

*Reprinted from*  
**GENES IN ECOLOGY**

The 33rd Symposium of  
The British Ecological Society  
University of East Anglia

Edited by  
**R.J. BERRY, T.J. CRAWFORD  
AND G.M. HEWITT**

Blackwell Scientific Publications  
Oxford London Edinburgh Boston  
Melbourne Paris Berlin Vienna  
19912

#### 4. LIFE-HISTORY EVOLUTION

RICHARD SIBLY\* AND JANIS ANTONOVICS†

\**Department of Pure and Applied Zoology, University of Reading, Reading RG6 2AJ, UK* and †*Department of Botany, Duke University, Durham, North Carolina 27706, USA*

##### SUMMARY

The life history is a focal point for the intersection of population genetics and population ecology. Nevertheless historically life-history variation has been studied either from a 'genetic' or from an 'ecological' point of view. The genetic approach has involved a detailed analysis of selection acting on multivariate age-specific life-history components. The ecological approach has used optimality analysis to determine the life-history features that will produce the highest population growth rate in a particular environment. We make explicit the relationship between these two approaches and show them to be complementary. Optimality analysis is illustrated by considering how big offspring should be, how fast they should grow, whether they should continue to grow after first reproduction, and what size and how fecund adults should be. We discuss various approaches to testing life-history theory and the special challenges that life-history traits present to the empiricist.

##### INTRODUCTION

The life history, defined as the schedule of age-specific birth and death rates of a population or class of individuals, has been the focal point for the merger of the disciplines of population genetics and population ecology. This merger, a belated evolutionary synthesis (Anderson & King 1970, Charlesworth & Giesel 1972a, b), converted the subject of ecological genetics from a discipline that simply studied genetic variation in an ecological (and by implication natural) context (Ford 1964), to a discipline that promised truly to integrate ecological and evolutionary thinking. The life history was an expression of fitness of a phenotype in the context of natural selection as well as an expression of the contribution of that class of phenotypes to population growth. Theoretical studies (e.g. Charlesworth & Giesel 1972a, b) showed clearly that the relative fitness of genotypes could depend critically on population growth rates, and that population

growth rates could be influenced by genotypic composition (King & Anderson 1971).

In an ideal world, all individuals should have an infinite number of offspring which have an infinite life span and which reproduce as soon as they are born! The biological reality is that different species have widely divergent life histories, and once this obvious fact was pointed out by Deevey (1947), the life history and the forces that mould its evolution became an object of fascination and study. This generated a research agenda that has lasted to the present day. Much of this fascination was fuelled by Cole's (1954) paper, which presented the now famous but by no means irresolvable dilemma that the fitness of an annual (semelparous) species will be equal to the fitness of a perennial (iteroparous) species if it produced one extra offspring. This made it hard to see why perennials would ever evolve.

In spite of these seminal papers, very little theoretical progress in understanding life-history evolution was made until the development of the ideas of  $r$ - and  $K$ -selection by MacArthur (1962). His theory integrated genetic and ecological ideas in that it was based on genetic variation in the parameters of the logistic population growth equation. He showed in populations obeying logistic growth dynamics, that under low density, genotypes with high  $r$  would be favoured, but that at high density, i.e. at carrying capacity,  $r$  was now irrelevant and that genotypes with high  $K$  would be favoured. Given a trade-off between high fecundity at low density and high performance in resource-limited conditions of high density, it was easy to see that organisms may indeed evolve quite different life histories.

The prospect of being able to explain life-history evolution by the  $r$ - $K$  continuum was a seductive one but the idea rapidly gained as many opponents as converts. At one level the theory fits what we know about the world (weeds versus trees, aphids versus elephants) but at the same time it was clearly over-simplified. A number of other classificatory schemes for life histories were therefore developed. However, because of the multitude of selective forces acting on life histories and the diversity of responses by different organisms to similar forces, none of these schemes has gained general acceptance (see Southwood 1988, for a review of 'ecological periodic tables').

Since the 1970s numerous approaches have been used to model life history evolution. The raw genetic approach is to use explicit single-locus or two-locus genetic models, where genotypes are assigned life-history schedules of births and deaths; this permits exploration of the dynamics of gene frequency change and equilibrium outcomes (e.g. Anderson &

King 1970). This approach can be extended to a quantitative genetics scenario, where now the life-history traits are described by a genetic variance-covariance matrix, and evolutionary trajectories are explored under different types and intensities of selection (e.g. Lande 1982). A very common method has been to compare the intrinsic rates of increase of contrasting life-history phenotypes, and to ask under what circumstances a particular phenotype will have the highest increase (e.g. Bell 1980). A similar approach is to use some form of options set or trade-off surface (see later) to predict which combination of life-history parameters will have the highest fitness under particular circumstances (e.g. Pianka & Parker 1975). Such ecological models are seemingly gene free but they can be conceptually grounded in genetic models given some not unreasonable assumptions. An explicit mathematical reconciliation of the optimality and quantitative genetics approaches has recently been described by Charlesworth (1990); such a reconciliation is dependent on weak selection and trade-off curves that can as a first approximation be treated as linear functions.

Not only has it come to be appreciated that the processes of life history evolution are diverse but the theoretical approaches taken by ecologists and geneticists in trying to understand life-history evolution have also been wide ranging (e.g. Schaffer 1974a, b, Lande 1982). The ecologists have focused on asking which specific life histories might produce higher population growth rates in which environments, and they have considered trade-offs among life-history processes as the inevitable outcome of individual limits to resource acquisition and allocation of these limited resources to competing physiological functions. The geneticists on the other hand have viewed life-history evolution as the result of selection of alleles with age-specific effects; they have considered trade-offs to be due to pleiotropic gene effects within populations that produced genetic covariances among traits that constrained the joint evolution of multiple (life history) character states. It is almost as if ecologists viewed the life history as a property of a population and trade-offs as a property of an individual, whereas the geneticists saw the life history as a property of individual alleles and trade-offs as a property of the population in which those alleles resided. These two approaches, for want of better terms we shall call the 'ecological approach' and the 'genetic approach'.

To understand the relationship between ecological and genetic approaches to life-history evolution, we begin by describing in the next section how the rate of increase of an allele depends on its effects on life-history components. We then describe how such a population genetic approach relates to optimality theories based on trade-off curves and

fitness functions. We illustrate the optimality approach by considering some general predictions of life-history theory. In the last section we discuss explicitly how life-history theory is testable but also emphasize why life-history evolution presents unique challenges for the empiricist.

#### EVOLUTION: PROCESS AND OUTCOME

We start our analysis by considering what happens in asexual populations because in this case there is a direct link with population dynamics in the concept of the rate of increase of a population. Later we proceed to the sexual case, which we introduce with a simple graphical approach (Figs 4.1 and 4.2).

Ecologists have traditionally translated the overall age-specific survivorship and fecundity schedules of individuals into estimates of intrinsic rates of increase of the population,  $r$ , using the Euler-Lotka equation:

$$1 = \sum_{x=1}^{\infty} n(x)l(x)e^{-rx}$$

where  $n(x)$ ,  $l(x)$  are the female age ( $x$ ) specific fecundity and survival respectively.

If we consider any population as a collection of genotypes, each with its own age-specific life-history characteristics, and for the moment assume that these genotypes are asexual, then the intrinsic rate of increase of the  $i^{\text{th}}$  genotype would be given by:

$$1 = \sum_{x=1}^{\infty} n_{ij}(x)l_{ij}(x)e^{-r_{ij}x} \quad (1)$$

The absolute fitness of the  $i^{\text{th}}$  genotype would be  $\lambda_{ij} = e^{r_{ij}}$ , which can easily be relativized to the most fit genotype to give the more traditional relative fitnesses of population genetics. However, this parallel between the ecological and genetic approaches is based on a large number of assumptions, the most important being that the genotypes are asexual. If the genotypes are interbreeding, then there will be Mendelian assortment of genes every generation.

Before proceeding to the algebraic treatment of what happens in sexual populations, consider Fig. 4.1, which provides a simple graphical account of the main ideas. The evolutionary process is envisaged, put very simply, as consisting of the creation (by mutation) of new alleles, which either displace or are displaced by their counterparts. In Fig. 4.1, alleles A-E affect two life-history traits of carriers. Note that most individuals carry the A allele in Fig. 4.1a and so have small values of both

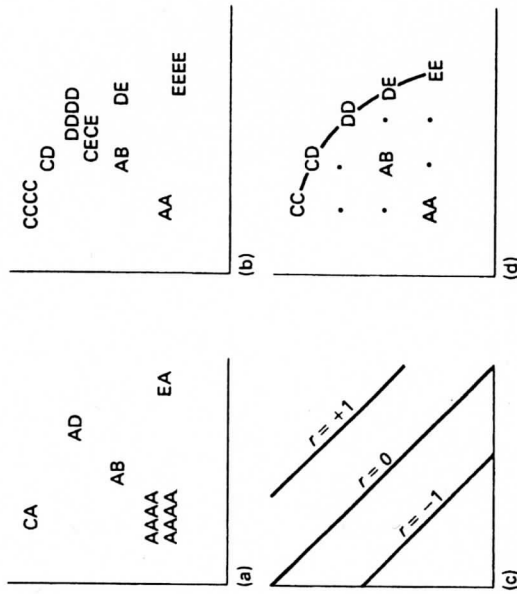


FIG. 4.1. Simple example of an evolutionary process. Axes represent two life-history traits. Note that the alleles far from the origin (C-E) have increased in numbers between (a) and (b) whereas those near the origin (A) have decreased. Per copy rates of increase (i.e. fitnesses) are shown in (c). The extant genetic options set with genotypes obtainable by recombination represented as dots is shown in (d). The boundary of the options set is the trade-off curve (thick line). See text for further details.

traits, but a few individuals have larger values so that overall there is a small positive correlation between individuals. If there is not much environmental variation, this reflects a positive genetic correlation (e.g. the two traits are correlated because they are determined by alleles that have an effect on the magnitude of both traits).

