PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Constraints in the Evolution of Life Histories [and Discussion]

Linda Partridge, Richard Sibly, R. J. H. Beverton and W. G. Hill

Phil. Trans. R. Soc. Lond. B 1991 **332**, 3-13
doi: 10.1098/rstb.1991.0027

Constraints in the evolution of life histories

LINDA PARTRIDGE[1] AND RICHARD SIBLY[2]

[1] *Institute of Cell, Animal and Population Biology, University of Edinburgh, Zoology Building, West Mains Road, Edinburgh EH9 3JT, U.K.*
[2] *Department of Pure and Applied Zoology, University of Reading, PO Box 228, Reading RG6 2AJ, U.K.*

SUMMARY

The life history favoured by natural selection maximizes fitness, and this implies maximization of fecundity and survival at all ages. The observed diversity in life histories suggests that there are constraints on what can be achieved in practice. Functional constraints occur if only certain combinations of age-specific fertility and survival are possible, either because of the physiology of the organism or because of the ecological impact of its environment. The resulting constrained optimization means that the organism is involved in making trade-offs between life-history characters. A major task for the future is the measurement of trade-off functions in the environment in which the life-history evolved. Natural variation between individuals and populations, genetic studies and experimental manipulations have all been used to detect trade-offs. The last two methods are the most satisfactory, and can be complementary. Experimental manipulations are at their best when based on sound physiological understanding of the traits under manipulation. Constraints can also operate on the long-term. Local optima, evolutionary lags and irreversible evolution may all have contributed to the diversity of life histories.

1. INTRODUCTION

The life history of an organism is the combination of age-specific survival probabilities and fecundities it displays in its natural environment. The physical forms of life cycles are extraordinarily variable, and different creatures march through their principal life events to very different drum-beats. Lifespan and fecundity vary over several orders of magnitude, and the age of first reproduction, itself highly variable, can mark the beginning of a period of repeated breeding that occupies most of the lifespan, or may instead herald a single, suicidal burst (Cole 1954; Stearns 1976).

It is the job of evolutionary biologists to make sense of this kind of diversity. Because the extent and timing of progeny production are characters very close to fitness itself (see, for example, Gustaffson 1986), life histories are of special interest, and raise some of the most challenging issues in evolutionary biology (Caswell 1989); what exactly is fitness, and what are the constraints on the characters and combinations of characters contributing to it? The connection between the life history and fitness is much closer than for characters more removed from demography, and any suspicion that life-history evolution may simply be an epiphenomenon of genetic drift or of selection on other characters can therefore be dismissed. There is therefore a real opportunity both to formulate explicit models of selection and to test their ability to explain the diversity of life histories we see in nature.

Many models of life-history evolution and tests of them have used optimality theory (Parker & Maynard Smith 1990). This approach to the study of adaptation specifies the options open to an organism, defines an optimization criterion as close as possible to Darwinian fitness, assigns pay-offs to the different options and deduces the optimal solution. This procedure has been accused both of circularity, if models are altered in the light of a mismatch with the data, and of ignoring constraints on the evolution of perfection by natural selection (Gould & Lewontin 1979). However, any model must be altered if it fails to fit the data. Furthermore, in many optimality models the idea of constraint is inherent in the way that the options are specified. For instance, optimality theories of life-history evolution explicitly include the notion of functional constraints (Charlesworth 1990), which means that only certain constrained combinations of the characters individually increasing fitness can be realized in practice.

An important area of debate for life historians has been the importance of genetics. There is a built-in assumption in optimality theory that there can exist genotypes capable of producing the optimal phenotype, and that such genotypes will evolve. On the other hand, some geneticists have voiced the suspicion that the inclusion of genetic details in the theoretical models may alter the outcome (see, for example, Charlesworth 1980; Lande 1982; Rose *et al.* 1987). Recent theoretical work using quantitative genetics (Charnov 1989; Charlesworth 1990) has suggested that optimality and genetic approaches produce similar equilibrium solutions, even with realistic assumptions about the effects of mutation (Charlesworth 1990). Furthermore, many life-history characters do have a demonstrated genetic basis (see Mueller & Ayala 1981; Rose 1984; Gustaffson 1986; Caswell 1989). There has also been a related debate about the need to use genetic techniques in empirical studies of life histories. This topic is considered in some detail later in the present paper.

Optimality models and tests have indeed proved powerful in several cases. For instance, almost all of our understanding of the evolution of avian clutch size (which has been shown to be heritable in some species (see van Noordwijk *et al.* 1980; Gustaffson 1986)) is based on optimality reasoning (see, for example, Charnov & Krebs 1974; Gustaffson & Sutherland 1988; van Noordwijk & de Jong 1986; Pettifor *et al.* 1988). However, it is clear that in some cases a genetic approach to theory and testing is essential. To understand the evolution of date of egg-laying in many birds, it is necessary to make a sharp distinction between genetic and purely environmental variation in the character, and to understand the origin of each (Price *et al.* 1988). Furthermore, gene flow between different populations can prevent optimization of clutch size within each (Dhondt *et al.* 1991).

Functional constraints on evolution are not the only ones. Organisms can become stuck in absorbing states; evolution is not necessarily reversible when selective forces return to an earlier form (Bull & Charnov 1985). Evolutionary history can also be important and there are constraints from design. They will all be discussed below.

2. NATURAL SELECTION ON LIFE HISTORIES

The consequences of natural selection acting on life-history variation within populations are well understood. If the age-specific fecundities and survival probabilities of all the individuals in a population are identical, and if no environmental change intervenes to alter these vital rates, then the population will come to have a stable age-structure, and the numbers of individuals present will change at a rate r, called the intrinsic rate of increase or Malthusian parameter (Cole 1954). There is general agreement that natural selection will favour the genotype that maximizes the value of r under the prevailing ecological conditions. r is determined by the life history, a generalized version of which is illustrated in figure 1. For a genotype producing this life history, r is defined by the Euler–Lotka equation:

$$1 = \tfrac{1}{2}\sum_{x} l_x m_x \mathrm{e}^{-rt_x}, \qquad (1)$$

where:

t_x = age at the x^{th} breeding attempt

l_x = survival probability to age t_x

m_x = fecundity at age t_x

(Schaffer 1974; Charlesworth & Leon 1976; Charlesworth 1980; Lande 1982; Caswell 1989; see Sibly (1989) for an exposition that defines r for a gene, and shows that selection favours the gene that maximizes the value of r under the prevailing ecological conditions). r is a measure of the fitness of the genotype in the environment in which its life history was measured.

