C & D). The evolutionary optimal age at maturation is found where these equilibrium curves have their maximum, hence both $\alpha \rightarrow R_0(\alpha, E)$ and $\alpha \rightarrow r(\alpha, E)$ need to be maximal.

The essence of Mylius & Diekmann's (1995) result is the simplification which follows from using the right fitness measure. By applying result (1), neither the ecological equilibrium nor the link with the maximum in R_0 and r has to be calculated. Instead, it suffices to calculate the maximal R_0, as the optimal age at first reproduction α^* has a maximum in R_0 for all values of E (dashed vertical line in Fig. 7 C). In contrast, the maximum of r does depend on E (Fig. 7 D) and maximisation of r *per se* will thus lead to a different conclusion concerning the optimum age at maturity.

(3) Back to Roff's example

There is an interesting difference between the interpretation of the ESS outlined in section III by Mylius & Diekmann (1995) and Pásztor *et al.* (1996). For Mylius & Diekmann (1995), fitness is characterised by the growth rate of the invader in the environment set by the resident. This environment incorporates the way in which density dependence functions in regulating the population. Thus, the population itself sets the environment. In contrast, Pásztor *et al.* (1996) studied the consequences of a slight perturbation of an optimum, where density dependence and environment are considered as two separate variables. This allows for the intuitive distinction of external (environmental) and internal factors. The latter view stands closer to the more traditional analyses discussed in section IV.

It is, however, apparent that the answer to the question which fitness measure to use is not a matter of taste (Pásztor *et al.*, 1996). Evolutionary and ecological equilibrium are linked. If changing a fitness measure in structurally similar models generates different predictions, one should make a choice regarding the way density dependence functions in regulating the population (Mylius & Diekmann, 1995). In fact, the choice of fitness measure itself implies a certain form of density dependence; it does not matter whether density dependence was incorporated explicitly, because it is implicit in the fitness measure chosen. Roff's (1992) example illustrates clearly that the 'right' fitness measure is usually implicit in the formulation of the
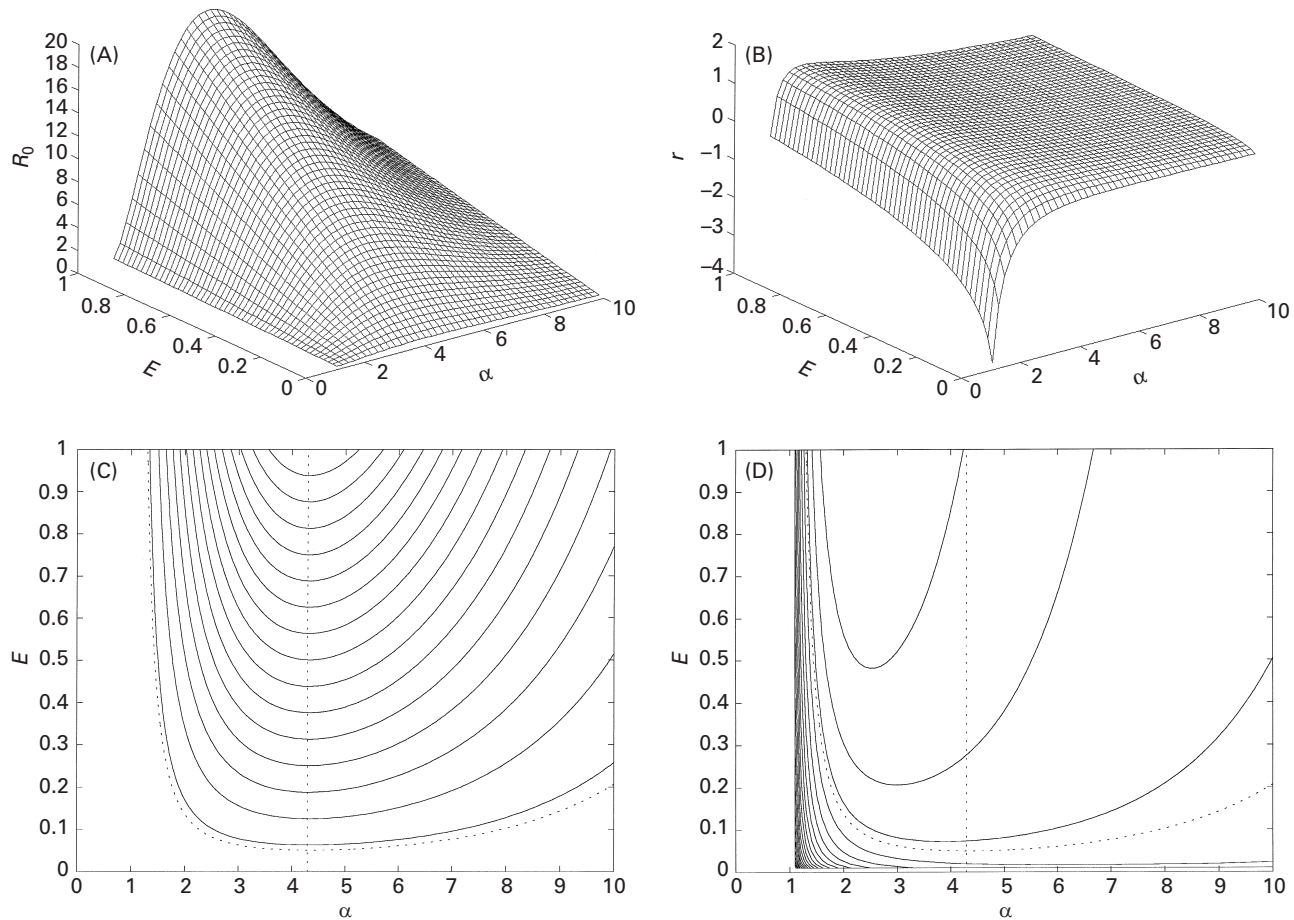
Fig. 7. Reconsideration of the example of section IV.3 [equation (22)] when incorporating the effect of the environment in an explicitly formulated model. Here, the fecundity of an organism maturing at age α, $m(\alpha) = 0$ for $\alpha < 1$, increases quadratically as $m(\alpha) = 5.5 \cdot (\alpha - 1)^2$ for $\alpha \geqslant 1$. Juvenile survival $j = 0.8$ and adult survival rate $p = 0.6$. The environment acts in reducing the fecundity with a multiplication factor E, thus $m(\alpha, E) = E \cdot m(\alpha)$. Therefore, Mylius & Diekmann's (1995) result (1) applies (see text) and R_0 is the fitness measure to be maximised. Drawn here for different values of α and E are the fitness values of R_0 (A) and r (B). In the corresponding contour plots, equal values of R_0 (C) and r (D) are connected. The dashed curve indicates the ecological equilibrium $R_0(\alpha, E) - 1 = r(\alpha, E) = 0$. Maxima of $\alpha \to R_0(\alpha, E)$ and $\alpha \to r(\alpha, E)$ correspond to minima of the contour-lines in the (α, E) plane as both R_0 and r decrease with a change in α and E being equal. The dashed vertical line indicates the maxima of $\alpha \to R_0(\alpha, E)$. Evolutionary and ecological equilibrium is given by $\max\{R_0(\alpha, E)\} - 1 = \max\{r(\alpha, E)\} = 0$ and corresponds to the intersection of the dashed vertical line with the dashed curve. When not incorporating density dependence, the optimal age at maturation corresponds to the maximum in either fitness measure where $E = 1$, which is in this case clearly incorrect for r.

model. In reconsidering Roff's (1992) example [equations (22) and (23)], it now becomes clear that the population density may be ignored in maximising r when only adult survival p is affected, since p will not appear in the derivative of r to α and hence not in inequality equation (23) [result (2) above]. A similar reasoning holds for R_0 and juvenile mortality j [result (1) above].