Figure 4.1b represents a hypothetical situation at some later time in the selection process. Now most of the small-trait A alleles have disappeared but the numbers of the large-trait alleles (C-E) have increased. Furthermore, the genetic correlation between individuals is now negative, whereas earlier it was positive. Empirical evidence for such a scenario has been given by Holloway *et al.* (1990).

Clearly all depends on whether or not an allele spreads in the population — i.e. on the rates of increase of the alleles (called *fitness* hereafter). Since these depend on their effects on life histories, they can be plotted out in the space of Fig. 4.1, as shown in Fig. 4.1c. In our

example the small-trait alleles have negative rates of increase, corresponding to their decline in the population, whereas the large-trait alleles have positive rates of increase, since they are spreading. Evolutionary change can also occur, however, if both small- and large-trait alleles increase but at different rates.

In general, as selection proceeds, the cloud of points in Fig. 4.1 changes shape. In the absence of environmental variation, the shape of the cloud is measured by genetic correlations and variances (i.e. the  $G$  matrix) and as the cloud changes shape, the genetic correlations and variances change accordingly. In the absence of further mutation, where would this process end up?

In considering the eventual outcome of this selection process it is natural to restrict attention to a constant environment, or one in which the environmental variation is specified by constant parameters (e.g. randomly changing or cycling annually). It is important to realize that the environment of an individual depends not only on physical features (e.g. temperature, rainfall) and biotic features determined by other species (e.g. food availability, predation) but also has characteristics determined by conspecifics, such as territory size, availability of mates, competition for food and so on.

In this environment many alleles will affect life-history components. Plotting out all these genetically-codable options (including all possible recombinants) in a space like that of Fig. 4.1a gives us a set of points we shall call the *extant genetic options set* (Fig. 4.1d). However, the evolutionary process is a dynamic one, and we consider that there also exists for any population (or set of populations) within any time scale a *potential genetic options set* which represents what is possible given mutation and recombination. When considering different genetic possibilities, care is needed in saying what we mean by the 'study organism' — how far are we allowed to change it before it is no longer the same organism (Maynard Smith 1991)? Technically this is the same problem as specifying the set of alleles defining a species. The potential genetic options set has also been variously referred to as a 'strategy set' (Parker & Maynard Smith 1990) or as a 'fitness set' when the traits contribute linearly and equally to fitness (e.g. Charnov 1982).

A three-dimensional example of an options set is shown in Fig. 4.2a. We will not here distinguish between a genotype options set (as in Fig. 4.1d) and an allele options set, representing the average characteristics of each allele, but note that the type of options set should match the fitness accounting system, so either both should use alleles, or both should use genotypes.

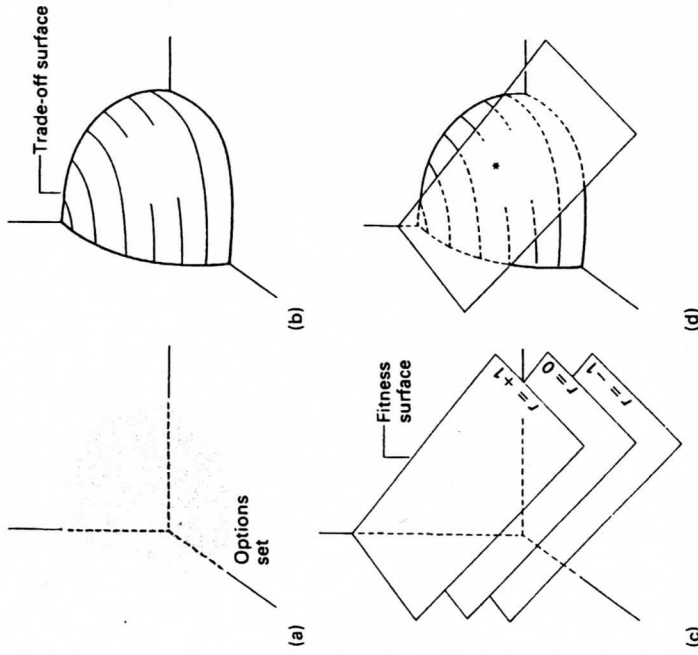


Fig. 4.2. The options set in three dimensions. (a) The options set comprises a volume. (b) The boundary of the options set is a trade-off surface. (c) Points giving equal fitness  $r$  now form surfaces (cf. Fig. 4.1c). (d) The outcome of selection — i.e. the optimal strategy — is the point (\*) in the options set giving the highest fitness in the study environment.

Of particular interest, because it limits selection, is the boundary of the options set. We shall call this the *trade-off curve* (two dimensions) or *trade-off surface* (three dimensions) or, in general, the *trade-off hypersurface* ( $n$  dimensions) (Fig. 4.2b). This trade-off (hyper)surface represents the best that this type of organism can achieve genetically in the study environment.

Putting together the information about fitness (Figs 4.1c and 4.2c) with the information on options sets (Figs 4.2a and b) the optimal strategy is readily identified (Fig. 4.2d) as that having the highest fitness in the study environment. This point, then, represents the eventual outcome of selection in this environment.

For short-term evolutionary predictions within local populations, the fitness surfaces together with the extant genetic options set as defined by the genetic variance-covariance matrix will determine the evolutionary trajectories. On the other hand if we wish to make predictions over a longer term, and/or for example, within a taxonomic group, there may be no direct method of estimating the potential options set (indeed, it may be in a strict sense 'unknowable', given the stochasticity of mutational events). However, within a particular taxonomic group, a number of aspects of the physiology and ecology of the group may be relatively invariant, thus allowing us to infer the likely shape of the trade-off surface. We can now caricature more precisely the views of the 'geneticist' and the 'ecologist' as to what a trade-off represents. For the geneticist, it is a population property because the trade-off is measured on an extant options set. The ecologist, on the other hand, views the trade-off in terms of the potential options set, best estimated by understanding the 'underlying physiology' of the individual. Such within-individual trade-offs must, however, have implications for the shape of the genetic options set (Smith *et al.* 1987, Partridge & Sibly 1991, Smith 1991).

In this section we have made a distinction between the process and the outcome of selection. This makes explicit the relationship between quantitative genetics, which models the process, and optimality theory (ecology) which locates the outcome of the selection process.

In the next section we give algebraic form to some of these ideas.

#### *How fitness (rate of increase) depends on life-history components*

As we have seen, whether or not an allele is able to spread in a population depends on its rate of increase. Suppose that at some locus there are only two alleles,  $A_1$  and  $A_2$ , in proportions  $p$  and  $q$ , with  $p + q = 1$ . Then the rate of increase of the proportion of  $A_1$  is  $dp/dt$ . How is gene frequency change related to the life-history characteristics of the two genotypes in which the  $A_1$  allele occurs, namely  $A_1A_1$  and  $A_1A_2$ ? The solution was given by Charlesworth (1980). The first step is to define the age-specific life-history characteristics of each genotype (Fig. 4.3a); thus let  $l_{ij}(x)$  be the chance of survival from birth to age  $x$  of individuals of the  $ij$  genotype (i.e. here  $A_1A_1$ ,  $A_1A_2$  or  $A_2A_2$ ), and let  $n_{ij}(x)$  be the expected number of daughters at age  $x$ . Intrinsic rate of increase of the  $ij$  genotype is then defined as the number,  $r_{ij}$ , which solves the Euler-Lotka (Eqn 1). We assume that the sexes have identical life histories and that the life-history characteristics do not change with allele frequencies (otherwise the formulations are more complex: Charlesworth 1980, Abugov 1988).

Charlesworth (1980, p. 206) showed that under weak selection the proportionate rate of increase of  $A_1$  is given approximately by:

$$dp/dt = pq(pr_{11} + (q - p)r_{12} - qr_{22}) \quad (2)$$

Examining Eqn (2), we now ask, what causes  $dp/dt$  to increase, or in other words what causes  $A_1$  to spread faster? Clearly anything increasing  $r_{11}$  will. When  $r_{12}$  is increased but  $r_{11}$  and  $r_{22}$  are unaffected  $dp/dt$  is increased when  $A_1$  is rare ( $p \approx 0$ ), so  $A_1$  will spread. However, if  $A_1$  were ever to approach fixation, it would be selected against, since then  $q = 0$ , and  $dp/dt$  is decreased. Thus  $A_2$ , not  $A_1$ , then spreads because of 'heterozygous advantage'.

Therefore, a new mutant will spread in the population (at least initially) if it results in a greater intrinsic rate of increase of the genotypes which now carry it. Intrinsic rate of increase, defined as in Eqn (1), therefore provides a measure of genotypic fitness.

A similar approach, but one which simplifies some of the calculations by restricting attention to dominant alleles, was suggested by Sibly and Calow (1986, see Sibly & Curnow, in press). In this case the life history of the heterozygote is the same as that of the homozygote, and it turns out that an allele's per copy rate of increase (hereafter called allelic fitness) is given by  $r$  in an equation looking like Eqn (1), viz.

$$1 = \frac{1}{x} \sum_{x=1}^{\infty} n(x) l(x) e^{-rx} \quad (3)$$

where  $l(x)$  and  $n(x)$  are characteristics of individuals carrying the allele:  $l(x)$  is the chance of carriers surviving from birth to age  $x$ , and  $n(x)$  is the number of offspring at age  $x$  (Sibly 1989). In Eqn (3) the  $\frac{1}{x}$  represents the chance of a given allele being transferred from parent to offspring: a given allele is transferred to half the offspring on average by Mendel's laws. However, if segregation is distorted, for example by meiotic drive, or if there is selfing, the  $\frac{1}{x}$  should be adjusted appropriately. Although  $A_2$  is contained in the heterozygote and it might seem that the per copy rate of increase of  $A_1$  would depend on the genotypes carrying it, with dominance one can show it is not necessary to take into account the frequency of  $A_2$ .

