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Functional Ecology, Vol. 3, No. 3. (1989), pp. 259-268.

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Trade-offs in life-history evolution

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Introduction

Trade-offs represent the costs paid in the currency of fitness when a beneficial change in one trait is linked to a detrimental change in another. If there were no trade-offs, then selection would drive all traits correlated with fitness to limits imposed by history and design. However, we find that many life-history traits are maintained well within those limits. Therefore, trade-offs must exist.

Trade-offs have played a central role in the development of life-history theory, from Gadgil & Bossert (1970), Charnov & Krebs (1973), Schaffer (1972, 1974a, b) and Bell (1980) on to the present. They have been measured through field observations (e.g. Clutton-Brock, Guinness & Albon, 1982, 1983), through experimental manipulations in laboratory (e.g. Partridge & Farquhar, 1981) and field (e.g. Askenmo, 1979), through phenotypic correlations in the laboratory (e.g. Bell, 1984a, b) and through genetic correlations (e.g. Rose & Charlesworth, 1981a, b), to mention only a few of the more prominent studies. They have been reviewed by Stearns (1976, 1977), Bell (1980), Charlesworth (1980), Warner (1984), Reznick (1985), Partridge & Harvey (1985, 1988) and most thoroughly by Bell & Koufopanou (1986). In addition, the methods used to measure trade-offs have been the subject of criticism (Tuomi, Hakala & Haukioja, 1983; Partridge, 1987) and controversy (Reznick, Perry & Travis, 1986; Bell, 1986).

The most prominent life-history trade-off involves the cost of reproduction. It has two major components, costs paid in survival and costs paid in future reproduction. Two approaches to analysing those costs were suggested by Williams: genetic costs represented by antagonistic pleiotropy (Williams, 1957) and phenotypic costs represented by negative correlations between current reproductive effort and future survival and reproduction (Williams, 1966a, b). A third, physiological approach to trade-offs has been developed by Hirshfield & Tinkle (1974) and Calow (1979), among many others (cf. Townsend & Calow, 1981).

In this extensive discussion, a few points have not always received the attention they deserve:

(1) That trade-offs can be measured and analysed at the level of the genotype, the phenotype and what lies between (intermediate structure) is well known and uncontroversial but it has not always been emphasized that each of those levels makes an essential contribution to our understanding. It is not a question of *either* genetic correlations *or* phenotypic correlations *or* physiological trade-offs but of how such measurements combine to deliver information about potential evolutionary responses. A study conducted at just one of these levels is likely to be of as little use as the information on the nature of the elephant delivered by one blind man holding its tail.

(2) One can draw a useful distinction between *intra*individual trade-offs — for example, between the reproductive effort made by a female in one season and the probability that *she* will survive to the next season — and *inter*generational trade-offs — for example, between a female's reproductive effort and the probability that her *offspring* will survive to the next season. Intraindividual trade-offs (and only some of them) have received most attention but intergenerational trade-offs, which are arguably just as important, have been relatively ignored. They deserve more attention.

(3) The genetic structure of a population, in particular the genetic variance-covariance matrix for a set of important life-history traits, reflects the very recent past, describes the present and predicts the near-term future. There is no logical or direct way to use the current genetic structure of a population to infer the trade-offs that constrained the past approach to the current state even if they occurred as recently as a few tens of generations ago (J. Travis, personal communication).

(4) Our understanding of a trade-off can be described as first order (slope known), second order (curvature known) or third order (all details, including interaction effects, known). In a few cases we have reliable information about first-order effects. In no case known to me do we have reliable information on second-order effects, which are important in the theory (e.g. Schaffer, 1974a). Measurement of third-order effects, however desirable (Pease & Bull, 1988), remains a matter for future research.

Levels of analysis

There are trade-offs at the phenotypic level, the genotypic level and in intermediate structure, which lies between the other two. By phenotypic level, I mean whole-organism measurements on traits directly connected with reproduction and survival. By genotypic level, I mean all types of evidence claimed to be genetic, whether arrived at through quantitative, Mendelian or molecular genetics. By intermediate structure, I mean all mechanisms connecting the genotypic to the phenotypic levels, as here defined. These include physiological and developmental mechanisms under endocrinological control that result in the allocation of resources among the functions of reproduction, growth, maintenance, storage and survival.

Knowledge of all three of these levels is necessary to understand how a trade-off works. Natural selection acts on phenotypes; phenotypic trade-offs determine the pattern of covariation presented to natural selection. The response to selection depends on genetic variation; genetic trade-offs measured by genetic covariance determine whether, and in what direction, a response to selection will occur. Intermediate structure modulates the expression of genetic trade-offs; it can change the expression of genetic covariances from positive to negative across a range of environmental conditions.