Unfortunately, little is usually known about the way in which density dependence operates in any population (Mylius & Diekmann, 1995). These ideas underline once more the importance of

understanding this mechanism; not only with respect to population dynamics, but also with respect to evolutionary dynamics.

(4) Defining fitness for general ecological scenarios

Many aspects of real life have not been considered in previous sections, while limiting assumptions have been made implicitly by the use of r or R_0 as fitness measures. One important assumption is that the

Table 3. *Population projection matrix and an individual projection matrix of the population of Table 1*
(A matrix describes all relevant transitions between stages in a population in a column-to-row fashion. In this case, the population has four age classes that survive with a certain probability to the next age class, except for the last age class, which does not survive. All age-classes produce individuals in the first age class (reproduction). The first row in the population's matrix denotes the effective fecundity $(m_x p_0)$ starting at age = 1, the sub-diagonal denotes the yearly survival p_x. The individual matrix (*sensu* McGraw & Caswell, 1996) denotes the contribution of one possible individual in that population. Here, on the first row, the individual's production of females, b_x, at each age x, starting again at age = 1. The survival in the sub-diagonal is 1, because this individual has survived to age = 3, after which it died. In both cases, the dominant eigenvalue of the matrix λ denotes the fitness.)

Population of organism B				Individual organism		
0.96	1.28	0.96	0.64	0	1	2
0.16	0	0	0	1	0	0
0	0.08	0	0	0	1	0
0	0	0.02	0			
$\lambda_{\text{pop}} = 1.14$				$\lambda_{\text{ind}} = 1.52$		

environment does not fluctuate. Another is that these models have not considered polymorphic populations with more than one type of strategy. Most importantly, however, it has become clear that a certain fitness measure can only be used in special circumstances to measure fitness correctly. Evolution can thus, for certain cases, be thought to maximise the quantities r and R_0, but these measures are certainly not automatically valid substitutes for fitness in a general sense. Metz *et al.* (1992) and Rand, Wilson & McGlade (1994) have argued for a framework of fitness based on the invasibility criterion as mentioned in section V.2 as the master fitness concept, this in contrast to r and R_0, which present fitness measures. The fitness concept conforms to a visualisation of how evolution operates (e.g. Eshel, 1996; Hammerstein, 1996). As such, the concept is generally applicable, allowing the incorporation of many realistic and complicating aspects, such as environmental variations, when considering life-history evolution.

To distinguish between the individual members of a population, Metz & Diekmann (1986) introduced so-called physiologically structured models, where each individual was characterised by its state, which represented physiological differences (e.g., age, size, condition, spatial location or a certain period at birth). A population at time t can thus be described as a vector $\mathbf{N}(t)$, with as its components the densities of individuals in each state. For a simple example of a population vector, consider that individuals can be characterised into a finite number of discrete states. In such a case, the population vector is

$$\mathbf{N}(t) = \begin{bmatrix} n_1(t) \\ n_2(t) \\ \vdots \\ n_\omega(t) \end{bmatrix},$$

with $n_i(t)$ the number of individuals in state i at time t and ω denoting the last state-class.

The fate of an individual, whether it changes state, reproduces or dies, depends on its current state and on the influence of the environment, denoted by the vector $\mathbf{E}(t)$, which could contain quantities such as predation rate, temperature, food supply and other factors for the different stages. In a density-independent situation $\mathbf{N}(t+1) = \mathbf{L}\,(\mathbf{E}(t))\,\mathbf{N}(t)$, with $\mathbf{L}$ a matrix composed of elements that depend on $\mathbf{E}(t)$. This matrix denotes the transitions between the states; possible transitions are for example birth, survival or changing habitat (Caswell, 1989). This means that the population at time t can be traced back to the initial population size, thus

$$\mathbf{N}(t) = \mathbf{L}\,(\mathbf{E}(t-1))\mathbf{L}(\mathbf{E}(t-2))\,\mathbf{L}\,(\mathbf{E}(t-3))\ldots\mathbf{L}\,(\mathbf{E}(0))\,\mathbf{N}(0).$$

According to the multiplicative ergodic theorem (Tuljapurkar, 1989) the relative sizes of the components of $\mathbf{N}$ eventually become independent of $\mathbf{N}(0)$. When the total population is denoted by $|\mathbf{N}(t)|$, population growth rate will converge in the limit of time to infinity, such that

$$\lim_{t\to\infty}\frac{\ln|\mathbf{N}(t)|}{t} = \Lambda \tag{31}$$

describes the asymptotic growth rate Λ. Here, Λ is also known as the dominant Lyapunov exponent of the matrix sequence $\mathbf{L}(\mathbf{E}(t))$, $t = 0, 1, 2, \ldots$ If this exponent is negative, the population goes extinct, if it is positive the population will grow exponentially. In a restricted scenario, i.e. when the environment is constant, the Lyapunov exponent will reduce to the logarithm of the dominant eigenvalue of the matrix $\mathbf{L}$. Note that if $\mathbf{L}$ denotes the Leslie matrix of a population with m_x and l_x values, $\ln(\Lambda)$ will be equivalent to the familiar measure r $[= \ln(\lambda)]$ as defined by the Euler-Lotka equation (1) (see also Caswell, 1989; Stearns, 1992, Table 3). That a
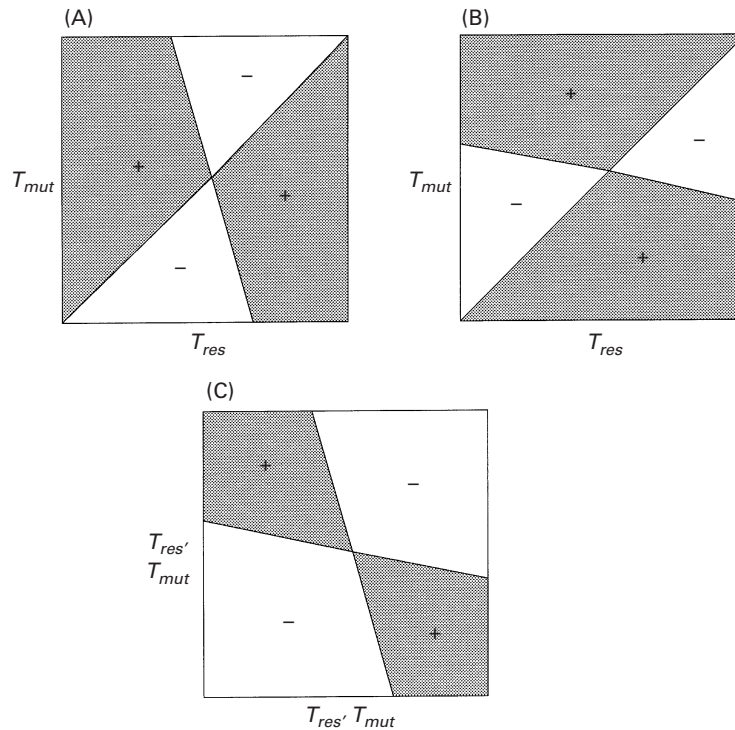
Fig. 8. Graphical illustration of invasibility, presented for two continuous strategies denoted by T_{res} and T_{mut}. In (A), the mutant with strategy T_{mut} can invade the resident with strategy T_{res} if the Lyapunov exponent $\Lambda T_{res}(T_{mut})$ is positive (grey area; see text for more details). In this case, the mutant strategy T_{mut} can invade. Nevertheless, in turn the invasibility of T_{res} in T_{mut} [$\Lambda T_{mut}(T_{res})$] may also be positive, which is illustrated in (B). In this case, by overlaying (A) and (B), one obtains (C), which visualises the region in the trait space where T_{res} and T_{mut} are mutually invasible (grey areas). In this case, no strategy can exclude the other and there will be a dimorphism.