An attraction of this approach is that general life histories can be handled directly — examples are given in Fig. 4.3. Note that although genotypic and allelic fitnesses are interchangeable for some purposes, they may not be interchangeable when timing of the life history is affected as in some of the models in Fig. 4.3, since genotypic equivalents have not been derived for all the allelic treatments. In Fig. 4.3b, the timing of the

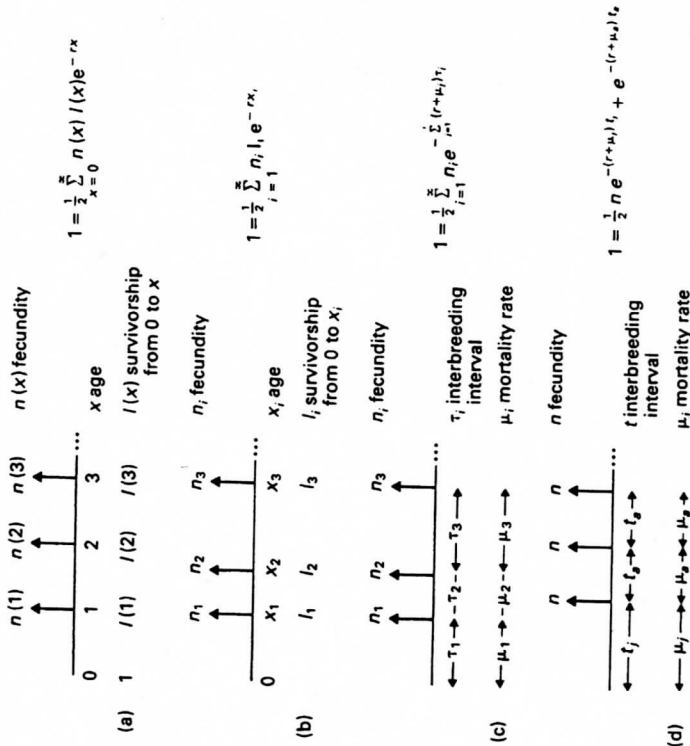


FIG. 4.3. The life histories and associated equations discussed in the text. (a) Life history with regular breeding. (b) Life history with irregular breeding. (c) Reparameterization of (b) to obtain independent variables  $\tau$  and  $\mu$ . (d) Simple regular life history in which parameters vary between juvenile,  $j$ , and adult,  $a$ , phases.

different breeding episodes is now one of the key life-history variables, allowing consideration of irregular breeding, which cannot be handled within the framework of Fig. 4.3a. The modified form of the Euler-Lotka equation is shown on the right of Fig. 4.3b.

The parameterization of the life history shown in Fig. 4.3b suffers from the disadvantage that the parameters are not independent of each other. Thus the timing of the  $i^{\text{th}}$  breeding event ( $x_i$ ) is likely to depend on the timing of the  $(i-1)^{\text{th}}$  event — if that is delayed, there are likely to be effects for subsequent reproduction. Similarly  $l_i$ , the probability of survival from birth until the  $i^{\text{th}}$  breeding attempt, obviously depends on when the  $i^{\text{th}}$  breeding attempt occurs — if it is delayed, the chances of survival are reduced because of extrinsic mortality. Furthermore, survivorship to the

$i^{\text{th}}$  breeding attempt depends on survivorship to the  $(i-1)^{\text{th}}$  breeding attempt, and so on. Thus the  $l_i$  variables are not independent of each other either. Both these problems can be circumvented by replacing the  $x$  and  $l$  variables by a set of independent variables  $\tau$  and  $\mu$  defined as in Fig. 4.3c. The mortality rates  $\mu$  are independent of each other, and in the absence of trade-offs they are independent of the timing of breeding events.

We shall later consider in some detail the case in which adult characteristics do not change after the age of first reproduction. The resultant life history and associated equation are shown in Fig. 4.3d.

In principle the fitness of alleles in organisms such as plants which use both sexual and vegetative reproduction can be handled by methods similar to those shown in Fig. 4.3 (Sibly 1989).

The above life-history components can be divided into two categories: those that depend on rate of production of new biomass and those that affect the survival of that biomass. We can call these 'production rate' (Sibly & Calow 1986) and 'mortality rate' variables. For example, production rate affects age to first reproduction, offspring size, fecundity and interval between breeding. In this way the timing and extent of reproduction are determined by production rate. The remaining life-history components represent mortality rates,  $\mu_i$  defined as in Fig. 4.3c. It is interesting to note that mortality rate always appears in the equations added to  $r$ .

Using the above formulation it is easy to show that in the absence of trade-offs there is always selection to increase fecundity, decrease mortality rate and breed early (Sibly 1989). In the next section we outline what happens when trade-offs occur, using the concepts of genetic options sets and fitness surfaces to illustrate the richness of life-history theory and the diversity of possible evolutionary outcomes, following the general approach of Sibly and Calow (1986). We go through an organism's life history, and consider the types of forces that might mould offspring size, juvenile growth rate, post-reproductive growth, adult size and adult fecundity. We then illustrate how this approach can be extended to considerations of sex allocation involving extension of the models to frequency-dependent processes.

### TRADE-OFFS BETWEEN LIFE-HISTORY COMPONENTS

Limits to life history evolution are obviously set by the fact that organisms cannot, to any large degree, simultaneously increase their fecundity, decrease their mortality and decrease the age at reproduction. There are

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trade-offs between these (and other) aspects of the life history. Trade-offs are often viewed by ecologists as the inevitable consequence of the physiological and behavioural allocations of an individual. Thus, resources can be allocated to growth or reproduction, or resources devoted to reproduction can be partitioned among a few large offspring or many small offspring; time spent handling prey items will be at a cost to time spent foraging; and so on. Functional relationships between life-history traits will almost certainly be evident whenever these traits vary. For present purposes we assume that each such trade-off has a genetic basis and we present an optimality analysis for the life history in Fig. 4.3d.

#### How big should offspring be?

The product of offspring size and offspring numbers is here taken to be fixed (equal to 'reproductive effort'). Offspring size can affect a number of life-history characters, for example juvenile mortality rate (Taylor & Williams 1984) but here we consider only development period (i.e. time to first reproduction). If we assume that size at first reproduction is fixed, then there will be a trade-off between offspring size and juvenile development period, since smaller offspring have further to grow (Fig. 4.4). Fitness contours can be calculated from the equation in Fig. 4.3c or d and have slope  $-1/(r + \mu_j)$  (Sibly & Calow 1985). Optimal offspring size is the point where one such line touches the trade-off curve (starred in

Fig. 4.4). One of the most interesting applications of this result is to use it to compare optimal strategies in habitats differing in production rate. Suppose the trade-off in Fig. 4.4a represented the situation when production rate was low and consider the likely changes if production rate was increased (Fig. 4.4b). Note that the trade-off in the good habitat is everywhere below and steeper than that in the poor one (Sibly & Calow 1985). Assuming for simplicity that  $\mu_j$  is the same in the two habitats and that ecological compensation (by other components of the life history, Sibly & Calow 1987) has resulted in  $r$  also being the same (e.g. zero), then it is easy to see that optimal offspring size in the good habitat is smaller than that in the poor (Fig. 4.4, Sibly & Calow 1985). In this way, if trade-offs with mortality are not involved, the effect of the habitat on production rate will determine offspring size, with smaller offspring being produced where production rate is higher.

#### How fast to grow?

After birth a variety of growth strategies may be possible but this may also affect the risks that the individual takes and hence the mortality rate. Thus it may be possible for animals to increase production rate by feeding more at increased cost in terms of personal safety, or for better quality food in more dangerous places or at more dangerous times of day. Alternatively, resources may be allocated to personal defence which could otherwise have gone to production. Thus energy, nutrient or water reserves may help avoid starvation or desiccation. Other examples would include thorns, toxins, protective coloration, or immune and detoxification systems. The relationships between mortality and allocation to defence can be plotted as an options set in a space with axes mortality rate and growth rate, and a trade-off curve defined as the boundary of such a set (Fig. 4.5). The resultant curve has the features that: (1) even when growth rate is maximal (zero allocation to defence) growth rate is finite — equal to the limiting production rate in the study environment; (2) even if all resources are allocated to defence, mortality rate is still greater than zero, equivalent to the 'extrinsic' mortality rate in that environment. The simplest shape the trade-off curve can take is therefore that shown in Fig. 4.5, i.e. convex seen from below. The  $r = 0$  fitness contour is a straight line through the origin (Sibly & Calow 1989).

What happens to the optimal strategy if the production or mortality regimes change? In general, such changes will change the shape as well as the position of the trade-off curve, but since we lack insight into how shape might change, we shall hold shape constant for the purposes of

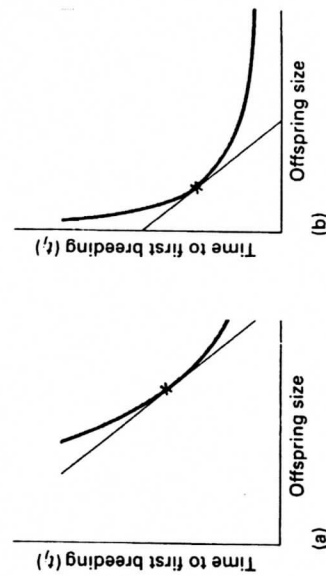


FIG. 4.4. The trade-off curve (thick line) relating offspring size to development period  $t_f$  in an environment with (a) low and (b) high production rate. In this and subsequent figures shaded areas represent genetic option sets, thick lines represent trade-off curves, thin lines represent contours and \* represents the selection outcome (optimal strategy). See text for further details.



fixed adult size is optimal, i.e. growth followed by reproduction, with no intermediate phase of simultaneous reproduction and growth. These conclusions are surprising given the ubiquity of growth after first reproduction in nature (but see also Gabriel (1982), who used numerical methods to show that intermediate strategies could be optimal if life span was finite and both production and mortality rates increased with size, and see also Kozlowski (1991), Pugliese and Kozlowski (1990) and Taylor and Gabriel (1992)).

From now on we assume for simplicity that there is no growth after first reproduction.

What size adults?