Assuming survival is not associated with age at breeding, timing of offspring production influences r only if population numbers are changing; if they are increasing, offspring produced early in the lifespan are more valuable than those produced late, while if population numbers are decreasing the opposite is true (Cole 1954). However, with the more realistic assumption that there is mortality throughout the juvenile and adult periods, it is always advantageous to produce offspring as early as possible, unless this induces a change in mortality rate (Sibly & Calow 1987). If population numbers are stable, average lifetime reproductive success is a sufficient measure of the fitness of a genotype (Lande 1982; Sibly 1989; Charnov, this symposium). There is justification for the use of this measure because in practice, for a species to persist over evolutionary time, its numbers cannot decline indefinitely, and none are in a permanent state of increase. Some life-history variables may none the less be under selection only during phases of population increase or decline. For instance, in many multivoltine temperate insects, the summer is a period of increase in numbers, when early offspring will be more valuable, while the decrease in numbers from late summer onwards may occur through adult mortality unrelated to life-history characteristics. The Euler–Lotka equation for r automatically includes the effects of population increase or decrease, because r is defined under specified environmental conditions.

Certain simplifying assumptions are necessary for either r or lifetime reproductive success to be accepted as measures of fitness. Perhaps the most important is that fitnesses are not frequency dependent. This assumption is clearly not true where the presence or frequency of one life-history morph affects the way that selection acts on another (see, for example, Gross 1985, this symposium), and then an ESS approach is necessary (Maynard Smith 1982; Parker & Maynard Smith 1990). The theory also assumes that individuals of the same genotype are identical and invariably in the same ecological environment, aspects of which depend on conspecifics; to the extent that individuals, environments and population parameters vary, the theory needs modification to include the effects of temporally- and spatially-variable selection (Orzack & Tuljapurkar 1989). Other assumptions are that mating is random with respect to life-history characters and to age, and that parent–offspring conflict is not limiting parental options (Godfray & Parker, this volume).

The life-history characters maximizing r were described by Cole (1954), and by Law (1979) who dubbed the hypothetical creature displaying them a 'Darwinian Demon'; it commenced reproduction at birth, and produced copious offspring during frequent breeding attempts throughout its infinite lifespan. If such a life history could be realized in practice then it would be universal. The observed diversity in life histories suggests that natural selection cannot be the only contributing factor, and that other forces, namely constraints, must be at work.

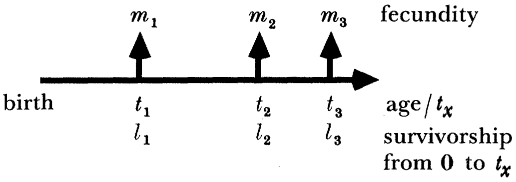

Figure 1. A general life history. The horizontal axis shows the individual's age.

3. FUNCTIONAL CONSTRAINTS

(*a*) *Ecological and physiological constraints*

In the study of life histories, most attention has been directed to the idea that only constrained combinations of the individual life-history characters contributing to r are possible, so that they cannot all be simultaneously maximized by natural selection. There seem to be two main reasons (Calow 1979). First, all organisms live in environments that are to some extent hazardous because of physical risks and the presence of biological enemies. Characters that would increase r can also increase the impact of these hazards, leading to ecological costs. For instance, male frogs *Physalaemus pustulosus* call to attract females, but are more vulnerable to predation by fringe-lipped bats *Trachops cirrhosus* when calling than when silent (Tuttle & Ryan 1981), leading to a survival cost of reproduction. Secondly, physiological costs can also occur if functional constraints are produced by processes internal to the organism. For instance, reproduction may lead to the diversion of resources away from repair or storage, causing a decline in survival or future fecundity (Fisher 1958; Williams 1966). This kind of reproductive cost has been particularly well studied in birds (Partridge 1989*a*; Linden & Moller 1989; Lessells 1991). An example is the demonstration that female collared flycatchers *Ficedula albicollis* allocated enlarged broods in their first year subsequently showed permanently lowered fecundity compared with control females (Gustaffson & Part 1990). Costs of reproduction can therefore affect both sexes, with an effect on mortality or fecundity, and can be exerted instantaneously (in the case of mortality) or with a time delay or both.

Functional constraints can also occur between the juvenile and adult period, although this type of effect is less well explored. For instance, the lifespan and late-life fecundity of female fruitflies *Drosophila melanogaster* can be increased by repeatedly breeding from adults late in their lives. However, this form of artificial selection can also result in a lengthening of the juvenile period and a reduction in larval survival (L. Partridge & K. Fowler, unpublished data). Physiological constraints on parents can also affect offspring characters; it may be impossible for a parent both to produce many offspring and to devote high levels of time or resources to each (Godfray & Parker, this symposium; Harvey & Keymer, this symposium).

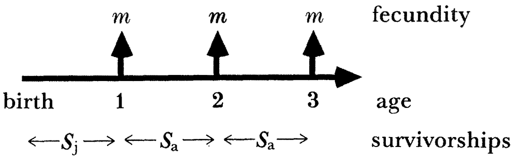

Figure 2. A simple life history first analysed by Schaffer (1974) (cf. figure 1). For this life history, equation (1) simplifies to $e^r = S_a + \frac{1}{2} S_j m$, where S_a and S_j are the adult and juvenile survivorship, respectively.

Organisms are therefore forced to reach some sort of compromise between the demands of competing costly activities, and the nature of that compromise is known as a trade-off. The nature of the constraints will vary between different taxa. These functional constraints are explicitly included in the theory of life-history evolution.

(*b*) *Functional constraints in the theory*

Williams (1966) used Fisher's (1958) idea of reproductive value to explore theoretically the consequences of a conflict between current and future reproduction, caused either by an increased likelihood of death of the parent, or by a negative effect on future fecundity. His important conclusion was that, depending upon the exact relation between possible combinations of current and future reproduction, it could pay to reduce current fecundity, because the loss of progeny would be more than compensated by the improvement in the prospects for reproduction in the future. The critical determinants of the optimal decision are the relative value of adults and progeny, and the function linking the possible combinations of current and future reproduction (Gadgil & Bossert 1970; Schaffer 1974; Pianka & Parker 1975; Sibly & Calow 1986).