system becomes eventually independent of its initial conditions is, in fact, a prerequisite for studying evolution on the basis of current information; knowledge on initial conditions is rarely available.

Neo-Darwinian evolution supposes a time-scale difference in short-term dynamics, such as population dynamics, as opposed to mutation dynamics, i.e. introduction of mutant types (Eshel, 1996). Thus, after a successful introduction of a mutant, a population will relatively quickly attain a new evolutionary equilibrium until it is again disturbed by another mutant. This 'stop-and-go' process goes on until no new types can invade any more; one can then view evolution as movements through a trait space (Metz *et al.*, 1992; Hammerstein, 1996; Weissing, 1996; Geritz et al., 1998). These mutations constitute a change of finite size in the trait under investigation, sufficiently close to the resident's trait value. The whole process has been compared to a tram ride, with stops to let new mutant on (and possibly old ones off) until the tram reaches the final stop (Hammerstein, 1996).

When evolution is mutation-limited, one has to evaluate the invasibility of mutant types when considering evolutionary scenarios. Given a vector $\mathbf{X}$ that is composed of the values of the traits under study, a successful mutation causes $\mathbf{X}$ to 'jump' to a new value. The possible jumps can be summarised by the invasibility criterion, using the dominant Lyapunov exponent to evaluate invasibility. A set of phenotypes $\mathbf{Y}$ can invade a resident set $\mathbf{X}$ if and only if the Lyapunov exponent of invasion is positive ($\Lambda_{\mathbf{X}}(\mathbf{Y}) > 0$); thus, $\mathbf{Y}$ can achieve a positive growth rate in an environment set by $\mathbf{X}$. Now, the sign of the $\Lambda_{\mathbf{X}}(\mathbf{Y})$ function summarises the evolutionary walk.

With this so-called 'adaptive dynamics' framework, it becomes possible to study not only whether a stable ESS exists, but also whether an ESS is convergence stable. The existence of an ESS does not necessarily mean that the population will actually evolve to reach such a strategy. As discussed above, an ESS is stable if no mutant strategy can invade, defined by the points $\mathbf{X}^*$, such that $\Lambda_{\mathbf{X}^*}(\mathbf{Y}) \leqslant 0$, for all possible $\mathbf{Y} \neq \mathbf{X}^*$. If we consider a one-dimensional trait, then a strategy is also convergence stable if all nearby phenotypes in the trait space can only be invaded by mutants playing a strategy closer to $\mathbf{X}^*$; thus, $\Lambda_{\mathbf{X}}(\mathbf{Y}) > 0$ for $\mathbf{X} < \mathbf{Y} < \mathbf{X}^*$ and, *vice*
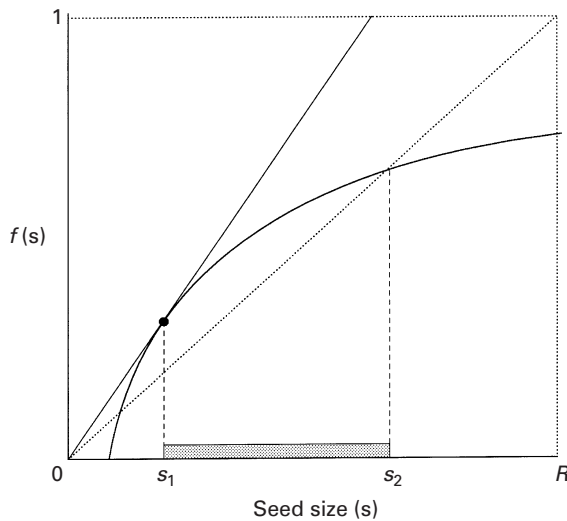
Fig. 9. Example of classical optimisation and the incorporation of individual differences. For seeds of a given size s, which denotes the amount of resource put into the seed, there is a probability function $f(s)$ describing the expected *per capita* yield. As the parent has R resources available, the maximum seed size equals R and the number of seeds produced can be described by R/s; the fitness of the plant thus equals $R/s\,f(s)$ (Smith & Fretwell, 1974). Therefore, maximising fitness for any R, equals maximising $f(s)/s$, which is graphically equivalent to maximising the slope of a line through the origin and $f(s)$. This is shown as a solid line and the Smith–Fretwell optimum s_1 is indicated by a filled circle. By introducing competition between individuals, the ESS is a range of seed size, as indicated by the grey bar. See text for further details. Figure drawn after Geritz (1995).

versa $\mathbf{X}^* < \mathbf{Y} < \mathbf{X}$ (Eshel, 1983; Kisdi & Meszéna, 1993; Geritz *et al.*, 1998). Thus, from any initial starting point, there is a successive 'path' of invasions through the trait space that leads to the ESS $\mathbf{X}^*$. Such a strategy is an evolutionary attractor, also called a 'continuously stable strategy' or CSS (Eshel, 1983).

Besides studying the very relevant question of convergence stability, the invasibility framework can explicitly deal with polymorphic populations. For example, a dimorphic population can exist if there are two strategies that can mutually invade, thus both $\varLambda_{\mathbf{X}}(\mathbf{Y}) > 0$ and $\varLambda_{\mathbf{Y}}(\mathbf{X}) > 0$; this mutual invasion can be visualised using pairwise-invasibility plots (see e.g. Geritz *et al.*, 1998) (Fig. 8).

The interest in polymorphism is fuelled by the frequent observations of variation in life-history traits; e.g. age at maturity is seldom fixed for the whole population. In the classical reaction norm approach, this may be viewed as an outcome of environmental variability within such a population. It may also be thought of as a bet-hedging strategy against environmental stochasticity (Kisdi & Meszéna, 1993; Bulmer, 1994). An alternative view is that there is frequency-dependent selection operating, such that rare strategies gain a fitness advantage, that would promote a so-called mixed ESS (Heino *et al.*, 1998). In one-dimensional environments, the ESS will be monomorphic (e.g. Mylius & Diekmann, 1995). However, in multi-dimensional environments the feedback environment is different between individuals and there may be strong frequency-dependence. Variation in a life-history trait may then be explained as adaptive, even when the population dynamics are stable (e.g. Heino, Metz & Kaitala 1997).