Now suppose that egg size is fixed so that, since it necessarily takes longer to grow to be bigger, larger adult size can only be achieved at the cost of a longer development period. As noted above, in the absence of trade-offs there is always selection to minimize development period, and hence adult size. Thus in the absence of trade-offs, adults should be as small as possible.

What usually prevents this happening in practice is a trade-off that arises because larger adults are more fecund. This produces a trade-off between development period and fecundity, as shown in Fig. 4.6a. If the options set is known, optimal body size can be readily identified.

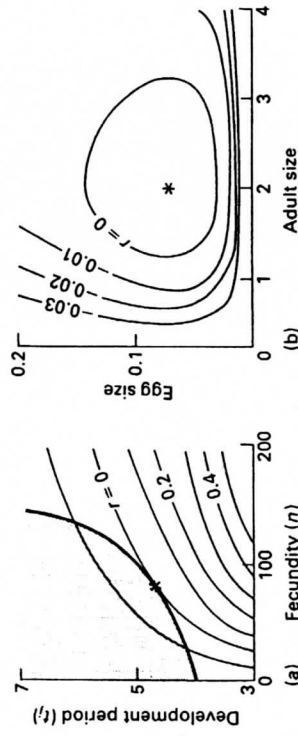


FIG. 4.6. Calculation of adult body size with offspring size fixed (a) or allowed to vary (b). Larger adults are more fecund but take longer to develop, so fecundity trades off against development period (a) (from Sibly *et al.* 1985). To construct the example in (b) it was supposed that  $n \times (\text{egg size}) = (1 - \exp(-0.3 \times (\text{adult size})) + 0.5(\log_e(\text{egg size}))^2 + 2$ .

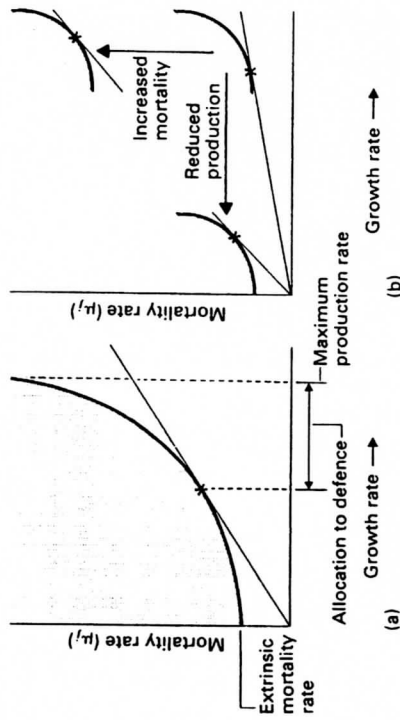


FIG. 4.5. (a) Allocation of resources to defence reduces mortality rate but simultaneously cuts growth, here defined as  $1/t_1$ , i.e. growth rate is inverse time to first reproduction. The  $r = 0$  fitness contour is a straight line through the origin. (b) If only the position of the trade-off curve is changed, by reducing maximum production or increasing mortality rate, the effect on optimal strategy is a reduced allocation to defence. See text for further details.

discussion. Allowing only the position of the trade-off curve to change, it is clear that increasing (extrinsic) mortality rate moves the curve vertically upwards, whereas decreasing production rate moves the curve horizontally to the left (Fig. 4.5b). Assuming ecological compensation acts elsewhere in the life history to keep  $r$  zero in all three situations, the optimal strategy lies in each case on a straight line through the origin (Fig. 4.5b). Thus, either sort of worsening of the environment (increasing mortality or decreasing production) results in a reduced optimal allocation to defence.

Should organisms continue to grow after first reproduction?

This is one of the classical problems of life-history theory: if production and mortality rates depend solely on body size, and if maximum life span is given, then what is the optimal size at first reproduction, and how (if at all) should the organism grow thereafter? It is usually assumed that production is split between growth and reproduction, and that birth rate and specific growth rate are linearly proportional to their allocations from production. Analyses so far include infinite life span models with general production and mortality regimes (e.g. Taylor *et al.* 1974 and Sibly *et al.* 1985), and models with limited life span but no size-dependent mortality (Ziolkowski & Kozlowski 1983). These analyses concluded that generally

What happens if both egg size and adult size are allowed to vary? Both have consequences for development period. A simple example to illustrate what might happen is shown in Fig. 4.6b.

#### How fecund?

A classic problem in life-history theory concerns the number of offspring to produce in the case that increased fecundity results in an increase in post-reproductive adult mortality. Other costs of reproduction, perhaps more serious in practice, but not considered here, include delays and decreases in subsequent reproduction (see for example, Lessells 1991). Also important, and also not treated here, is the Lack case in which number of offspring trade off against their individual survivorship, in species with parental care (Lack 1954, Nur 1984).

Certain features of the curve specifying the trade-off between fecundity and mortality can be deduced *a priori*. Even when fecundity is nil, mortality must be greater than zero (extrinsic mortality), but maximum fecundity is finite, and then, since all resources are devoted to reproduction, no resources are left for maintenance, so the organism dies (i.e. infinite mortality rate). Hence the options set is likely to be convex (Fig. 4.7). In this case there is no very easy way to find the optimal strategy. However, the optimal strategy can be characterized by a differential equation:

$$\frac{\delta \mu_a}{\delta n} = \frac{S_j}{t_a S_a} e^{-r_j + r_a} \quad (4)$$

where  $\mu_a$ ,  $S_a$  and  $t_a$  represent adult mortality rate, survivorship between breedings and interval between breedings respectively;  $t_j$  represents age

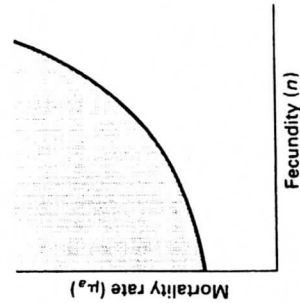


Fig. 4.7. The classic cost of reproduction trade-off.

at first reproduction, and  $S_j$  is survivorship to first reproduction (model of Fig. 4.3d).

What happens if the production or mortality regime changes? Keep, as ever, the shape of the trade-off curve constant (for simplicity) and consider comparisons made with  $r = 0$ . Ecological compensation is unusually difficult to take into account because so many life-history components have an effect on the optimal strategy (Eqn (4), Sibly & Calow 1987). For example if  $S_j$  is better in one environment, then to keep  $r = 0$ , if  $n$  were unchanged,  $S_a$  must decrease. These complications can, however, be handled mathematically, and the conclusion is that however ecological compensation acts (through extrinsic adult mortality or  $t_a$ ) the result is the same: selection acts to increase  $n$  if  $S_j/t_a S_a$  is increased (Sibly & Calow 1987). Thus, environments that offer higher  $S_j/t_a S_a$ , through an improvement in either production or mortality, select for increased fecundity, i.e. towards semelparity.

#### Male and female, or hermaphrodite?

The approach developed so far is quite general and can be applied directly to sex-allocation theory, as developed principally by Charnov (1982). We illustrate this in the next two sections.

Given two types of gamete (sperm and eggs), it is easy to imagine that their production requires specialist structures, which may be carried by all individuals (hermaphrodites, monoecious) or may alternatively be more efficiently carried by specialized individuals (males/females, dioecious). This may be examined formally by considering whether a given individual should be male or female or both (hermaphrodite), and whether gender should be constant or change through life, and if so when? The modern approach to these questions was pioneered by E.O. Charnov in the 1970s and is synthesized in his 1982 book. Suppose the options set is concave (Fig. 4.8a) so that more offspring are obtained by single-sex individuals than by hermaphrodites. It is easy to imagine this coming about as a result of advantages of specialization. For example, since only one type of reproductive organ needs to be built, the costs of building the other type are saved by specialists. Hermaphrodites, by contrast, have to pay the costs of building and maintaining both male and female organs. Since fitness depends on the total number of offspring produced, fitness contours are straight lines with slope  $-1$ , and so the optimal strategies are to be either male or female. On the other hand, if the options set was convex (Fig. 4.8b) the optimal strategy would be hermaphrodite.

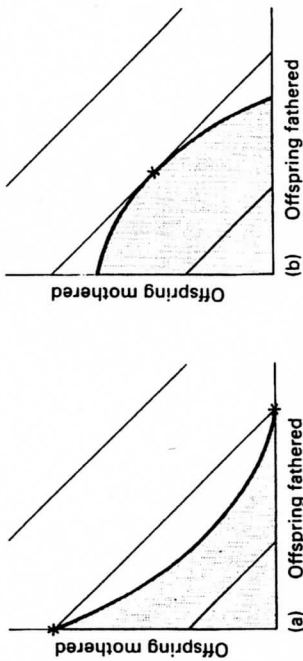


FIG. 4.8. Options sets for hermaphrodites. Offspring fathered is the number of offspring to which sperm have been contributed via male organs. Offspring mothered is defined analogously. A concave options set (a) has twin optima corresponding to dioecy whereas a convex options set (b) has a single optimum corresponding to hermaphroditism. (After Charnov 1982 and Maynard Smith 1989).

The analysis can be extended to consider when to change sex by changing the axes in Fig. 4.8 so that the x-axis now represents the number of offspring fathered in the male part of the life history, and the y-axis the number mothered in the female part. The options set now shows the consequences of spending different amounts of time as a male — the longer spent, the more offspring fathered, and so on. The optimality analysis proceeds as before. Sex change is advantageous if the options set is convex as in Fig. 4.8b, but not if the options set is concave, as in Fig. 4.8a.

Accepting the form of reproductive system is now chosen, we continue the analysis of life history by considering the allocation of resources between sons and daughters in the two-sex system.