These can be illustrated using the modified life history shown in figure 2. For any pair (or more) of life-history characters, the options open to an individual can be described using what have been variously known as strategy sets (Maynard Smith 1978; Parker & Maynard Smith 1990), options sets (Sibly 1991), in a modified form as fitness sets (Levins 1968; Pianka & Parker 1975), and which can sometimes be derived from the principle of allocation (Cody 1966). All refer to an n-dimensional space defined by a set of orthogonal axes, each representing one life-history character. Only a restricted region of this space contains character combinations which the organism is capable of achieving in its natural environment. Two possible functions are illustrated in figure 3*a* and *b* for fecundity at age x and adult survivorship in the life history shown in figure 2. The best combination or trade-off for the organism to adopt can be determined by the use of fitness contours along which r is constant and which are plotted in the same space as the options set. In figure 3 these are straight lines of negative slope S_j, the juvenile survival rate, with r increasing as lines are crossed moving away from the origin. In figure 3*a* the options set is drawn as convex out, as might occur if each increment of reproduction eats increasingly further into a budget for personal maintenance. The trade-off leading to the highest value of r (*) is given by the point of contact of the options set with the outermost fitness contour it touches, leading in this case to intermediate values of reproduction and survival

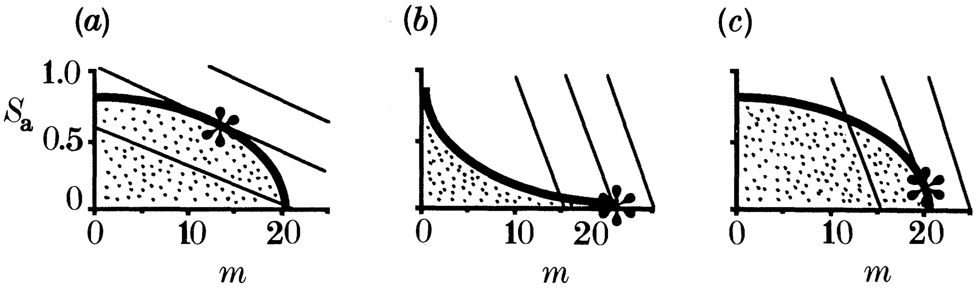

Figure 3. Options sets (dotted) with associated trade-off curves, which are their boundaries, for the life-history variables m and S_a defined in figure 2. In (*a*) and (*c*) the options sets are convex out, in (*b*) it is concave out (see text for biological interpretation). Fitness contours have been superimposed (straight lines), calculated from the equation $S_a = e^r - \frac{1}{2}S_j m$ (see figure 2) and so have slope $-\frac{1}{2}S_j$. * denotes optimal trade-off. Note that low juvenile survivorship selects for iteroparity (*a*), whereas high juvenile survivorship selects for semelparity (*c*).

(iteroparity). If the options set is concave out (figure 3*b*), as might occur if the marginal cost of each offspring reduces with increasing fecundity, suicidal levels of reproduction are optimal (semelparity). The effect of increasing the level of juvenile survival when the options set is convex out (figure 3*c*) is to increase the optimal reproductive rate despite the resulting lower adult survival. This theoretical prediction has recently been elegantly confirmed in field introduction experiments with guppies *Poecilia reticulata* (Reznick *et al.* 1990). If the trade-off varies in curvature over its range, multiple optima may be possible, which could itself explain some life-history diversity.

An important conclusion to emerge from optimality theory is that the shape of the options set is critical in determining the form of the life history. This conclusion is not apparent from quantitative genetic theory, in which the options set is represented by the genetic variance-covariance or G matrix. Genetic models assume linearity of the G matrix in the region of evolutionary equilibrium. In this way the quantitative genetic theories obscure an object of interest, namely the shapes of the trade-off curves (Charnov 1989).

The theory of life-history evolution is well developed. The current state of empirical work is less advanced, and the theory has outstripped our ability to test it. A major difficulty is that we know almost nothing about the shapes of the options sets that determine the possible shapes of trade-off curves.

4. MEASURING OPTIONS SETS

To understand the evolution of life histories we need to know, for specific organisms in specified environments, the set of achievable combinations of different life-history variables. A start in this direction has been made by the detection of the presence of ecological and physiological constraints between pairs of variables; some examples have already been mentioned. Ultimately we wish to extend this knowledge to cases where all the life-history variables and the shapes of the surfaces relating their best achievable values are understood, in at least a few organisms. We need to know where the most important restrictions occur, why they occur and what they look like. The options sets can then be related to the fitness contours for the life histories being studied, to determine if they explain the different trade-off values seen.

There has been much discussion about the appropriate methods for measuring options sets. Is it sufficient to make observations on undisturbed populations? Must we work in the field? What is the best method for an experimental approach? Is it always necessary to do genetic studies? A point of general importance is that the circumstances under which the options set is measured should be those in which the life history evolved, including the impact of ecological hazards and the population density of the study species. These criteria are hard to satisfy, and raise the spectre that we may be dealing with a theory couched in terms of unmeasurable relations. Only time will tell, but a simple conclusion to energe from the approaches about to be discussed is that we need to understand much more about mechanisms if we are to make headway with measuring options sets.

(*a*) *Theoretical considerations*

Options sets can be defined theoretically for some optimization problems (Parker & Maynard Smith 1990). For instance, where male and female progeny are of equal cost and value to their parents, the options set for the proportion of males versus proportion of females in the progeny would be a straight line of negative slope 1. For sex determination systems such as haplo-diploidy, any of the points along the line could also be achieved in practice. Unfortunately, most life-history options sets cannot be so easily defined.

Tantalizingly, it might be possible to identify a *physiological* options set in this way using Cody's (1966) Principle of Allocation. An organism's life history can be viewed at the output of three biological processes, namely maintenance (which affects survival), growth (which affects the timing of reproduction) and reproduction, and these three processes are in competition for nutrients. The Principle of Allocation asserts that, in accordance with the conservation of matter, nutrients allocated to one process are not available to the others. It follows that the options regarding allocations between the three biological processes lie in a plane in the three-dimensional space, the axes of which represent the allocations to each process. So far so good, but how do we get from this set to the life-history variables m_x, l_x and t_x? The relations with m_x and t_x are relatively straightforward (Calow & Sibly 1990), and indeed there have been many measurements of 'reproductive effort', defined as the fraction of the total amount of resources of time and energy available to the individuals at a given age that is devoted to reproduction (Tinkle 1969; Gadgil & Bossert 1970; Hirshfield & Tinkle 1975). The problems arise with the relation between maintenance and mortality rate. Little can be said in general except that the relation is likely to be decreasing and nonlinear. Thus, reducing allocation to maintenance may increase mortality rate gradually until a threshold at which any further increase would pose a serious risk to life. In short, the gain and cost functions for the life-history variables affected by altered nutrient allocation may often be nonlinear. A similar problem occurs when the trade-off spans two generations. For instance, in birds that feed their dependent young, an increase in clutch size is eventually likely to be accompanied by a law of diminishing returns in the number of young fledged, because the total amount of food that can be delivered to the brood is limited by the parents' ability to forage (Lack 1954; Charnov & Krebs 1974). Another problem with this approach is that only some nutrients may be limiting, and these only at particular times. Lastly, the approach concerns itself only with different ways of dividing the cake of available resources, but there is no reason why the size of the cake should not be increased, albeit at some ecological cost to the individual. Such a cost, however, necessarily brings into play new trade-offs, the impact of which cannot be deduced from the Principle of Allocation alone.