An example of adaptive polymorphism is seed size variation in plants (Geritz, 1995). In the Smith & Fretwell (1974) model, the number of s-sized seeds a plant can produce is determined by the resource R, and equals R/s. The expected reproductive yield $f(s)$ is a non-linear function of seed size s. The Smith–Fretwell optimal seed size is fixed, no matter what amount of resources are available (Fig. 9). Differences in seed size can only be explained between populations with a different $f(s)$, but the model fails to account for variation within the population or intra-individual variation in seed size.

Geritz (1995) has extended this approach to considering inter-individual competition in germination site (e.g. for sunlight), whereby competition is assumed to be 'honest' (i.e. the largest seed size will always win the sole use of the germination site in competition with other seed sizes). The fitness benefits are thus frequency-dependent, since producing smaller seeds allows also for a production of more seeds, which will reach many different sites. Alternatively, producing a lower number of larger seeds gives a competitive advantage for within-site competition. Geritz (1995) proved that the ESS consists of a range of seed sizes (Fig. 9); within this range, a continuum of seed size productions are mutually invasible (see Fig. 8) and there is no single optimum seed size.

The verbal interpretation of Geritz's (1995) result is that the Smith–Fretwell (global) optimum represents the point where the maximum number of sites is reached (the fitness $f(s)/s$ relationship, Fig. 9). Seeds larger than this size s_1 decrease in their ability to reach sites, but, as they are bigger, gain a competitive advantage. Producing seeds smaller then s_1 is never optimal, as they are inferior both competitively and in reaching sites. Thus, strategies

for producing seeds larger than s_1 can invade because of the competitive advantage of larger seeds. However, the maximum seed size is reached when the slope of $f(s)/s$ equals $1/R$; producing larger seeds will result in a *per capita* reproduction of less than 1 (see the formulation of fitness in Fig. 9), which means that a population producing such large sized seeds will decline.

VI. IMPLICATIONS

The controversy regarding the 'right' measure of fitness has shifted the focus in life history towards an explicit ESS formulation. There are two main implications that stem from this development. Firstly, the environment plays an important role and has truly come to the foreground in recent approaches. Second, the phenotypic response of individuals to their environment has received more attention; individuals can be considered to have more plasticity.

(1) The role of the environment

Throughout the literature on life history, the term 'environment' and its role in fitness considerations has shifted considerably. With the increasing focus on reaction norms, the role of the environment has increased in importance. Originally, however, the environment was thought of as a 'template for ecological strategies' (Southwood, 1977), which implies a certain rigidity. In the simplest case, the environment may be described as a fixed 'point'. For one individual, a range of these environmental points may be qualitatively different and thus the consequences of a certain action may differ. This is the source of the genotype–environment $(G \times E)$ interaction in quantitative genetic considerations (e.g. Lande, 1982). This interaction is because certain genotypes perform well in one environment but poorly in another. For example, a genotype can have a relatively high fertility at a low ambient temperature, but not at a high ambient temperature and *vice versa*.

However, the realisation that all local distinguishable environmental points are connected, either spatially or temporally (McNamara, 1991; Houston & McNamara, 1992; Kawecki & Stearns, 1993), broadened the term environment conceptually. It is important to consider not only the range of local conditions, but also the connection between these environmental conditions, e.g. through dispersal.

As previously discussed, when recognising the game aspect in natural selection, the success (fitness) of any action becomes dependent on the strategies of the other members of the population (Maynard Smith & Price, 1973; Maynard Smith, 1982). Thus, for a correct evaluation, the number and strategies of the other players have to be incorporated, and explicit consideration of density dependence becomes necessary (Mylius & Diekmann, 1995; Pásztor *et al.*, 1996). Selection processes may therefore become frequency dependent (Maynard Smith & Price, 1973; McNamara, 1995; Heino *et al.*, 1998). Depending on the formulation (see section V.3), the concept of 'environment' has to be enlarged to include the density of conspecifics (e.g. Metz *et al.*, 1992; Mylius & Diekmann, 1995). Hence, the properties of the environment are essentially determined by the individuals themselves and the environment has become integrated in the concept of fitness.

There is thus a continuous interplay between individual-level and population-level processes. The actions of a set of individuals determine the dynamics of the population. For example, the allocation to reproduction will directly determine the growth or decline of the population size as this determines the fertility and survival schedule. Nevertheless, processes at the population level determine whether individual actions are in fact optimal (Fig.10A); e.g. when all individuals are competitively equal in the competition for resources, the *per capita* resource availability will decrease linearly with increasing population density. In considering optimal strategies, the whole dilemma of mutual feedback has to be solved simultaneously. In the above sketched example, the environment can be described by the *per capita* resource availability, which is one-dimensional. The optimal strategy will be a pessimisation strategy, where all individuals follow the same strategy that maximises *per capita* resource availability and population size (e.g. Hastings, 1978).

Currently, the role of feedback in a multi-dimensional environment is receiving increasing attention. Such multi-dimensional environments allow polymorphisms to evolve. A feedback environment is that part of the environment which is influenced by the actions and the density of the population. The feedback is multi-dimensional when it cannot be described by a single scalar (one-dimensional) variable any more in calculating the population dynamics. For example, in the light of the above given example, individuals might differ in

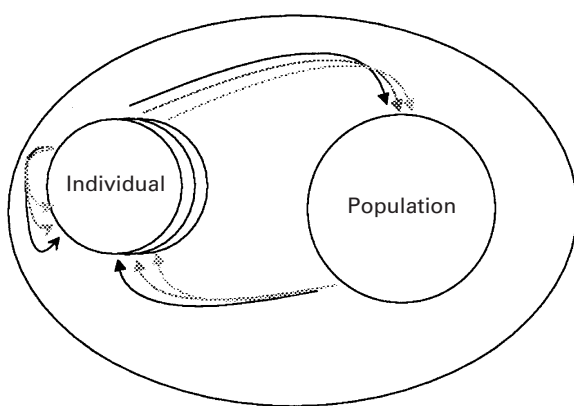(A) One-dimensional feedback
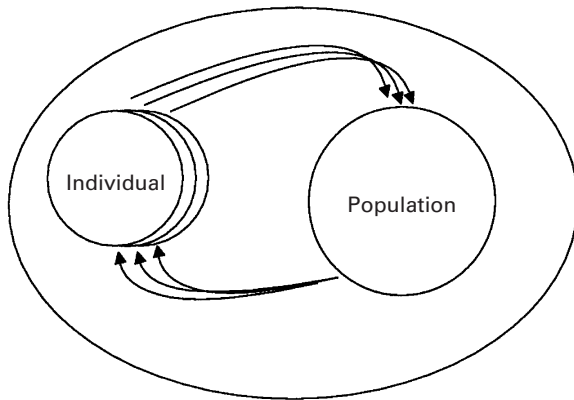
(B) Multi-dimensional feedback