#### Sons or daughters?

This is one of the classic trade-offs first considered by Fisher (1930). If sons and daughters cost the same to produce, in terms of resources, then the trade-off between them is linear (Fig. 4.9a). What then is the optimal ratio of sons to daughters? The answer depends on whether sons or daughters can be expected to pass on more alleles to future generations. Suppose an allele causing mothers to produce only sons spreads initially — this could not continue for long, since a very fundamental feedback operates against such alleles. If initially successful, they thereby tip the balance of advantage against themselves. This comes about because

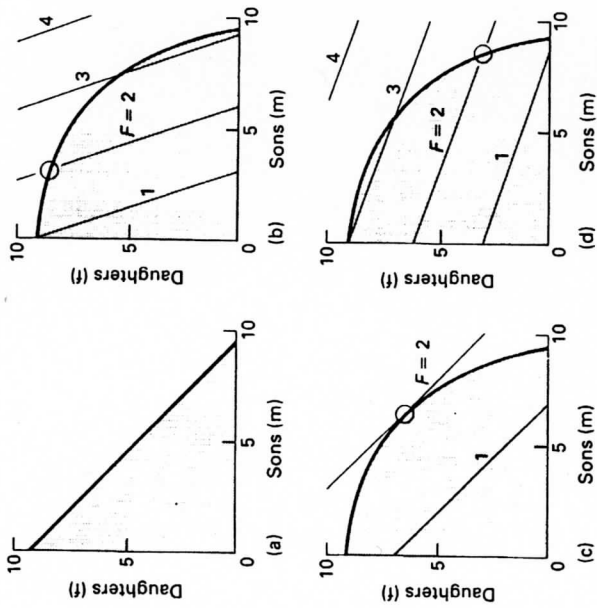


FIG. 4.9. Trade-off constraining offspring production. Sons can theoretically be traded for daughters on a one-to-one basis if they cost the same (a). (b)–(d) show a convex options set with fitness contours from Eqn (5) giving the fitness of a rare mutant.  $\circ$  represents the population strategy ( $m', f'$ ). See text for discussion.

after their initial success there are more breeding males than females in the population, so the success of males becomes lower than that of females. Resources invested in sons would then be more profitably invested in daughters and alleles that do not make sons are favoured over those that do.

The argument can be formalized using fitness contours calculated using the Shaw–Mohler equation (Charnov 1982, p. 14) for the fitness of a rare mutant producing  $m$  sons and  $f$  daughters:

$$\text{fitness} = \frac{m}{m'} + \frac{f}{f'} \quad (5)$$

where  $m'$  and  $f'$  are the numbers of sons and daughters, respectively, produced by individuals not carrying the mutant allele. Fitness contours are shown in Fig. 4.9b–d for a non-linear trade-off curve (application to the linear case is discussed by Charnov 1982, p. 14). In the case shown in

Fig. 4.9b, where there are more females than males in the population, mutants producing more sons have higher fitness. The converse holds in Fig. 4.9d. Only in Fig. 4.9c, where the fitness contours are parallel to the options set, do mutants have lower fitness than non-mutants. Note that both the fitness contours and the direction of selection are frequency dependent. Only the situation in Fig. 4.9c is evolutionarily stable (*sensu* Maynard Smith 1982). For a recent review of the topics covered in the last two subsections see Frank (1990).

#### General patterns of productivity and mortality

In this section we have distinguished two types of life-history variable — production variables and mortality variables. We have analysed what happens when they are traded off against each other, and we have considered the impact of production stress and mortality stress. Throughout we have taken some account of the basic requirement of existence, that, put simply, production has to balance mortality. Do any general life-history patterns emerge?

In the search for general patterns, consider first the case that extrinsic mortality is low throughout life. This might be true of some top carnivores, for example. If mortality rate is low, then production rate must be low too, to balance the low mortality rate. What offspring size is favoured by selection if both production and mortality rates are low? Low production implies low growth rate, and with juvenile mortality rate also low, selection favours offspring about as large as possible, and offspring produced one at a time (Fig. 4.4). This is a feature of many top carnivores, from freshwater flatworms to albatrosses. The prediction does, however, need formal testing.

Next, what growth rate of juveniles is favoured? Should resources be allocated to defence or should juveniles grow as fast as possible? Since production rate is low, relatively low allocation to defence is favoured (Fig. 4.5b), and juveniles are therefore expected to grow nearly as fast as possible — though limited, of course, by low production rate.

Will the organism be semelparous or iteroparous? Semelparity can here be ruled out on other grounds — if only one offspring is produced at a time a semelparous population could not sustain itself. Fixed-size populations with unit fecundity are necessarily iteroparous. Furthermore, since fecundity is already fixed, at one, no further analysis of the cost of reproduction trade-off is needed.

The above has dealt with the case in which extrinsic mortality is low. If extrinsic mortality is higher, for example as a result of transplanting the population to a new environment, production rate must also be higher

if the population persists, and now selection favours smaller offspring. Allocation to defence is again expected to be relatively low (Fig. 4.5b) though the rationale this time is the existence of mortality stress (as opposed to production stress, before). The reproductive strategy is not this time constrained, and could be either semelparous or iteroparous, but in predicting which, ecological compensation has to be taken into account. All the above assumes the shapes, though not the positions, of the trade-off curves are invariant.

#### TESTING LIFE-HISTORY THEORY

Over the past 20 years, empirical and theoretical studies of life histories and their evolution have generated a body of broad and generally accepted knowledge that may be termed 'life-history theory'. The main achievement of this theory has been to answer the question posed by Deevey in the 1940s, namely, how do diverse life histories arise and what is their selective significance. However, while some answers have been given to the 'how possibly' questions of life-history evolution, a much more difficult task is to answer the 'how actually' question, i.e. whether the process posited by a model has actually occurred, or is occurring, in a group of organisms. As we will see, this problem is particularly challenging given the difficulty of measuring life histories, their sensitivity to environmental conditions, and the closeness of life-history traits to fitness itself.

A model of a biological process can be 'tested' in two ways. One way is to demonstrate that the assumptions of the model are met for many (or several) biological situations, i.e. that the phenomena and processes posited in the model actually occur. The other way is to test the model's predictions, i.e. that given a range of starting conditions the outcomes of the hypothesized process are actually as expected. Clearly, both types of test are desirable. Assumptions may be met but other unknown forces may impinge on the process; or outcomes may be correct but for the wrong reasons. When we are dealing with evolutionary predictions about outcomes, we can study these outcomes either at a 'microevolutionary' level (i.e. by looking at evolution as an ongoing phenomenon in present-day populations) or at a 'macroevolutionary' level (i.e. by using the comparative method in a phylogenetic context). In the present paper we mainly consider microevolutionary approaches.

There are two major requirements for testing evolutionary predictions about life-history outcomes. One is to measure the shapes and positions of the trade-off surfaces that bound the options set. The other is to measure the associated fitness surface.

young. The two control groups did not differ in terms of young fledged, indicating that the manipulation procedure did not itself affect the results. There was, however, no detectable cost of reproduction in terms of male survival to the following year (Fig. 4.10a). However, sample size was small for the detection of survivorship differences, being about 20 per group. Figure 4.10b shows there were costs in terms of the number fledged the following year. Note that these data suggest a curvilinear trade-off (but see also Smith *et al.* 1991).

In an experiment of this type, it is obviously not possible to obtain evidence about the initial cost of growing a tail, nor of the effects sacrifices earlier in the life history might have on tail length. This illustrates a general point about experimental manipulations — they can only inform us about trade-offs with events later in the life history, never about trade-offs with events before the manipulation occurred (Partridge & Sibly 1991).

Experiments of this sort are much more easily performed with plants. The pink Lady's Slipper orchid *Cypripedium acaule* is well suited to such designs because naturally occurring flowering plants only rarely fruit, whereas virtually all hand-pollinated flowers develop into fruits. Plants manipulated to fruit more grew and flowered less later, thereby demonstrating a cost of reproduction (Primack & Hall 1990). In *Plantago lanceolata* it is possible to induce flowering by exposing plants to 30 minutes of very dim light during the night. Plants manipulated to flower more grew fewer leaves (Antonovics 1980). Experimental manipulation has also been used to measure the cost of nectar production in Christmas Bells (*Blandfordia nobilis*) (Pyke 1991).

#### ESTIMATION OF TRADE-OFFS: GENETIC METHODS

As explained earlier, direct short-term predictions of life-history evolution are possible from a knowledge of the extant genetic options set; this genetic options set is normally described by a genetic variance-covariance matrix, under the assumption its shape is multivariate normal. The interpretation of genetic covariances in terms of trade-offs has to be done cautiously if there are more than two interacting traits (i.e. the options set is multidimensional). For example, two traits may be negatively correlated given a uniform genetic background for all other traits but this may be obscured if there is a strong correlation of these two traits with another third trait that varies. In this way, the genetic covariances among some pairs of traits may be positive (Charlesworth 1990, Smith 1991) even though their trade-off functions are negative.

A large number of difficulties are associated with the estimation of genetic correlations. Sample sizes have to be large, there are problems in estimating confidence intervals, and estimates (though not the true values) can and do exceed the range (-1, +1). However, the statistical problems are being addressed by a number of recent studies (for example, Shaw 1991). Another weakness of the genetic correlation *per se* is that it gives no information about the curvilinearity of the trade-off relationship. However, this can perhaps be assessed by appropriate data transformations, or by non-linear regressions of breeding values of the two traits.

If the population is 'at equilibrium' (i.e. has been in the same environment for a long time, it has not undergone a radical change in its breeding system, and there is a low mutation rate), it is often assumed that the extant genetic options set will be at or close to the boundary (see Fig. 4.1) and will therefore reflect the trade-off curve. There is some evidence for this assumption (Holloway *et al.* 1990), and the converse can certainly be expected to be true. Thus, a novel environment, inbreeding in a normally outbred population (Rose 1984), or a high mutation rate (Houle 1991), can be expected to produce genes that have very different fitnesses, resulting in correlations among life-history traits which in principle could be positive. The trade-off surface of the extant options set is therefore ideally estimated from the genetic correlations measured using progeny from crosses among parents derived from a long-standing population, where those progeny are transplanted back into the same natural environment.

We present, as an example, a study by Moller *et al.* (1989) of the cowpea weevil, *Callosobruchus maculatus*, a stored product pest. An advantage of working on stored product pests is that their ancestral environment is readily re-created in the laboratory. As mentioned above, this is an important point, because the values of genetic parameters are in general environment dependent, so studies that have moved populations to the laboratory to make measurements have generally also changed their environments, making the measurements of doubtful value.