An empirical approach to options sets is, therefore, usually desirable. The key question is: what kind of empirical approach? The aim is to persuade an organism to operate over the possible range of values for one life-history variable, and to give its corresponding best possible performance on another, using all the developmental, physiological and behavioural machinery at its disposal. The empirical studies so far described all involved testing the null hypothesis of absence of functional constraints, and all rejected it. Indeed, trade-offs are a logical necessity in a world of risk and finite resources (Stearns 1989). The important questions are whether it is possible empirically to deal directly with the constraints imposed by ecological hazards and by finite resources, and so to measure the shapes of options sets. Possible techniques for doing so will now be considered.

(*b*) *Individual variation*

A method that has frequently been used to detect costs of reproduction is to record data on the naturally occurring variation between the individuals within a population under field or laboratory conditions. The data can be used to test, for instance, for an association across individuals between reproduction and subsequent survival or fecundity. Examples of the use of this method include a demonstration that red deer *Cervus elaphus* females giving birth to calves in one season had lower subsequent survival and fecundity than non-reproductive females (Clutton-Brock *et al.* 1982); work showing that subsequent fecundity is higher in female collared flycatchers *F. albicollis* breeding for their first time at the age of 2 years than in females breeding in their first year (Gustaffson & Part 1990); and the study already mentioned (Tuttle & Ryan 1981) showing a higher rate of predation by bats on calling male frogs *P. pustulosus* than on non-calling males.

These studies all suggest the existence of reproductive costs, and for none of them is it easy to suggest an alternative explanation. Such studies are therefore valuable in revealing the kinds of constraints that can occur. However, correlational studies have been criticized (see, for example, Partridge & Farquhar 1983; Reznick 1985; Bell & Koufopanou 1986; van Noordwijk & de Jong 1986; Partridge & Harvey 1985, 1988; Partridge 1989*a*, *b*). The main reason is that confounding variables are likely to reduce the true magnitude of the effect or even to produce spurious correlations, for example positive correlations when the true values are negative. Individuals can differ in phenotype as a result of their environment in early life or in adulthood. For instance, opportunities for feeding during growth may affect adult body size, identity of parents may affect the social status of offspring, and recent feeding may affect fat reserves of adults. This sort of variation can cause individuals to differ in the size of their options sets; some individuals will then have the potential for high scores on all life-history variables. The environments occupied by different individuals may also differ, affecting both current reproductive success and subsequent survival and fecundity. Both individual phenotype and environment may also differ between populations, and will tend to produce positive correlations between life-history variables.

There have been several surveys of the effect of using correlational studies to deduce options sets (see, for example, Reznick 1985; Bell & Koufopanou 1986; Partridge 1989*a*, *b*). The general picture to emerge is inconsistent, with many positive correlations between life-history characters, which individually lead to high fitness, suggesting that individual phenotype and environmental differences may have a potent influence on the form of individual life histories. This is in itself both a phenomenon of interest and a problem for life-history theory (Partridge 1989*a*).

It is no coincidence that natural variation between individuals has been used to search for reproductive costs, but not for other forms of functional constraint on the life history. It would not be possible to use this technique to look for an association between juvenile survival probability and subsequent adult performance, because once the creature is dead it can yield no data on later parts of its life history. Characters costly in terms of earlier survival must therefore be investigated by other means.

(*c*) *Comparisons of populations or taxa*

The comparative approach is one way of detecting adaptation. If an independent character, such as haplodiploidy, causes a predisposition for the evolution of a dependent character, such as eusociality, then they would be expected to co-occur. The technique has been highly successful in revealing patterns in nature (see, for example, Harvey & Pagel 1991).

In principle, the comparative approach might be used as well to detect constraints on adaptation as to detect adaptation itself, and hence could be useful for measuring options sets. For life histories, species comparisons have been used to show that the large males of highly polygynous species suffer a higher death rate before reaching adulthood. The association probably occurs because males achieve their size excess by rapid growth, at the expense of fat deposition, increasing the chance of starvation (Clutton-Brock *et al.* 1985). Unlike individual variation, the units compared are populations, and so the comparative method can be used to examine functional constraints involving early death. Comparative work has also been useful in studying the trade-off between number and size of offspring (Godfray & Parker, this symposium; Harvey & Keymer, this symposium).

There are difficulties with using the comparative approach to measure options sets. The problem of confounding variables producing spurious correlations, mentioned above in the context of the use of individual differences, applies equally here. In addition, gene–environment interactions can be a problem where different populations or species are placed in a common environment to which they are not equally well adapted (Partridge 1989*b*); this procedure is likely to take less well adapted species away from the boundary and into the interior of their options sets. This may explain why several comparative studies of different species in the laboratory have revealed positive correlations between life history variables (see Snell & King 1977; Schnebel & Grossfield 1988).

Population dynamics pose an additional complication. An association between high seasonal fecundity and low adult survival rates has been reported across species of lizards (Tinkle 1969), birds (O'Connor 1985; Saether 1988) and mammals (Sutherland *et al.* 1986). However, populations in steady state necessarily have equal birth and death rates, so that higher adult fecundity is inevitably accompanied by increased adult or juvenile mortality (Sutherland *et al.* 1986; Sibly & Calow 1987; Gustaffson & Sutherland 1988). One way out of this difficulty would be to confine the use of the technique to life-history characters that make at most only a small contribution to population dynamics. Male reproductive characters could qualify where males contribute only gametes to their progeny. An interesting association between bright male coloration (and hence high reproductive rate?) and short adult lifespan has been reported in lizards (Tinkle 1969), and in general, semelparity seems to be associated with extreme development of male secondary sexual characters (Partridge & Endler 1987), perhaps showing a trade-off between fecundity and longevity for males.

The comparative method was devised to study adaptation, but it is always possible that correlated life-history characters could be independent adaptations to the different study environments. Their association would then not imply any functional constraint. So, for instance, high rates of predation on small individuals might be expected independently to select for speedy development and thus earlier age of first breeding to minimize the time spent in the dangerous size classes, but also to reduce adult reproductive rate as a consequence of the lower value of juveniles. An association between these two sets of characters would therefore not necessarily show a functional constraint between them.