Fig. 10. Schematic representation of the structure of the feedback environment. In (A) there is an example of a one-dimensional interaction between the individual level and the population level. All individuals are equal within the population (e.g. in terms of reproduction and survival) and the population feedback works the same on each individual. Consider, for example, the density dependence in a logistic growth model $\mathcal{N}(t+1) = b[1 - \mathcal{N}(t)/K]\mathcal{N}(t)$, where population growth in population size $\mathcal{N}$ at time t is determined by the reproduction b. The feedback environment is the same for all individuals, because the limitation on population growth stems from the carrying capacity K, which affects all individuals equally. In contrast, there may be a multi-dimensional feedback, as in (B), where population level processes have a differential effect on the individual level, due to for example differences in age, resource availability or predation risk between these individuals. Likewise, there may be direct interactions between individuals (e.g. competition, cannibalism).

their response to the environment (e.g. juvenile and adult age classes may respond differently) and this information has to be included in describing the population dynamics (e.g. Bulmer, 1994; Geritz, 1995; Kaitala, Mappes & Ylönen, 1997; Heino *et al.*, 1997) (Fig. 10B). Polymorphic strategies are com-

mon in nature and the exploration of these exciting areas outside the rather restricted outline of classical optimisation presents an exciting and different view on the complexity of variation in nature.

The fitness of life histories can be described by at least two variables, the life-history strategy and the environment (Mylius & Diekmann, 1995). Both these variables may have several dimensions; for example, in determining the seasonal decline of clutch size in birds, the life-history strategy may be described by reproductive effort and laying date. Likewise, the environment may be described by the food supply and the population size, determining the *per capita* food availability. From descriptive and experimental life-history data, one may be able to infer the consequences of different life history strategies on an individual's fitness component, but these effects are particular for a certain environment. Any formulation of life-history optimisation, based on these measurements, is thus also constrained to that environment. If the objective is to model the observed life-history patterns in a population which has been studied intensively in fixed environments, density dependence is not always essential. However, one should be careful in using these models to make a comparison between populations living in a different environment.

(2) The individual in the life history

Fitness, in more recent approaches, is viewed as the growth rate associated with individual phenotypes in the population. The emphasis is on the plasticity of an individual's response to its environmental condition. One is therefore taking the whole individual's reaction norm and not a subset of its genes (those genes that code for some life-history trait), as the unit of selection. This is a notion that is purely demographic. By doing away with the problems of (unknown) genetics underlying such a complex phenomenon as life history, vastly more intricate ecological relationships may be explored. When comparing approaches, genetics-based approaches with Mendelian inheritance or quantitative genetics proved compatible to ESS analyses within certain restrictions (Charlesworth, 1990; Abrams, Harada & Matsudo, 1993; Eshel, 1996; Hammerstein, 1996; Weissing, 1996).

Populations may be composed of different individuals, which can be characterised by a state variable. Current state is affected by the individual's previous actions (in, for instance, reproductive output or survival) and the current environmental

circumstances; the consequences of an individual's actions are dependent on its state (McNamara, 1991, McNamara & Houston, 1996). The optimal life history is thus a description of the optimal action an individual should play given that it is in a certain state. Again, optimality should be defined in relation to the actions and number of the other players; density of conspecifics may play an important role in determining state (Houston & McNamara, 1999).

By describing a life history of a population in a Table format (Table 1), one considers only the 'average individual'. In reality, however, there are no such individuals. Populations are typically structured in some sense, both spatially and individually. For example, breeding sites may be of different quality and effectively constitute 'sources' and 'sinks' (Pulliam, 1988). This implies that life histories evolve as a description of optimal actions in each habitat (section IV.2; Fig. 6). More generally, this concept should be interpreted for any distribution of states, which can be spatially fixed habitats, but individual states as well. The distribution of future states of both parents and offspring can be defined either spatially or temporally. Using this interpretation, the 'patches' of different quality in Fig. 6 represent different states. As an end-result of life-history evolution, individuals then carry a policy of state-dependent actions, the reaction norm.

Mechanisms shaping reaction norms are structurally similar when considering a variety of scenarios. For example, in discussing reaction norms in section IV.1 (Fig. 4), environments were characterised by growth rate. The reaction norm was a resultant of timing and a fecundity-related trait (age and size in Fig. 4). Reasoning in an analogous fashion for birds, these environments may represent different territories and the optimal response concerns a seasonal decline in clutch size between territories (Rowe, Ludwig & Schluter, 1994). Analogous reasoning also applies to insects and other taxa (e.g. Abrams et al., 1996; Leimar, 1996). Generally, the fecundity component increases with advancing time (e.g. due to increase in size, or simply because of a higher realised fecundity with equal reproductive effort), but the value of this component decreases (e.g. value of offspring or value of being of a certain size). The optimal solution describes the balance between these two factors. The time component itself is restricted to a certain window, where the minimum is dictated by the fecundity achieved, there is for example a minimum clutch size or minimum size at maturity that allows reproduction.

The maximum time may be restricted as well, due to for example the onset of winter in a seasonal scenario or a physiological maximum in developmental time or age.

Nevertheless, as argued above, the ESS concept is essential for a correct evaluation of reaction norms. The optimality of the reaction norm should be defined through the invasibility concept as the policy of state-dependent actions that cannot be beaten when played (Kisdi et al., 1998). Optimisation arguments are sensitive to the separation of current and future states, as offspring produced by an individual in a certain state are not necessarily of the same state and nor are their offspring and so on.

Recently, the concept of reaction norms has been enlarged to include a wide variety of behavioural decisions, besides 'classical' life-history decisions (McNamara & Houston, 1996; Houston & McNamara, 1999). For example, individuals may base their action to breed or not on the quality of the available habitat patch; it can then be shown that the optimal strategy maximises the population size of non-breeding 'floaters' (Kokko & Sutherland, 1998) in contrast to the breeding population size (e.g. Hastings, 1978). Other examples include divorce rate (McNamara & Forslund 1996), foraging behaviour when balancing foraging against predation (McNamara, Houston & Lima, 1994; Houston, McNamara & Hutchinson, 1993) and hoarding of food (Brodin & Clark, 1997; McNamara & Houston, 1997).

These models combine behavioural aspects with life history that allows for both inter- and intra-individual differences in state to underlie the optimality of each action (Clark, 1993; McNamara & Houston, 1996; Houston & McNamara, 1999). These so-called state-dependent models centre on individuals making a calculated decision where the consequences of each action are incorporated in the expression of an individual's reproductive value (Grafen, 1999). In this sense, the fitness concept has come full circle back to the formulation of Williams (1966) [section II.3], which was originally formulated on a behavioural basis. The concept behind this type of optimisation can be thought of as an enumeration of Pianka & Parker's (1975) visualisation of individuals in the life history. As these authors explicitly noted, the relationship between current reproductive output and residual reproductive value (as in Fig. 3) is not a fixed volume, but changes constantly with the actions taken by the individual and how the environment affects these actions. Current state is a reflection of the previous

actions of an individual and any action taken will, dependent on the current state, affect the shape and intercepts of the solid presenting an individual's life history, as presented by Fig. 3. The power of this type of thinking stems from the explicit incorporation of decision-making at the individual level. Such models and their assumptions can be tested critically in experimental or field situations; a quality which is obviously desirable.