A specially designed breeding study was used to allow efficient calculation of genetic parameters such as breeding value (Fig. 4.11), which provides an estimate of the effects of the alleles carried by each individual (here, each male). Figure 4.11a shows that genetically larger individuals produced more eggs, but Fig. 4.11b shows that this was at a cost in terms of juvenile growth rate — because it takes longer to grow to be bigger. The methods of quantitative genetics allowed accurate estimation of genetic correlations from these data, and these are shown in Table 4.1.

The requirement that the genetic correlation be measured in the

## ESTIMATION OF TRADE-OFFS: PHENOTYPIC METHODS

### *Observation of phenotypes*

Observational studies of phenotypes, either within species, or comparative studies between species, often stimulate hypotheses about the trade-offs that influence the evolution of a particular type of organism. Sometimes, indeed, it is hard to think of explanations other than trade-offs to account for observed character correlations (see for example, Tuttle & Ryan 1981, Clutton-Brock *et al.* 1982, Gustaffson & Part 1990).

In general, however, because phenotypic correlations confound genetic and environmental influences, and these may act on character combinations in quite different ways, extreme caution has to be exercised in their interpretation. Environmentally induced correlations can come about for many reasons. There may be ecological compensation such that under density-dependent limitation, an environmentally induced increase in local mortality may result in a corresponding increase in individual size and fecundity. Or accidents and chance events early in life (e.g. an individual's location) may affect an individual's overall 'quality' (e.g. size) which then affects more than one life-history variable.

### *Experimental manipulation*

Changing the phenotype of an individual with regard to one trait experimentally, and examining the response in a second trait, has the advantage that it ensures that the covariance of the life-history characteristics is not due to some common environmental factor affecting each trait independently. It also has the advantage that phenotypes can be produced that are more extreme than the extant types in a given population; the potential options set may therefore be better explored by this method. However, there is still no guarantee that a genetic change, and the ensuing correlated genetic change in the other trait, will be in the same direction as in the experimentally manipulated system. To translate the experimental effect into a genetic effect, one has to assume that the experimental manipulation provides an exact 'phenocopy' of the genetic effect. It is well-known that actual alleles can have seemingly quite bizarre pleiotropic effects (Gromko *et al.* 1991), and an actual genetic change in a trait may have repercussions on other traits that are different from the effects of a manipulation.

We illustrate this method using Møller's (1988, 1989) study of swallows. The basis of the study was that Møller was able: (1) to catch 83 males

shortly after arrival at their breeding colonies; (2) to manipulate male tail length, with scissors and superglue; and (3) to observe males thereafter and to record various features of their behaviours and life histories. Males caught at the start of the breeding season were assigned to one of four groups: short tails, long tails, and two control groups with tails of normal length, one unmanipulated, and the other cut and stuck. The males with experimentally lengthened tails were more successful in attracting mates, and fledged more young in the year their tails were lengthened (Fig. 4.10a). Conversely, the group with shortened tails fledged fewer

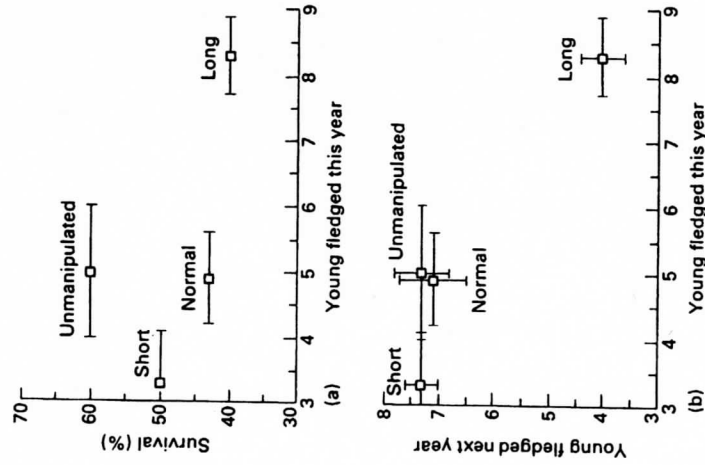


FIG. 4.10. Experimental manipulation of swallow tail length to identify costs of reproduction (data of Møller 1988, 1989). The lengths of male tails were manipulated into four groups, 'short', 'long', 'normal' and 'unmanipulated' (bars indicate standard errors). (a) shows the effects on number of offspring fledged in the year the manipulation was performed, and on the survival of the male until the following year (standard error was not calculated for survivorship). (b) shows the effects on the number of offspring fledged in the following year. See text for further details.

sizes, the technique would seem to be well suited to the job of mapping the options set. The principal difficulty from the point of view of identifying the trade-off surface is that one cannot be certain that the genetic options so identified lie on the boundary rather than in the interior of the extant genetic options set. However, this can be overcome by maintaining the populations in the study environment for several generations; lack of change would indicate they were on the boundary.

Transplant experiments can also be used to study microevolutionary processes within populations directly. If transplants into a novel environment are the result of a formal crossing design, then it should be possible from measurements in this new habitat to identify both the genetic options set and, using the methods suggested above, the fitness surface for that environment. If the population is allowed to persist in that environment, actual changes in life-history characteristics can then be examined.

In one such study (Jordan 1989, also Jordan 1991), but involving morphological and growth characteristics rather than life history traits, families of a non-weed ecotype of *Diodia teres* were transplanted into a dense stand of soybeans. This permitted calculation of genetic variances and covariances, as well as forces of selection on a number of covarying traits. Comparing the weed and non-weed ecotypes, the direction of selection was as predicted in four out of five characters studied.

In a reciprocal transplant experiment a further prediction can be made. If the transplanted populations are genetically distinct, it is unlikely that the alleles evolved in other habitats will be superior in the study environment to the alleles that evolved there. Hence, in each habitat the population that evolved there should outperform the others. This prediction has often been confirmed by reciprocal transplant experiments (especially in plants) showing that resident populations outperform aliens (Briggs & Walters 1984, Levin 1984). The life history components that result in such overall fitness differences have, however, rarely been studied explicitly (for exceptions see McGraw & Antonovics 1983, Jordan 1991) or put in the context of expectations from life history theory (Antonovics & Primack 1982). More explicit use of transplant experiments to test life-history theory, rather than overall fitness differences, could be rewarding.

#### DIRECT STUDY OF THE EVOLUTIONARY PROCESS

A particular challenge is to test life-history theory in prospective, micro-evolutionary studies, where there can be direct observation of evolutionary changes in life history. Such studies may involve laboratory selection experiments or may be field based.

An interesting example of the latter approach is the work of Reznick *et al.* (1990). Earlier work had shown that guppies (*Poecilia reticulata*) occurred in streams differing with respect to whether juveniles or adults were more affected by predation. Where predation was mainly on adults, guppies matured at an earlier age, had higher reproductive effort, and had more and smaller offspring per brood (Reznick & Endler 1982, Reznick *et al.* 1990). These differences were heritable and could be explained on the following basis. First, where predation is mainly on juveniles, production rate is thought to be lower (on the basis of temperature and food supply, Reznick 1982). This selects for larger eggs. In addition, larger eggs would give juveniles a 'head start' and so allow them to hurry through the juvenile stages (Reznick 1982, Taylor & Williams 1984). Second, where predation is mainly on juveniles, juvenile survivorship is lower but adult survivorship is higher, and this combination selects for lower reproductive effort assuming the costs of reproduction are paid after reproduction has occurred. Lastly, although we have not treated it formally here, it would seem adaptive to mature earlier and therefore at lower size where adult predation is more intense, since the increased mortality on larger fish can thereby be to some extent avoided (Reznick *et al.* 1990). To show that predation was the cause of the observed life-history differences, Reznick *et al.* (1990) introduced 200 guppies from a site with predominantly adult predation to one with mainly juvenile predation. By the end of the study 11 years (30–60 generations) later, field phenotypes had lower reproductive effort, and fewer and larger offspring, as predicted. To see if these differences were heritable, Reznick *et al.* first reared fish from both localities in a common environment for two generations, to eliminate environmental influences on the life histories. When they then measured the life histories they found they had changed in the predicted directions (Table 4.2).

Other examples of selection experiments include Rose and Charlesworth (1981), Luckinbill *et al.* (1983) and Moller *et al.* (1990) (for a review see Lessells 1991).

#### ESTIMATION OF FITNESS SURFACES

In theoretical studies such as those described earlier, fitness surfaces are estimated by solving the Euler-Lotka equation to calculate  $r$  for the relevant trait variables. In any particular real-world situation, the actual observed relationship between the trait combination and fitness may be different from this theoretical expectation for many reasons. For example, the trait 'seed number at age  $x$ ' might seem easily equatable with  $\pi(x)$  in a

TABLE 4.2. Life-history traits of two lines of guppies (*Poecilia reticulata*) exposed to either adult or juvenile predation in the field for 11 years (SE in brackets, data from Reznick *et al.* 1990). \*,  $p < 0.05$ ; NS,  $p > 0.05$ . Although the overall difference in reproductive effort was not significant, as shown, the difference at 8 weeks was

Life-history trait	Adults predated	Juveniles predated	
Male age at maturity (days)	48.5 (1.2)	58.2 (1.4)	*
Female age at first parturition (days)	85.7 (2.2)	92.3 (2.6)	*
Brood size, litter 1	4.5 (0.4)	3.3 (0.4)	*
Brood size, litter 2	8.1 (0.6)	7.5 (0.7)	NS
Offspring size (mg-dry), litter 1	0.87 (0.02)	0.95 (0.02)	NS
Offspring size, litter 2	0.90 (0.03)	1.02 (0.04)	*
Interbrood interval (days)	24.5 (0.3)	25.2 (0.3)	NS
Reproductive effort (%)	22.0 (1.8)	18.5 (2.1)	NS

fitness function but such a measure may fail to take into account seed quality (inbred versus outbred, large versus small), may fail to take into account dispersal differences (due to, for example, variation of plant height with age), may fail to consider the level of interaction among the seedlings from the same sibship in the next generation, etc. Ideally we would like to know the actual relationship between the traits in question and fitness. However, an important empirical problem arises if we attempt to measure the traits and fitness on the same individuals because of confounding by environmental variables that affect both (Rausher 1992). There is also the problem that the life-history character should not be part of the fitness measure of those self-same individuals.