(*d*) *Genetic studies*

Genetic approaches to measuring functional constraints estimate the extent to which genetic variation affecting one life-history character also affects another, measured as the genetic correlation between them. Genetic correlations can be estimated from correlated responses to selection, as in the *Drosophila* example already mentioned (p. 5), or in two-generation studies. An example of the latter is provided by a study of cowpea weevils *Callosobruchus maculatus*, which examined some life-history characters of the female progeny of single males mated to a series of different females. The results showed a negative genetic correlation between adult fecundity and development rate, consistent with the existence of a trade-off constraining the animal's evolutionary options in the culture environment (Moller *et al.* 1989*a*, *b*).

Genetic studies avoid the pitfalls so far mentioned, and they allow all parts of the life history to be studied. It has indeed been argued that only the demonstration of a negative genetic correlation between two traits, caused by pleiotropy, is sufficient to show that there is a functional constraint between them (see, for example, Charlesworth 1980; Lande 1982; Reznick 1985). From this perspective options sets are viewed as a result of genetic constraints imposed by pleiotropy. It is of course true that if, for instance, nutrients are limiting for reproduction and growth, then a genetic variant, the primary mode of action of which is to cause the diversion of nutrients towards reproduction, will also lower growth. To view this as a genetic constraint is perhaps a little perverse; the primary level of action of constraint in the example just described is nutritional, not genetic.

The main argument advanced for the necessity of genetic studies is that, because we are interested in evolutionary options, we need a demonstration that these can be genetically coded. This could be provided by a selection experiment, or by the measurement of genetic correlation (or more generally, the genetic variance-covariance matrix). However, it is not clear that either approach will necessarily reveal the options set. The *reductio ad absurdum* of that position would be to assert that because cheetahs, say, appear to lack any significant genetic variance, their life histories cannot involve trade-offs. Even for persistently large populations, genetic variances give a guide only to the very short term evolutionary future. To find out what could be achieved in the long term in response to a genetic change in the value of one life-history character, two further items of information are needed. The first is the range of effects of new mutational variance. Second, if the initial correlated responses are not the best possible ones, there may be selection on other loci, not initially involved in the response, to modify them. In short, the level of genetic variance available on a reasonable timescale allows exploration of only a very restricted part of the options set.

There is also a pragmatic point, which is that genetic techniques will allow only very slow progress. They confine attention to a small subset of the organisms; it is no coincidence that most genetic studies have been done on insects in the laboratory. The genetic techniques which stand the most chance of being used in the field are selection experiments (see Reznick *et al.* 1990) and two-generation studies. The latter, however, requires the use of controlled breeding designs in an appropriate environment (Clark 1987). There are also problems with large standard errors on estimates of genetic correlation. Even in the carefully controlled laboratory study of weevils described above, in which 761 individuals were scored, several of the estimates of genetic correlation lay outside the theoretical limits of minus and plus one. Such problems frequently occur, and this means that impractically large breeding designs are often required. For this reason perhaps, and because selection magnifies genetic effects (Pease & Bull 1988), correlated responses to selection have provided more evidence for the existence of genetic constraint than has the two generation approach (Reznick 1985; Lessells 1991). However, both approaches are limited by the amount of genetic variation available, and genetic studies are therefore probably not going to reveal why an albatross lays one egg and a blue tit ten.

These sorts of considerations provide a strong motivation for finding other avenues of approach. The main alternative avenue is experimental manipulation. However, use of this approach involves assumptions, which require empirical validation.

(*e*) *Experimental manipulations*

Experimental manipulations examine the effect of manipulation of one life-history variable on others. For instance, the cost of reproduction in female fruitflies *D. subobscura* was investigated by exposing them briefly to X-irradiation or high temperatures, both of which had the apparently paradoxical effect of extending the lifespan. There was, however, no significant effect on mutant ovaryless females, suggesting that the manipulations abolished ovarian activity, and that ovarian activity reduced longevity (Maynard Smith 1958; Lamb 1964). The geographical strain of flies used in the experiments mated only once. In the related *D. melanogaster* remating is common, and here mating reduces female lifespan even more than does the production of eggs (Fowler & Partridge 1989).

Surveys of the results of experiments have shown that, like correlated responses to selection, they reveal fairly consistent evidence for the existence of functional constraints (Reznick 1985; Bell & Koufopanou 1986; Partridge 1989*a*). Could experiments of this general kind be used to measure options sets? The approach has potential strengths and weaknesses.

A strength of experiments is that they have the potential for exploration of a large range of character values, much greater than could be achieved in practice for most organisms by artificial selection. In addition, experiments are strictly prospective; they will reveal only effects occurring after the point in the life history at which the intervention is made. This allows precise examination of the present and future effects of decisions at each point in the life history in isolation from others but, on the other hand, would not necessarily reveal the most likely evolutionary response to a change in the manipulated life-history variable, because the correlated response could involve an event earlier in the life history. For instance, male swallows *Hirundo rustica* with experimentally elongated tails had higher reproductive success (Moller 1988) but incurred a cost in terms of their reproductive success in the ensuing breeding season (Moller 1989). However, there could be additional earlier survival costs for a bird growing a longer tail. Experiments have so far been used mainly to study costs of reproduction, for which some manipulative techniques are available. Ignorance of the machinery controlling developmental decisions has impeded manipulation of earlier parts of the life history.

Experiments are not free of pitfalls. One is that the manipulation used may alter the options set. For instance, using food to induce a female fruitfly to lay more eggs or a male swallow to grow a longer tail could also have a direct effect on the dependent variables survival and future reproduction. This is a serious difficulty, which can only be circumvented by an understanding of physiological control mechanisms. Manipulations should ideally alter all aspects of the target variable in a coordinated way. For instance, some brood size manipulation experiments, aimed at investigating the cost of chick-rearing, have revealed that the parents do not alter their rate of feeding the brood in response to a change in its size (reviewed in Lessells 1991). Even in simpler systems there can be pitfalls. Abolition of ovarian activity increased the lifespan of female *D. subobscura*, but these experiments may not have fully abolished reproductive costs, because the fat body synthesis and degradation of yolk polypeptides may have continued in the absence of an ovary.

If experiments are to be used successfully to measure options sets, then the mechanisms underlying the response to the manipulation must be studied; an understanding of how the organism controls its own life-history events is needed for effective intervention. This problem is especially acute if we want to understand the effects of decisions made in the juvenile period on events then and in adulthood. As a result, we really have very little idea of how much adult survival and fecundity are determined by decisions made in adulthood and how much on ones made earlier in life.