For example, considering seasonal timing of size and development in insects, many studies have manipulated perceived time in the season by manipulating the photoperiod (e.g. Lutz, 1968; Veerman, 1994; Leimar, 1996). However, individuals that perceive the closing of the time-window for completing their development may increase their foraging rate, which may affect their growth rate and confound the measured life history response; behaviour and life history may be dependent on each other (Leimar, 1996). Johansson & Rowe (1999) separated these effects and showed that damselflies, when manipulated to a later time period by adjustment of the photoperiod, did increase their foraging intensity and their developmental rate (reduced age at maturity), but growth rate itself was independent of these two actions.

A second implication of the increasing importance of the role of the individual, concerns the focus on an individual's fitness. One can study evolutionary processes by following the long-term reproductive success of individually marked organisms. In this type of study, one needs a measure of fitness based on individual lifetime success in order to show any selectional differences between individuals. The use of R_0, in field studies measured as lifetime reproductive success (LRS, studies in Clutton-Brock, 1988; Newton 1989), has been ambiguous (e.g. Grafen, 1988; Murray, 1992). Lifetime reproductive success is usually measured simply as the sum of all offspring produced, because of difficulties in estimating the mortality fractions and average fecundity needed to calculate $R_0 (= \Sigma l_x m_x)$.

Showing the fitness consequences as measured by LRS of a traditionally important life-history trait, such as age at first reproduction, has proven unsuccessful in many studies (examples in Clutton-Brock, 1988). LRS, as a fitness measure, is insensitive to differences in reproductive timing; only the production of one extra offspring is incorporated and not when it was produced. To incorporate intra-individual differences in timing into a fitness measure, one can structure the population *sensu* Metz *et al.* (1992; section V.3) all the way down to

the individual level. Individuals can then be characterised according to their 'reproductive type'. Analogous to constructing a Leslie matrix that contains all relevant transactions of the life-history table (Table 3; Caswell, 1989), one can use the lifetime reproductive success as a trait and compare their growth rates, as estimates of fitness (Table 3; McGraw & Caswell, 1996). Fitness, as measured by the intrinsic rate of increase λ, is in both cases calculated as the dominant eigenvalue of the projection matrix. Often (lifetime) reproductive success and age at first breeding are viewed as separate fitness measures and the incorporation of these two aspects into one fitness measure is necessary for a correct evaluation.

Both the extension of the reaction norm to include behavioural actions and the formulation of a measure of individual fitness, are examples of the change of the position of the individual in life history. In early work, individuals were grouped together *in extremis* by thinking in populations of identical individuals (e.g. Cole, 1954). Starting with the characterisation of individuals by their age (e.g. Gadgil & Bossert, 1970; Schaffer 1974), more and more information on an individual's state was incorporated into theoretical considerations, e.g. habitat (Houston & McNamara, 1992; Kawecki & Stearns, 1993; Kisdi *et al.*, 1998). The formulation of the ESS framework is explicitly based on intra-individual differences and has highlighted the role of the individual. For empirical studies, the ESS concept may also present a powerful alternative way of analysing important processes in life-history evolution. For example, Both, Visser & Verboven (1999) found an effect of relative mass (mass of a fledgling compared to the other fledglings hatched in the same year) on recruitment in great tits and used an ESS-reasoning in motivating and discussing this result.

Ultimately, all factors, be it abiotic, spatial location, individual history or condition that contribute to a classification of state can be, at least in principle, incorporated. Nevertheless, an extensive incorporation of individuals making decisions on the basis of their state, begs the question what state actually stands for in real-life scenarios.

VII. CONCLUSIONS

(1) After Cole (1954) formulated his paradox (why are there iteroparous/perennial species?), interest in life-history problems and especially in the

use of the intrinsic rate of increase r increased. By incorporating more and more biological realism, the principles behind life history were refined.

(2) Especially crucial was the formulation of reproductive effort. The appreciation that individuals can be thought of as balancing costs and benefits and how these could be expressed by Fisherian reproductive value led to an increasing focus on the associated fitness measure r and a rich development of empirical work. Life-history optimisation was thought of as maximising r *per se*.

(3) With the incorporation of the concept of the evolutionarily stable strategy (ESS) in considering evolution of life history, the concept of fitness optimisation was refined. A strategy being played by a population was optimal when no 'mutant' strategy could invade. In practice, this was formulated as a maximisation of the fitness measures r or R_0 with respect to the strategy (typically reproductive effort) under consideration. This reflected the notion that all other strategies were not optimal, because their r or R_0 was lower. Moreover, the importance of the way density dependence acted in optimality considerations was recognised (Charlesworth & Leon, 1976; Michod, 1979).

(4) With the consideration of life histories as presenting individual reaction norms, the environment became a focal issue in explaining life-history variation. Nevertheless, it was soon realised that there was a predictive difference in the use of the fitness measures r and R_0, such that a structurally similar model could generate different predictions, depending on the fitness measure maximised. This problem with predictive differences became, in fact, practically accepted (Stearns, 1992; Roff, 1992).

(5) The problem of predictive differences between fitness measures was solved with an explicit incorporation of density dependence. Evolutionary games are, in essence, frequency dependent; i.e. the success of any strategy depends on the strategy and the frequency of the other players (*sensu* Maynard Smith & Price, 1973). Thus, the number of other players (i.e. density dependence) needs to be explicitly incorporated when considering evolutionary scenarios. Fitness is affected by at least two variables, the life-history action and the environment. When including both, the fitness measures r and R_0 are linked in evolutionary and ecological equilibrium when $r = R_0 - 1 = 0$ and both are maximal (Mylius & Diekman, 1995). Consequently, maximisation of any fitness measure *per se* is only valid in restricted scenarios.

(6) The fitness of any strategy can, conceptually, be thought of as the invasibility of this strategy in a resident population (Metz *et al.*, 1992; Rand *et al.*, 1994). The strategy which cannot be invaded is the ESS and thus optimal. This fitness concept allows to consider whether a population will actually attain the optimal life history strategy (ESS as an evolutionary attractor) (e.g. Geritz *et al.*, 1998). The dimensionality and feedback from the environment, which may include both abiotic and biotic factors, plays a crucial role in determining the outcome (Heino *et al.*, 1998).

(7) Using invasibility as the master fitness-concept, individual plasticity in life-history strategies is highlighted. When individuals are characterised by their state, evolution shapes the individual's policy of state-dependent actions, the reaction norm (e.g. Houston & McNamara, 1999). The consequences of an action depend on an individual's current state, the future state of itself and its offspring and the actions of the other individuals in the population.

VIII. ACKNOWLEDGEMENTS

IX. REFERENCES

ABRAMS, P. A., HARADA, Y. & MATSUDA, H. (1993). On the relationship between quantitative genetic and ESS models. *Evolution* **47**, 982–985.

ABRAMS, P. A., LEIMAR, O., NYLIN, S. & WIKLUND, C. (1996). The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. *American Naturalist* **147**, 381–395.

BOTH, C., VISSER, M. E. & VERBOVEN, N. (1999). Density dependent recruitment rates in great tits: the importance of being heavier. *Proceedings of the Royal Society (London) B*, **266**, 465–469.