There are ways out of these difficulties but none of them is easy. One could measure the trait in question on one set of individuals and measure fitness on another related (e.g. same family or clone) set of individuals. Alternatively, one can look at the correlations among breeding values (Rausher 1992). Another approach is to use two (or multiple) generation experiments, where life histories of individuals from a crossing design are measured in one generation, and the contribution of these individuals to the next generation are estimated using genetic markers (see Lacey *et al.* 1983, for a discussion of this issue). An example of such a study is that of Meagher (in press) which although it did not explicitly investigate life-history traits, showed using paternity analysis based on genetic markers, that large males of the dioecious plant *Chamaelirium luteum* actually tended to sire fewer offspring (perhaps because of reduced pollinator movement from those males).

Another possible source of error arises if the options set is multidimensional but some relevant characters are omitted ('the missing character problem'). One method to test for whether all the relevant traits have been identified is to ask how completely variation (and covariation) observed traits predict the observed variation in fitness. If there is residual unexplained variation in fitness, then one can assume that relevant traits (or their correlates) have been identified. If, however, residual variation is high, then clearly important traits are missing. A study of selection for herbivore resistance, 91% of the variance in breeding value of individuals for fitness (as measured by seed production) could be accounted for by variation in their breeding values for leaf area damage by four different herbivores (Rausher & Simms 1989, calculated from their Table 3).

Of particular interest are cases where there is a large amount of unexplained genetic variance in a component life-history trait but genetic variance in fitness (Mousseau & Roff 1987). Such a discrepancy could have two interpretations; either the trait is neutral, or it indicates that there is a negatively covarying fitness component that has not been measured. If the negative correlation is close to  $-1$  then these possibilities are hard to distinguish empirically.

In conclusion, the estimation of the fitness surface presents non-trivial issues for the evolutionary biologist interested in life-history evolution. These issues are common to any rigorous quantitative analysis of natural selection acting on multivariate traits but are exacerbated in life-history work by the closeness of the traits to fitness and by their phenotypic flexibility. The resolution of this issue may well be dependent on growing use of genetic markers to trace parentage. Such methods therefore likely to play a large role in empirical studies of life-history evolution.

## CONCLUSIONS

Detailed consideration of the fate of individual alleles affecting life history traits to a large extent reconciles the 'ecological' and the 'genetic' approaches that were juxtaposed in the introduction to this chapter. The genetic approach gives a predictive framework within which to study the microevolutionary process, and the ecological approach identifies expected outcomes in particular environments using optimality analysis. Both assumptions trade-offs among life-history traits and knowledge of the form of the trade-offs is critical to predicting evolutionary outcomes.



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Reproductive effort (%)	22.0 (1.8)		18.5 (2.1)	NS

fitness function but such a measure may fail to take into account seed quality (inbred versus outbred, large versus small), may fail to take into account dispersal differences (due to, for example, variation of plant height with age), may fail to consider the level of interaction among the seedlings from the same sibship in the next generation, etc. Ideally we would like to know the actual relationship between the traits in question and fitness. However, an important empirical problem arises if we attempt to measure the traits and fitness on the same individuals because of confounding by environmental variables that affect both (Rausher 1992). There is also the problem that the life-history character should not be part of the fitness measure of those self-same individuals.

There are ways out of these difficulties but none of them is easy. One could measure the trait in question on one set of individuals and measure fitness on another related (e.g. same family or clone) set of individuals. Alternatively, one can look at the correlations among breeding values (Rausher 1992). Another approach is to use two (or multiple) generation experiments, where life histories of individuals from a crossing design are measured in one generation, and the contribution of these individuals to the next generation are estimated using genetic markers (see Lacey *et al.* 1983, for a discussion of this issue). An example of such a study is that of Meagher (in press) which although it did not explicitly investigate life-history traits, showed using paternity analysis based on genetic markers, that large males of the dioecious plant *Chamaelirium luteum* actually tended to sire fewer offspring (perhaps because of reduced pollinator movement from those males).

Another possible source of error arises if the options set is multidimensional but some relevant characters are omitted ('the missing characters' problem). One method to test for whether all the relevant traits have been identified is to ask how completely variation (and covariation) in the observed traits predict the observed variation in fitness. If there is little residual unexplained variation in fitness, then one can assume that the relevant traits (or their correlates) have been identified. If, however, the residual variation is high, then clearly important traits are missing. In a study of selection for herbivore resistance, 91% of the variance in breeding value of individuals for fitness (as measured by seed production) could be accounted for by variation in their breeding values for leaf area and damage by four different herbivores (Rausher & Simms 1989, calculated from their Table 3).

Of particular interest are cases where there is a large amount of unexplained genetic variance in a component life-history trait but little genetic variance in fitness (Mousseau & Roff 1987). Such a discrepancy could have two interpretations; either the trait is neutral, or it indicates that there is a negatively covarying fitness component that has not been measured. If the negative correlation is close to  $-1$  then these two possibilities are hard to distinguish empirically.

In conclusion, the estimation of the fitness surface presents non-trivial issues for the evolutionary biologist interested in life-history evolution. These issues are common to any rigorous quantitative analysis of natural selection acting on multivariate traits but are exacerbated in life-history work by the closeness of the traits to fitness and by their phenotypic flexibility. The resolution of this issue may well be dependent on the growing use of genetic markers to trace parentage. Such methods are therefore likely to play a large role in empirical studies of life-history evolution.

## CONCLUSIONS

Detailed consideration of the fate of individual alleles affecting life-history traits to a large extent reconciles the 'ecological' and the 'genetic' approaches that were juxtaposed in the introduction to this chapter. The genetic approach gives a predictive framework within which to study the microevolutionary process, and the ecological approach identifies expected outcomes in particular environments using optimality analysis. Both assume trade-offs among life-history traits and knowledge of the form of these trade-offs is critical to predicting evolutionary outcomes.

The present status of life-history theory can best be described as being in the 'work-horse' phase. We now have a wealth of theories and more useful ideas continue to be forthcoming. We also have a large number of empirical investigations which are important in having shown life-history variation within and among species, in showing these are correlated with habitat/community features, and in illustrating at least the potential occurrence of trade-offs. However, few if any studies have rigorously delineated the forces responsible for the evolution of a particular life history.

We can liken the present status of life-history theory to that of the theory of natural selection after the publication of Darwin's book *Origin of Species*. It is clear that the general mechanisms and the environmental conditions that can lead to the evolution of diverse life histories are well established; similarly, the theory of natural selection was first posed as a logical inference from well-supported biological phenomena. But just as the theory of natural selection remained in need of 'testing' for a long period, so there is now a need to instantiate life-history theory, so as to establish which mechanisms are general or important in which groups, and under what ecological circumstances.

#### ACKNOWLEDGEMENTS

R.S. has benefitted greatly in the development of some of these ideas from discussions with Robert Smith and Nicolas Perrin.

#### REFERENCES

- Abugov, R. (1988). A sex-specific quantitative genetic theory for life history and development. *Journal of Theoretical Biology*, **132**, 437-447.
- Anderson, W. W. & King, C. E. (1970). Age-specific selection. *Proceedings of the National Academy of Sciences, USA*, **66**, 780-786.
- Antonovics, J. (1980). Concepts of resource allocation and partitioning in plants. *Limits to Action* (Ed. by J. R. Staddon), pp. 1-35. Academic Press, London, UK.
- Antonovics, J. & Primack, R. B. (1983). Experimental ecological genetics in *Plantago*. VI. The demography of seedling transplants of *P. lanceolata*. *Journal of Ecology*, **70**, 55-75.
- Bell, G. (1980). The costs of reproduction and their consequences. *American Naturalist*, **116**, 45-76.
- Berven, K. A. (1982). The genetic basis of altitudinal variation in the Wood frog *Rana sylvatica*. I. An experimental analysis of life history traits. *Evolution*, **36**, 962-983.
- Briggs, D. & Walters, S. M. (1984). *Plant Variation and Evolution* (2nd edn). Cambridge University Press, Cambridge, UK.
- Charlesworth, B. (1980). *Evolution in age-structured populations*. Cambridge University Press, Cambridge, UK.