If appropriate experimental manipulations can be found, will they help us to understand life-history evolution? For them to do so, two things would have to be true. The system would have to give its best response to the manipulation, which is tantamount to saying that the relevant phenotypic plasticity would have to be optimal. It would also have to have the same characteristics as the probable evolutionary response to a genetic change of the same magnitude. These are empirically testable assumptions, and there is a need for studies of the relation between responses to experimental manipulations and correlated response to selection. If the two methods give the same results, then the genetical relevance of the experimental manipulations has been shown. Otherwise two types of differences are possible. Experimental manipulation could show options not revealed by a genetical study, and this is the likely outcome if there is an insufficiency of genetic variation for selection to act on. Alternatively, the genetical study might show options not revealed by experimental manipulation, if genes can achieve more than the experimental manipulator. It may be that evolutionary responses and correlated responses are achieved by a multiplicity of intermediate mechanisms that cannot be reproduced without going through the evolutionary process itself; it would certainly be worth trying to find out.

Thus, no one approach to the elucidation of options sets is likely to be sufficient on its own. There will always be a place for individual studies that reveal correlations hard to explain except in terms of trade-offs. If these trade-offs are real, it should be possible to show them using genetic techniques, and where this can be achieved it is the method of choice, since it is certain that all the options revealed are genetically codable. The major problems with the genetic approach are that it may not reveal all possible genetic options, and that it is limited by the amount of genetic variation present in the study populations. These problems may be to some extent circumvented using experimental manipulation, successful application of which depends on a secure understanding of the physiological mechanisms involved in the control of life-history variables. However, an indication is needed that what was achieved by experimental manipulation could also be achieved by genetic engineering. This may not be implausible, however. For instance, in the experiment of Fowler & Partridge (1989) discussed above, it was shown that in an environment containing two males per female, reducing mating by $\frac{2}{3}$ improved female survivorship. It seems clear that in that environment, genes that achieved that reduction in mating would obtain the survivorship advantage. In principle, reduction in mating could be achieved by many mechanisms, although whether these could all be achieved in the study environment is less sure.

5. LONG-TERM CONSTRAINTS

Variation in the shapes of trade-off curves and differences in selection pressures may not be a sufficient explanation for life-history diversity. There are many instances where organisms with otherwise similar biology and inhabiting similar environments show marked differences in their life histories.

Part of the explanation could be provided by trade-off curves themselves if they are complex in shape, and hence allow more than one locally optimum solution. For instance, among the Salmonidae, the Genus *Salmo* is iteroparous, while *Oncorhynchus* is nearly always semelparous. These two genera coexist, spawning and maturing in the same areas. Schaffer (1974) suggested that the difference might be caused by a complex trade-off curve between fecundity and subsequent survival, with optima at both semelparity and iteroparity. Under these circumstances the point on the trade-off curve initially occupied could be important in determining the response of the life history to natural selection.

Even with multiple optima, the shapes of trade-off curves will be informative only about the short-term courses available. Over evolutionary time, options sets themselves can change. The extent to which they can do so will depend upon whether the underlying constraint is universal or local (Maynard Smith *et al.* 1985). Local constraints, which apply only to specific taxa, will mean that differences in design between organisms will affect the way that they evolve in a common environment. For instance, pre-existing contact with offspring appears to make it easier for fish to evolve parental care (Gross & Shine 1981).

Evolutionary lags may be another source of variation in life histories. Time is necessary both for the possible mutational variance to occur, and for a response to selection to be effected, so that the observed phenotype may lag behind the optimal one during periods of evolution, especially if selection is weak. Evolutionary delays of this kind could both withhold a population from the optimum, and cause diversity among populations subject to similar selection pressures for different lengths of time. The history of a population will then be a determinant of its life history.

Under some circumstances historical effects can take the extreme form of irreversibility, so that organisms can become stuck in absorbing states (Bull & Charnov 1985). One reason is that some evolutionary paths may involve loss of structures or processes which are then difficult to re-evolve. For instance, it could be easy to evolve semelparity from iteroparity by loss of late reproduction, but more difficult to evolve in the reverse direction, if the genetic substrate for post-reproductive survival has been lost. Natural selection itself can also cause irreversibility. For instance, in parasitic wasps, clutch size is bimodal, with clutch sizes of one giving rise to larvae equipped with large mandibles that are used to kill any introduced larvae, and clutch sizes above three giving rise to gregarious non-armed larvae.

This situation seems to be a consequence of parent–offspring conflict rather than a reflection of the distribution of parental optima. A theoretical analysis (Godfray 1987) suggested that a rare gene for gregariousness could only with difficulty invade a population of fighting larvae unless fitness increases with clutch size. The reason is that a rare gregarious larva is likely to find itself with at least one fighter, and will hence perish. Under these circumstances it pays the parent to reduce the clutch size to one, because only one larva will give rise to an adult, and clutch size one becomes an absorbing state. Evolving fighting larvae from gregarious ones would not present the same difficulty.

These kinds of long-term constraints are not easy to investigate. Theoretical studies like the one just described are likely to prove extremely valuable, but so also are empirical studies of trade-off curves and of the life histories, of populations with well known evolutionary histories.

REFERENCES

Bell, G. & Koufopanou, V. 1986 The cost of reproduction. In *Oxford surveys in evolutionary biology*, vol. 3 (ed. R. Dawkins & M. Ridley), pp. 83–131. Oxford University Press.

Bull, J. J. & Charnov, E. L. 1985 On irreversible evolution. *Evolution* **39**, 1149–1155.

Calow, P. 1979 The cost of reproduction: a physiological approach. *Biol. Rev.* **54**, 23–40.

Calow, P. & Sibly, R. M. 1990 A physiological basis of population processes: ecotoxicological implications. *Funct. Ecol.* **4**, 283–288.

Caswell, H. 1989 Life history strategies. In *Ecological concepts* (ed. J. M. Cherrett), pp. 285–307. Oxford: Blackwell Scientific Publications.

Charlesworth, B. 1980 *Evolution in age-structured populations*. Cambridge University Press.

Charlesworth, B. 1990 Optimization models, quantitative genetics and mutation. *Evolution* **44**, 520–538.

Charlesworth, B. & Leon, J. A. 1976 The relation of reproductive effort to age. *Am. Nat.* **110**, 449–459.

Charnov, E. L. 1989 Phenotypic evolution under Fisher's Fundamental Theorem of Natural Selection. *Heredity* **62**, 113–116.

Charnov, E. L. & Krebs, J. R. 1974 On clutch size and fitness. *Ibis* **116**, 217–219.

Clark, A. G. 1987 Genetic correlations: the quantitative genetics of evolutionary constraints. In *Genetic constraints on adaptive evolution* (ed. V. Loeschcke), pp. 25–45. Berlin: Springer-Verlag.

Clutton-Brock, T. H., Albon, S. D. & Guiness, F. E. 1985 Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature, Lond.* **313**, 131–133.

Clutton-Brock, T. H., Guiness, F. E. & Albon, S. G. 1982 *Red deer – behaviour and ecology of two sexes*. University of Chicago Press.