BRADSHAW, A. D. (1965). Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* **13**, 115–155.

BRODIN, A. & CLARK, C. W. (1997). Long-term hoarding in the Paridae: a dynamic model. *Behavioral Ecology* **8**, 178–185.

BRYANT, E. H. (1971). Life history consequences of natural selection: Cole's result. *American Naturalist* **105**, 75–76.

BULMER, M. (1994). *Theoretical evolutionary ecology.* Sinauer Associates, Sunderland, Massachusetts.

CASWELL H. (1989). *Matrix Population Models*. Sinauer Associates, Sunderland, Massachusetts.

CASWELL, H., KOENIG, H. E., RESH, J. A. & ROSS, Q. E. (1972). An introduction to system science for ecologists. *Systems Analysis and Simulation in Ecology* (ed. B. C. Patten), pp. 3–78. Academic Press, New York.

CHARLESWORTH, B. (1971). Selection in density-regulated populations. *Ecology* **52**, 469–474.

CHARLESWORTH, B. (1980). *Evolution in age-structured populations*. Cambridge University Press, Cambridge.

CHARLESWORTH, B. (1990). Optimisation models, quantitative genetics, and mutation. *Evolution* **44**, 520–538.

CHARLESWORTH, B. & LÉON, J. A. (1976). The relation of reproductive effort to age. *American Naturalist* **110**, 449–459.

CHARNOV, E. L. & SCHAFFER, W. M. (1973). Life history consequences of natural selection: Cole's result revisited. *American Naturalist* **107**, 791–793.

CLARK, C. W. (1993). Dynamic models of behavior: an extension of life-history theory. *Trends in Ecology and Evolution* **8**, 205–209.

CLUTTON-BROCK, T. H. (ed.) (1988). *Reproductive Success*. University of Chicago Press, Chicago.

COLE, L. C. (1954). The population consequences of life history phenomena. *Quarterly Review of Biology* **19**, 103–137.

DAAN, S., DEERENBERG, C. & DIJKSTRA, C. (1996). Increased daily work rate precipitates natural death in the Kestrel. *Journal of Animal Ecology* **65**, 539–544.

DAAN, S., DIJKSTRA, C. & TINBERGEN, J. M. (1990). Family planning in the kestrel (*Falco tinnunculus*): the ultimate control in covariation of laying date and clutch size. *Behavior* **114**, 83–116.

DIEKMANN, O., HEESTERBEEK, J. A. P. & METZ, J. A. J. (1990). On the definition and the computation of the basic reproductive ratio R_0 in models for infectious diseases in heterogenous populations. *Journal of Mathematical Biology* **28**, 365–382.

ESHEL, I. (1983). Evolutionary and continuous stability. *Journal of Theoretical Biology* **103**, 99–111.

ESHEL, I. (1996). On the changing concept of evolutionary population stability as a reflection of a changing point of view in the quantitative theory of evolution. *Journal of Mathematical Biology* **34**, 485–510.

FISHER, R. A. (1930). *The genetical theory of natural selection*. Clarendon Press, Oxford.

GADGIL, M. & BOSSERT, W. (1970). Life history consequences of natural selection. *American Naturalist* **104**, 1–24.

GERITZ, S. A. H. (1995). Evolutionary stable seed polymorphism and small-scale spatial variation in seedling density. *American Naturalist* **146**, 685–707.

GERITZ, S. A. H., KISDI, É, MESZÉNA, G. & METZ, J. A. J. (1998). Evolutionary singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology* **12**, 35–57.

GLEESON, S. K. (1987). Fitness, reproductive value, and Cole's result. *Oikos* **48**, 116–119.

GOODMAN, D. (1974). Natural selection and cost ceiling on reproductive effort. *American Naturalist* **108**, 247–268.

GRAFEN, A. (1988). On the uses of lifetime reproductive success. *Reproductive Success* (ed. T. H. Clutton-Brock), pp 454–471. University of Chicago Press, Chicago.

GRAFEN, A. (1999). Formal Darwinism. *Proceedings of the Royal Society (London) B* **266**, 799–803.

GUSTAFSSON, L. & SUTHERLAND, W. J. (1988). The costs of reproduction in the collared flycatcher *Ficedula albicollis*. *Nature* **335**, 816–815.

HAMMERSTEIN, P. (1996). Darwinian adaptation, population genetics and the streetcar theory of evolution. *Journal of Mathematical Biology* **34**, 511–532.

HASTINGS, A. (1978). Evolutionary stable strategies and the evolution of life history strategies: I. Density dependent models. *Journal of Theoretical Biology* **75**, 527–536.

HEINO, M., METZ, J. A. J. & KAITALA, V. (1997). Evolution of mixed maturation strategies in semelparous life histories: the crucial role of dimensionality of feedback environment. *Philosophical Transaction of the Royal Society (London) B* **352**, 1647–1655.

HEINO, M., METZ, J. A. J. & KAITALA, V. (1998). The enigma of frequency dependence. *Trends in Ecology and Evolution* **13**, 367–370.

HIRSCHFIELD, M. F. & TINKLE, D. W. (1975). Natural selection and the evolution of reproductive effort. *Proceedings of the National Acadamy of Sciences USA* **72**, 2227–2231.

HOUSTON, A. I. & MCNAMARA, J. M. (1992). Phenotypic plasticity as a state-dependent life-history decision. *Evolutionary Ecology* **6**, 243–253.

HOUSTON, A. I. & MCNAMARA, J. M. (1999). *Models of adaptive behaviour*. Cambridge University Press, Cambridge.

HOUSTON, A. I., MCNAMARA, J. M. & HUTCHINSON, J. M. C. (1993). General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society (London) B* **341**, 375–397.

JOHANSSON, F. & ROWE, L. (1999). Life history and behavioral responses to time constraints in a damselfly. *Ecology* **80**, 1242–1252.

KAITALA, V., MAPPES, T. & YLÖNEN, H. (1997). Delayed female reproduction in equilibrium and chaotic populations. *Evolutionary Ecology* **11**, 105–126.

KAWECKI, T. J. & STEARNS, S. C. (1993). The evolution of life histories in spatially heterogeneous environments: optimal reaction norms revisited. *Evolutionary Ecology* **7**, 155–174.

KISDI, É & MESZÉNA, G. (1993). Density dependent life history evolution in fluctuating environments. In: *Adaptation in a stochastic environment* (eds. C. W. Clark and J. Yoshimura), *Lecture Notes in Biomathematics*, **98**, 26–62.

KISDI, É, MESZÉNA, G. & PÁSZTOR, L. (1998). Individual optimisation: Mechanisms shaping the optimal reaction norm. *Evolutionary Ecology* **12**, 211–221.

KOKKO, H. & SUTHERLAND, W. (1998). Optimal floating and queuing strategies: consequences for density dependence and habitat loss. *American Naturalist* **152**, 354–366.

KOZŁOWSKI, J. (1992). Optimal allocation of resources to growth and reproduction: implications for age and size at maturity. *Trends in Ecology and Evolution* **7**, 15–19.

KOZŁOWSKI, J. (1993). Measuring fitness in life-history studies. *Trends in Ecology and Evolution* **8**, 84–85.