- Charlesworth, B. (1990). Optimization models, quantitative genetics and mutation. *Evolution*, **44**, 520-538.
- Charlesworth, B. & Giesel, J. T. (1972a). Selection in populations with overlapping generations. II. Relations between gene frequency and overlapping generations. *American Naturalist*, **106**, 388-401.
- Charlesworth, B. & Giesel, J. T. (1972b). Selection in populations with overlapping generations. IV. Fluctuations in gene frequency with density-dependent selection. *American Naturalist*, **106**, 402-411.
- Charnov, E. L. (1982). *The Theory of Sex Allocation*. Princeton University Press, Princeton, NJ, USA.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. (1982). *Red Deer*. University of Chicago Press, Chicago IL, USA.
- Cole, L. C. (1954). The population consequences of life history phenomena. *Quarterly Review of Biology*, **29**, 103-137.
- Deevey, E. S. (1947). Life tables for natural populations. *Quarterly Review of Biology*, **22**, 283-314.
- Fisher, R. A. (1930). *The Genetical Theory of Natural Selection*. Oxford University Press, Oxford, UK.
- Ford, E. (1964). *Ecological Genetics*. Methuen, London, UK.
- Frank, S. A. (1990). Sex allocation theory for birds and mammals. *Annual Review of Ecology and Systematics*, **21**, 13-55.
- Gabriel, W. (1982). Modelling reproductive strategies of *Daphnia*. *Archiv für Hydrobiologie*, **95**, 69-80.
- Gromko, M. H., Briot, A., Jensen, S. C. & Fukui, H. (1991). Selection on copulation duration in *Drosophila melanogaster*: predictability of direct response versus unpredictability of correlated response. *Evolution*, **45**, 69-81.
- Gustafsson, L. & Pärri, T. (1990). Acceleration of senescence in the collared flycatcher *Ficedula albicollis* by reproductive costs. *Nature*, **347**, 279-281.
- Holloway, G. J., Povey, S. R. & Sibly, R. M. (1990). The effect of new environment on adapted genetic architecture. *Heredity*, **64**, 323-330.
- Houle, D. (1991). Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. *Evolution*, **45**, 630-648.
- Jordan, N. (1989). Predicted evolutionary response to selection for tolerance of soybean (*Glycine max*) and intraspecific competition in a non-weed population of poorjoe (*Diodia teres*). *Weed Science*, **37**, 451-457.
- Jordan, N. R. (1991). Multivariate analysis of selection in experimental populations derived from hybridization of two ecotypes of the annual plant *Diodia teres* W. (Rubiaceae). *Evolution*, **45**, 1760-1772.
- King, C. E. & Anderson, W. W. (1971). Age-specific selection. II. The interaction between  $r$  and  $K$  during population growth. *American Naturalist*, **105**, 137-156.
- Kozlowski, J. (1992). Optimal allocation of resources of growth and reproduction: implications for age and size at maturity. *Trends in Ecology and Evolution*, **7**, 15-19.
- Lacey, E. P., Real, L., Antonovics, J. & Heckel, D. (1983). Variance models in the study of life histories. *American Naturalist*, **122**, 114-131.
- Lack, D. (1954). *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford, UK.
- Lande, R. (1982). A quantitative genetic theory of life history evolution. *Ecology*, **63**, 607-615.
- Lessells, C. M. (1991). The evolution of life histories. *Behavioural Ecology* (3rd edn) (Ed. by J. R. Krebs & N. B. Davies), pp. 32-68. Blackwell Scientific Publications, Oxford, UK.

- Levin, D. A. (1984). Immigration in plants: an exercise in the subjunctive. *Perspectives on Plant Population Biology* (Ed. R. Dirzo & J. Sarukhan), pp. 242-260. Sinauer, Sunderland, MA, USA.
- Luckinbill, L. S., Arking, R., Clare, M. J., Cirocco, W. C. & Buck, S. A. (1983). Selection for delayed senescence in *Drosophila melanogaster*. *Evolution*, **38**, 996-1003.
- MacArthur, R. H. (1962). Some generalized theorems of natural selection. *Proceedings of the National Academy of Sciences, USA*, **38**, 1893-1897.
- Maynard Smith, J. (1982). *Evolution and the Theory of Games*. Cambridge University Press, Cambridge, UK.
- Maynard Smith, J. (1989). *Evolutionary Genetics*. Oxford University Press, Oxford, UK.
- Maynard Smith, J. (1991). The evolution of reproductive strategies: a commentary. *Philosophical Transactions of the Royal Society of London*, **B**, **332**, 103-104.
- McGraw, J. B. & Antonovics, J. (1983). Experimental ecology of *Dryas octopetala* ecotypes I. Ecotypic differentiation and life-cycle stages of selection. *Journal of Ecology*, **71**, 879-897.
- Meagher, T. R. Analysis of paternity within a natural population of *Chamaelirium luteum*. II. Male reproductive success. *American Naturalist* (in press).
- Møller, A. P. (1988). Female choice selects for male sexual tail ornaments in the monogamous swallow. *Nature*, **332**, 640-642.
- Møller, A. P. (1989). Viability costs of male tail ornaments in a swallow. *Nature*, **339**, 132-135.
- Møller, H., Smith, R. H. & Sibly, R. M. (1989). Evolutionary demography of a bruchid beetle. I. Quantitative genetic analysis of the female life history. *Functional Ecology*, **3**, 673-681.
- Møller, H., Smith, R. H. & Sibly, R. M. (1990). Evolutionary demography of a bruchid beetle. III. Correlated responses to selection and phenotypic plasticity. *Functional Ecology*, **4**, 489-493.
- Mousseau, T. A. & Roff, D. A. (1987). Natural selection and the heritability of fitness components. *Heredity*, **59**, 181-197.
- Nur, N. (1984). The consequences of brood size for breeding blue tits. II. Nestling weight, offspring survival and optimal brood size. *Journal of Animal Ecology*, **53**, 497-517.
- Parker, G. A. & Maynard Smith, J. (1990). Optimality in evolutionary biology. *Nature*, **348**, 27-33.
- Partridge, L. & Sibly, R. (1991). Constraints in the evolution of life histories. *Philosophical Transactions of the Royal Society of London*, **B**, **332**, 3-13.
- Planka, E. R. and Parker, W. S. (1975). Age-specific reproductive tactics. *American Naturalist*, **109**, 453-464.
- Primack, R. B. (1979). Reproductive effort in annual and perennial species of *Plantago* (Plantaginaceae). *American Naturalist*, **114**, 51-62.
- Primack, R. B. & Hall, P. (1990). Costs of reproduction in the pink lady's slipper orchid: a four-year experimental study. *American Naturalist*, **136**, 638-656.
- Pugliese, A. & Kozłowski, J. (1990). Optimal patterns of growth and reproduction for perennial plants with persisting or not persisting vegetative parts. *Evolutionary Ecology*, **4**, 75-89.
- Pyke, G. H. (1991). What does it cost a plant to produce floral nectar? *Nature*, **350**, 58-59.
- Rauscher, M. D. (1992). The measurement of selection on quantitative traits: biases due to environmental covariances between traits and fitness. *Evolution*, **46**, 616-626.
- Rauscher, M. D. & Simms, E. L. (1989). The evolution of resistance to herbivory in *Ipomoea purpurea*. I. Attempts to detect selection. *Evolution*, **43**, 563-572.
- Reznick, D. A. (1982). Genetic determination of offspring size in the guppy (*Poecilia reticulata*). *American Naturalist*, **120**, 181-188.

- Reznick, D. A. & Endler, J. A. (1982). The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution*, **36**, 160-177.
- Reznick, D. A., Bryga, H. & Endler, J. A. (1990). Experimentally induced life-history evolution in a natural population. *Nature*, **346**, 357-359.
- Roach, D. A. (1986). Life history variation in *Geranium carolinianum*. I. Covariation between characters at different stages of the life cycle. *American Naturalist*, **128**, 47-57.
- Rose, M. R. (1984). Genetic covariation in *Drosophila* life history: untangling the data. *American Naturalist*, **123**, 565-569.
- Rose, M. R. & Charlesworth, B. (1981). Genetics of life-history in *Drosophila melanogaster*. II. Exploratory selection experiments. *Genetics*, **97**, 187-196.
- Schaffer, W. M. (1974a). Optimal reproductive effort in fluctuating environments. *American Naturalist*, **108**, 783-790.
- Schaffer, W. M. (1974b). Selection for optimal life histories: the effects of age structure. *Ecology*, **55**, 291-303.
- Shaw, R. G. (1991). The comparison of quantitative genetic parameters between populations. *Evolution*, **45**, 143-151.
- Sibly, R. M. (1989). What evolution maximizes. *Functional Ecology*, **3**, 129-135.
- Sibly, R. M. & Calow, P. (1985). Classification of habitats by selection pressures: a synthesis of life-cycle and *r/K* theory. *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (Ed. by R. M. Sibly & R. H. Smith), pp. 75-90. (The 25th Symposium of The British Ecological Society). Blackwell Scientific Publications, Oxford, UK.
- Sibly, R. M. & Calow, P. (1986). *Physiological Ecology of Animals*. Blackwell Scientific Publications, Oxford, UK.
- Sibly, R. M. & Calow, P. (1987). Ecological compensation - a complication for testing life-history theory. *Journal of Theoretical Biology*, **125**, 177-186.
- Sibly, R. M. & Calow, P. (1989). A life-cycle theory of responses to stress. *Biological Journal of the Linnean Society*, **37**, 101-116.
- Sibly, R. M., Calow, P. & Nichols, N. (1985). Arc patterns of growth adaptive? *Journal of Theoretical Biology*, **112**, 553-574.
- Sibly, R. M. & Curnow, R. N. An alleloentric view of life-history evolution. *Journal of Theoretical Biology* (in press).
- Sibly, R. M., Smith, R. H. & Møller, H. (1991). Evolutionary demography of a bruchid beetle. IV. Genetic trade-off, stabilizing selection and a model of optimal body size. *Functional Ecology*, **5**, 594-601.
- Smith, H. G., Montgomerie, R., Poldmaa, T., White, B. N. & Boag, P. T. (1991). DNA fingerprinting reveals relation between tail ornaments and cuckoldry in barn swallows. *Hirundo rustica*. *Behavioural Ecology*, **2**, 90-98.
- Smith, R. H. (1991). Genetic and phenotypic aspects of life-history evolution in animals. *Advances in Ecological Research*, **21**, 63-120.
- Smith, R. H., Sibly, R. M. & Møller, H. (1987). Control of size and fecundity in *Pieris rapae*: towards a theory of butterfly life cycles. *Journal of Animal Ecology*, **56**, 341-350.
- Southwood, T. R. E. (1988). Tactics, strategies and templates. *Oikos*, **52**, 3-18.
- Taylor, B. & Gabriel, W. (1992). Models for optimal growth and reproduction of *Daphnia*. *American Naturalist*, **139**, 248-266.
- Taylor, P. D. & Williams, G. C. (1984). Demographic parameters at evolutionary equilibrium. *Canadian Journal of Zoology*, **62**, 2264-2271.
- Taylor, H. M., Courley, R. S., Lawrence, C. E. & Kaplan, R. S. (1974). Natural selection of life history attributes: an analytical approach. *Theoretical Population Biology*, **5**, 104-122.

- Tuttle, M. D. & Ryan, M. J. (1981). Bat predation and the evolution of frog vocalizations in the neotropics. *Science*, **214**, 677-678.
- Ziolko, M. & Kozłowski, J. (1983). Evolution of body size: an optimization model. *Mathematical Biosciences*, **64**, 127-143.