Cody, M. L. 1966 A general theory of clutch size. *Evolution* **20**, 174–184.

Cole, L. C. 1954 The population consequences of life history phenomena. *Q. Rev. Biol.* **29**, 103–137.

Dhondt, A. A., Adriaensen, F., Matthysen, E. & Kempenaers, B. 1991 Non-adaptive clutch sizes in tits: evidence for the gene flow hypothesis. *Nature, Lond.* **348**, 723–725.

Fisher, R. A. 1958 *The genetical theory of natural selection*. New York: Dover.

Fowler, K. & Partridge, L. 1989 A cost of mating in female fruitflies. *Nature, Lond.* **338**, 760–761.

Gadgil, M. & Bossert, W. H. 1970 Life historical consequences of natural selection. *Am. Nat.* **104**, 1–24.

Godfray, H. C. J. 1987 The evolution of clutch size in parasitic wasps. *Am. Nat.* **129**, 221–233.

Gould, S. J. & Lewontin, R. C. 1979 The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. Lond.* B **205**, 581–598.

Gross, M. R. 1985 Disruptive selection for alternative life histories in salmon. *Nature, Lond.* **313**, 47–48.

Gross, M. R. & Shine, R. 1981 Parental care and mode of fertilization in ectothermic vertebrates. *Evolution* **35**, 775–793.

Gustaffson, L. 1986 Lifetime reproductive success and heritability: empirical support for Fisher's fundamental theorem. *Am. Nat.* **128**, 761–764.

Gustaffson, L. & Part, T. 1990 Acceleration of senescence in the collared flycatcher *Ficedula albicollis* by reproductive costs. *Nature, Lond.* **347**, 279–281.

Gustaffson, L. & Sutherland, W. J. 1988 The costs of reproduction in the collared flycatcher *Ficedula albicollis*. *Nature, Lond.* **335**, 813–815.

Harvey, P. H. & Pagel, M. D. 1991 *The comparative method*. Oxford University Press.

Hirshfield, M. F. & Tinkle, D. W. 1975 Natural selection and the evolution of reproductive effort. *Proc. natn. Acad. Sci. U.S.A.* **72**, 2227–2231.

Lack, D. 1954 *The natural regulation of animal numbers*. Oxford University Press.

Lamb, M. J. 1964 The effects of radiation on the longevity of female *Drosophila subobscura*. *J. Insect Physiol.* **10**, 487–497.

Lande, R. 1982 A quantitative genetic theory of life history evolution. *Ecology* **63**, 609–615.

Law, R. 1979 Ecological determinants in the evolution of life histories. In *Population dynamics* (ed. R. M. Anderson, B. D. Turner & L. R. Taylor), pp. 81–103. Oxford: Blackwell Scientific Publications.

Lessells, C. M. 1991 The evolution of life histories. In *Behavioural ecology: an evolutionary approach*, 3rd edn. (ed. J. R. Krebs & N. B. Davies). Oxford: Blackwell Scientific Publications. (In the press.)

Levins, R. 1968 *Evolution in changing environments*. Princeton University Press.

Lewontin, R. C. 1965 Selection for colonising ability. In *The genetics of colonising species* (ed. H. G. Baker & G. Ledyard Stebbins), pp. 77–94. New York: Academic Press.

Linden, M. & Moller, A. P. 1989 Cost of reproduction and covariation of life history traits in birds. *Trends Ecol. Evol.* **4**, 367–371.

Maynard Smith, J. 1958 The effects of temperature and of egg-laying on the longevity of female *Drosophila subobscura*. *J. exp. Biol.* **35**, 832–842.

Maynard Smith, J. 1978 Optimization theory in evolution. *A. Rev. Ecol. Syst.* **9**, 31–56.

Maynard Smith, J. 1982 *Evolution and the theory of games*. Cambridge University Press.

Maynard Smith, J., Burian, R., Kauffman, S., Alberch, P., Campbell, J., Goodwin, B., Lande, R., Raup, D. & Wolpert, L. 1985 Developmental constraints and evolution. *Q. Rev. Biol.* **60**, 265–287.

Moller, A. P. 1988 Female choice selects for male sexual tail ornaments in the monogamous swallow. *Nature, Lond.* **332**, 640–642.

Moller, A. P. 1989 Viability costs of male tail ornaments in a swallow. *Nature, Lond.* **339**, 132–135.

Moller, H., Smith, R. H. & Sibly, R. M. 1989 Evolutionary demography of a bruchid beetle. I. Quantitative genetical analysis of the female life history. *Funct. Ecol.* **3**, 673–681.

Moller, H., Smith, R. H. & Sibly, R. M. 1989 Evolutionary demography of a bruchid beetle. II. Physiological manipulations. *Funct. Ecol.* **3**, 683–691.

Mueller, L. D. & Ayala, F. J. 1981 Trade-off between *r*-selection and *K*-selection in Drosophila populations. *Proc. natn. Acad. Sci. U.S.A.* **78**, 1303–1305.

O'Connor, R. J. 1985 Behavioural regulation of bird populations: a review of habitat use in relation to migration and residency. In *Behavioural ecology: ecological consequences of adaptive behaviour* (ed. R. M. Sibly & R. H. Smith), pp. 105–142. Oxford: Blackwell Scientific Publications.

Orzack, S. H. & Tuljapurkar, S. 1989 Population dynamics in variable environments. VII. The demography and evolution of iteroparity. *Am. Nat.* **133**, 901–923.

Parker, G. A. & Maynard Smith, J. 1990 Optimality theory in evolutionary biology. *Nature, Lond.* **348**, 27–33.

Partridge, L. 1989*a* Lifetime reproductive success and life history evolution. In *Lifetime reproduction in birds* (ed. I. Newton), pp. 421–440. London: Academic Press.

Partridge, L. 1989*b* An experimentalist's approach to the role of costs of reproduction in the evolution of life histories. In *Toward a more exact ecology* (ed. P. J. Grubb & J. B. Whittaker), pp. 231–246. Oxford: Blackwell Scientific Publications.

Partridge, L. & Endler, J. 1987 Life history constraints on sexual selection. In *Sexual selection: testing the alternatives* (ed. J. Bradbury & M. Andersson), pp. 265–277. Chichester: Wiley.

Partridge, L. & Farquhar, M. 1983 Lifetime mating success of male fruitflies *Drosophila melanogaster* is related to their size. *Anim. Behav.* **31**, 871–877.

Partridge, L. & Harvey, P. H. 1985 Costs of reproduction. *Nature, Lond.* **316**, 20–21.

Partridge, L. & Harvey, P. H. 1988 The ecological context of life history evolution. *Science, Wash.* **241**, 1449–1454.