KOZŁOWSKI, J. & UCHMANSKI, J. (1987). Optimal individual growth and reproduction in perennial species with indeterminate growth. *Evolutionary Ecology* **1**, 214–230.

KOZŁOWSKI, J. & WIEGERT, R. G. (1987). Optimal age and size at maturity in annuals and perennials with determinate growth. *Evolutionary Ecology* **1**, 231–244.

LANDE, R. (1982). A quantitative genetic theory of life history evolution. *Ecology* **63**, 607–615.

LEIMAR, O. (1996). Life history plasticity: influence of photo-

period on growth and development in the common blue butterfly. *Oikos* **76**, 228–234.

LESSELS, C. M. (1991). The evolution of life histories. *Behavioural ecology* 3rd *edition* (eds J. R. Krebs & N. B. Davies), pp 32–68. Blackwell Scientific Publications, Cambridge.

LUTZ, P. E. (1968). Effects of temperature and photoperiod on larval development in *Lestes eurinus* (Odonata: Lestidae). *Ecology* **49**, 637–644.

MAYNARD SMITH, J. (1982). *Evolution and the theory of games*. Cambridge University Press, Cambridge.

MAYNARD SMITH, J. (1993). Life history, symmetry and evolution. *Quarterly review of biology* **68**, 557–559.

MAYNARD SMITH, J. & PRICE, G. R. (1973). The logic of animal conflict. *Nature* **246**, 15–1.

MCGRAW, J. B. & CASWELL, H. (1996). Estimation of individual fitness from life-history data. *American Naturalist* **147**, 47–64.

MCNAMARA, J. M. (1991). Optimal life histories: a generalisation of the Perron–Frobenius Theorem. *Theoretical Population Biology* **40**, 230–245

MCNAMARA, J. M. (1993). Evolutionary paths in strategy space: An improvement algorithm for life-history strategies. *Journal of Theoretical Biology* **161**, 23–37.

MCNAMARA, J. M. (1995). Implicit frequency dependence and kin selection in fluctuating environments. *Evolutionary Ecology* **2**, 185–203.

MCNAMARA, J. M. & FORSLUND, P. (1996). Divorce rates in birds: predictions from an optimisation model. *American Naturalist* **147**, 609–640.

MCNAMARA, J. M. & HOUSTON, A. I. (1996). State-dependent life histories. *Nature* **380**, 215–221.

MCNAMARA, J. M. & HOUSTON, A. I. (1997). Currencies for foraging based on energetic gain. *American Naturalist* **150**, 603–617.

MCNAMARA, J. M., HOUSTON, A. I. & LIMA, S. L. (1994). Foraging routines of small birds in winter: A theoretical investigation. *Journal of Avian Biology* **25**, 287–302.

METZ, J. A. J. & DIEKMANN, O. (1986). *The dynamics of Physiologically Structured Populations*. Springer-Verlag, Berlin.

METZ, J. A. J., NISBET, R. M. & GERITZ, S. A. H. (1992). How should we define 'fitness' for general ecological scenarios. *Trends in Ecology and Evolution* **7**, 198–202.

MICHOD, R. E. (1979). Evolution of life histories in response to age-specific mortality factors. *American Naturalist* **113**, 531–550.

MURRAY, B. G. (1992). The evolutionary significance of lifetime reproductive success. *The Auk* **109**, 167–172.

MYLIUS, S. D. & DIEKMANN, O. (1995). On evolutionary stable life histories, optimisation and the need to be specific about density dependence. *Oikos* **74**, 218–224.

NEWTON, I. (ed.) (1989). Lifetime Reproduction in Birds. Academic Press, London.

PÁSZTOR, E. & LOESCHKE, V. (1989). The coherence of Cole's result and Williams' refinement of Lack's principle. *Oikos* **56**, 416–420.

PÁSZTOR, L., MESZÉNA, G. & KISDI, É. (1996). R_0 or r: A matter of taste? *Journal of Evolutionary Biology* **9**, 511–518.

PIANKA, E. R. & PARKER, W. S. (1975). Age-specific reproductive tactics. *American Naturalist* **109**, 453–464.

PULLIAM, H. R. (1988). Sources, sinks, and population regulation. *American Naturalist* **132,** 652–661.

RAND, D. A., WILSON, H. B. & MCGLADE, J. M. (1994). Dynamics and evolution: evolutionary stable attractors invasion exponents and phenotypic dynamics. *Philosophical Transactions of The Royal Society (London)* B **343**, 261–283.

ROFF, D. A. (1992). *The evolution of life histories*. Theory and analysis. Chapman and Hall, New York, London.

ROWE, L., LUDWIG, D. & SCHLUTER, D. (1994). Time, condition and the seasonal decline of avian clutch size. *American Naturalist* **143**, 698–722.

SCHAFFER, W. M. (1974) Selection for optimal life histories: the effect of age structure. *Ecology* **55**, 291–303.

SCHAFFER, W. M. & ROSENZWEIG, M. L. (1977). Selection for optimal life histories II: multiple equilibria and the evolution of alternative reproductive strategies. *Ecology* **58**, 60–72.

SMITH, C. C. & FRETWELL, S. D. (1974). The optimal balance between size and number of offspring. *American Naturalist* **108**, 499–506.

SOUTHWOOD, T. R. E. (1977). Habitat, the templet for ecological strategies? *Journal of Animal Ecology* **46**, 337–365.

STEARNS, S. C. (1976). Life history tactics: A review of the ideas. *Quarterly review of biology* **51**, 3–47.

STEARNS, S. C. (1992). *The evolution of life histories*. Oxford University Press, Oxford.

STEARNS, S. & KOELLA, J. (1986). The evolution of phenotypic plasticity in life history traits: Predictions for norms of reaction for age and size at maturity. *Evolution* **40**, 893–913.

TAYLOR, H. M., GOURLEY, R. S. & LAWRENCE, C. E. (1974). Natural selection on life history attributes: an analytical approach. *Theoretical Population Biology* **5**, 104–122.

TINBERGEN, J. M. & DAAN, S. (1990). Family planning in the great tit (*Parus major*): Optimal clutch size as integration of parent and offspring fitness. *Behaviour* **114**, 161–190.

TULJAPURKAR, S. (1989). An uncertain life: demografy in random environments. *Theoretical Population Biology* **35**, 227–294.

VEERMAN, A. (1994). Photoperiodic and thermoperiodic control of diapause in plant-inhabiting mites: A review. *Netherlands Journal of Zoology* **44**, 139–155.

WEISSING, F. J. (1996). Genetic versus phenotypic models of selection: can genetics be neglected in the long-term perspectives? *Journal of Mathematical Biology* **45**, 533–555.

WILLIAMS, G. C. (1966). Natural selection, the costs of reproduction and a refinement of Lack's principle. *American Naturalist* **100**, 687–690.

WOLTERECK, R. (1909). Weitere experimentelle Untersuchungen über Artveränderung, speziell über das Wesen quantitativer Artunderschiede bei Daphniden. *Verhaltungen des Deutsches Zoologisches Gesellschaft* **1909**, 110–172.

YODZIS, P. (1981). Concerning the sense in which maximising fitness is equivalent to maximising reproductive value. *Ecology* **62**, 1681–1682.