Pease, C. M. & Bull, J. J. 1988 A critique of methods for measuring life history trade-offs. *J. evol. Biol.* **1**, 293–303.

Pettifor, R. A., Perrins, C. M. & McCleery, R. H. 1988 Individual optimization of clutch size in great tits. *Nature, Lond.* **336**, 160–162.

Pianka, E. R. & Parker, W. S. 1975 Age-specific reproductive tactics. *Am. Nat.* **109**, 453–464.

Price, T. R., Kirkpatrick, M. & Arnold, S. J. 1988 Directional selection and the evolution of breeding date in birds. *Science, Wash.* **240**, 798–799.

Reznick, D. 1985 Costs of reproduction: an evaluation of the empirical evidence. *Oikos* **44**, 257–267.

Reznick, D. A., Bryga, H. & Endler, J. A. 1990 Experimentally induced life history variation in a natural population. *Nature, Lond.* **346**, 357–359.

Rose, M. 1984 Laboratory evolution of postponed senescence in *Drosophila melanogaster*. *Evolution* **38**, 1004–1010.

Rose, M. R., Service, P. M. & Hutchinson, E. W. 1987 Three approaches to trade-offs in life history evolution. In *Genetic constraints on adaptive evolution* (ed. V. Loeschcke), pp. 91–105. Berlin: Springer-Verlag.

Saether, B-E. 1988 Pattern of covariation between life history traits of european birds. *Nature, Lond.* **331**, 616–617.

Schaffer, W. M. 1974 Selection for life histories: the effects of age structure. *Ecology* **55**, 291–303.

Sibly, R. M. 1989 What evolution maximises. *Funct. Ecol.* **3**, 129–135.

Sibly, R. M. 1991 The life-history approach to physiological ecology. *Funct. Ecol.* (In the press.)

Sibly, R. M. & Calow, P. 1986 *Physiological ecology of animals*. Oxford: Blackwell Scientific Publications.

Sibly, R. M. & Calow, P. 1987 Ecological compensation – a complication for testing life history theory. *J. theor. Biol.* **125**, 177–186.

Snell, T. E. & King, C. E. 1977 Life span and fecundity patterns in rotifers: the cost of reproduction. *Evolution* **31**, 882–890.

Schnebel, E. M. & Grossfield, J. 1988 Antagonistic pleiotropy: an interspecific *Drosophila* comparison. *Evolution* **42**, 306–311.

Stearns, S. C. 1976 Life-history tactics: a review of the ideas. *Q. Rev. Biol.* **51**, 3–47.

Stearns, S. C. 1989 Trade-offs in life history evolution. *Funct. Ecol.* **3**, 259–268.

Sutherland, W. J., Grafen, A. & Harvey, P. H. 1986 Life history correlations and demography. *Nature, Lond.* **320**, 88.

Tinkle, D. W. 1969 The concept of reproductive effort and its relation to the evolution of life histories of lizards. *Am. Nat.* **103**, 501–516.

Tuttle, M. D. & Ryan, M. J. 1981 Bat predation and the evolution of frog vocalizations in the neotropics. *Science, Wash.* **214**, 677–678.

van Noordwijk, A. J. & de Jong, G. 1986 Acquisition and allocation of resources: their influence of variation in life history tactics. *Am. Nat.* **128**, 137–142.

van Noordwijk, A. J., van Balen, J. H. & Scharloo, W. 1980 Heritability of ecologically important traits in the great tit. *Ardea* **68**, 193–203.

Williams, G. C. 1966 Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.* **100**, 687–690.

Discussion

R. J. H. Beverton (*Montana, Old Roman Road, Langstone, Gwent NP6 2JU, U.K.*). Although commending your comparative approach to life-history dynamics, care is needed about the extent to which quantitative relations such as that between pre-mature mortality rate and subsequent spawning strategy (semelparity against iteroparity) are valid between different animal groups. Perhaps I could give three examples from fish to illustrate this. Populations of American shad (*A. shapidissima*) at the southern end of their range are semelparous and have a high fecundity, whereas at the northern end they are predominantly iteroparous and have a low fecundity, which fits your prognosis. However, the Pacific pink salmon (*O. gorbuscha*) is strictly semelparous, spawning and dying at two years of age, whereas the Atlantic salmon (*S. salar*) is iteroparous, being able (if allowed to survive) to spawn a number of times; yet both species have a similar fecundity and pre-mature mortality rate. Lastly, elasmobranchs produce a very few young each year and have a low pre-mature mortality rate; whereas many teleosts are highly fecund, laying up to a million or so eggs per adult annually, and have a correspondingly high pre-mature mortality rate. Yet iteroparity is common in both groups. Clearly, fecundity and pre-mature mortality rate must vary inversely for the population to be balanced, and different kinds of fish have solved that part of the life-history equation in quite different ways independently of subsequent spawning strategy.

L. Partridge and R. Sibly. As we have suggested, great care is needed in applying the comparative approach. When different species are compared, it is necessary first to consider whether they have the same options sets – in general we imagine the answer is no. Complexity of the shape of the options sets could also produce multiple optima. But with no information about the shape of the options sets, no predictions can be made from optimality theory. For the elasmobranch and teleost comparison you mention, there is likely to be a trade-off between egg size and number, which would explain the fecundity difference, and which would not be expected to influence the degree of iteroparity.

W. G. Hill (*University of Edinburgh*, *Edinburgh*, *U.K.*). Different species adopt widely different reproductive strategies in what appear quite similar environments, for example, elasmobranchs and teleosts as mentioned previously. This would suggest that organisms can utilize their energy and other resources effectively in many ways. Further, it suggests that curves relating total fitness to any single component of fitness, providing all other components are altered appropriately, are very flat: there is no, or a very weak, global optimum. However, a curve relating fitness to any component on its own, or any pair or more of components with others ignored, would not be flat. Thus, I am concerned as to what, if any, conclusions one can obtain from studies on subsets of traits, or am I missing something important?

It seems to me that an experimental approach, albeit not necessarily a practical one, to answering the question of whether there is a global optimum strategy, i.e. a fitness maximum, and how pronounced it is, would be to maintain in a constant laboratory environment two or more species with very different current strategies and observe their evolution. Convergence should be expected, but at what rate?

L. Partridge and R. Sibly. We fully accept that a multidimensional approach is desirable, indeed essential for a full understanding. However, even if the fitness hypersurface is flat in the *n*-dimensional space with axes the life-history characters, it does not follow that the trade-off hypersurface, bounding a species' options set, will also be flat. Thus, the elasmobranchs and the teleosts probably have very different options sets, owing in part to their different body designs.