If a negative genetic correlation between two traits exists but the population is growing under environmental conditions in which most of the variation within and between the two traits is environmentally induced and the genetic differences are not expressed in the phenotypes, then the trade-off will not be present in the phenotype and no selection will occur (e.g. Groeters & Dingle, 1988). On the other hand, if there are strong negative phenotypic correlations between two traits that have, however, no genetic basis whatsoever, a selection pressure may exist but no evolutionary response is possible. Further, if mechanisms associated with growth and phenotypic plasticity modulate the expression of genetic covariation between two traits, so that the correlation is positive under some conditions and negative under others, then we would perceive a trade-off as existing under the latter but not under the former circumstances (Gebhardt & Stearns, 1988). Finally, whenever a variable environmental factor affects one trait more than another, the phenotypic correlation between the two traits will also change across environments and will alter the

selection gradients. For example, the phenotypic correlation between developmental rate and size at metamorphosis in frogs can be altered from positive to negative within a full-sib family by varying food level and distribution (Travis, 1984). These effects are all important. They determine whether a trade-off is exposed to selection in the phenotype, whether the genetic response to selection behaves like a trade-off and whether the trade-off appears at all, depending on the environment.

Phenotypic and genetic trade-offs are both well anchored in the literature. That intermediate structure can modulate the expression of genetic correlations is not as well appreciated. This effect is therefore illustrated here for two trade-offs: (1) age vs size at maturity and (2) reproductive investment vs survival. (These examples are intended to illustrate what *can* happen, not what must happen in every case. Necessary conditions are not yet known.)

Age vs size at maturity. Consider a population living in an environment heterogeneous for growth conditions. In some places and at some times, growth is rapid; in others, growth is slow. Organisms living in such an environment should evolve a reaction norm for the maturation event. The commonest type of reaction norm for age and size at maturity is one in which the organisms mature early at a large size when growth is rapid and later at a smaller size when growth is slow (Stearns & Koella, 1986). Each polygenic genotype will have a different reaction norm. There are many relations among reaction norms that will produce a sign change in genetic correlations. Two of these are not uncommon and could explain many observations of sign change:

(a) the largest and latest maturing genotype under good growth conditions is the largest but earliest maturing genotype under poor growth conditions, and the rest of the genotypes preserve this ordering (Fig. 1). The reaction norms may cross, as depicted here but this is not a necessary condition;

(b) growth rates have negative genetic correlations with maximal size, i.e. the fastest-growing genotypes produce the smallest adults, so that the extrapolated growth curves of the different genotypes would intersect if followed far enough. Under this assumption, the reaction norms of the different genotypes need not intersect. (If they do, their intersection strengthens the effect.) Fig. 2 plots growth curves and reaction norms for the maturation event for three genotypes. The growth curves change their rank order, measured early in

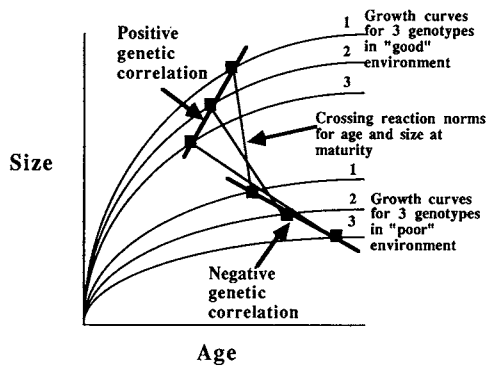


Fig. 1. One mechanism for producing a change in sign of genetic covariance: the reaction norms of the genotypes cross. Hypothetical growth curves for three genotypes are drawn for two environments; rapid and slow growth. The squares denote the age and size at maturity for each genotype in each environment. The word 'genotype' should be taken to mean the polygenic genotype of quantitative genetics, representing the whole genome, not the single-locus, two-allele genotype of population genetics.

life, across environments but the reaction norms do not. The heavy points indicate maturation events for each genotype under each growth condition. The genetic correlation between age and size at maturity changes from positive under good growth conditions, at the left, to negative under poor growth conditions, at the right.

Thus genetic covariance changes from positive to negative either when the growth curves of the genotypes cross or when their reaction norms have different slopes or ranges. When growth condi-

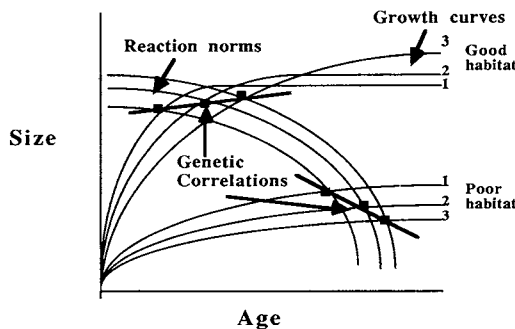


Fig. 2. A second mechanism for producing a change in sign of genetic covariance: the growth curves cross (growth rate and asymptotic size have negative genetic correlations). Hypothetical growth curves for three genotypes — fast (1), intermediate (2) and slow (3) growth — are plotted for two environments. The squares denote the age and size at maturity for each genotype in each environment; the heavy lines represent the reaction norms of different genotypes.

tions vary, we can expect genetic covariances to vary from positive to negative as well.

This effect is more than a theoretical possibility. Giesel, Murphy & Manlove (1982) measured large changes in genetic correlations between various life-history traits in *Drosophila melanogaster* Meigen raised at three different temperatures. Preliminary evidence indicates that the genetic covariance between age and size at hatching in *Drosophila mercatorum* Patterson & Wheeler changes from positive when larval growth is rapid on a rich diet to negative when larval growth is slow on a poor diet (Gebhardt & Stearns, 1988). G. de Jong (personal communication and in preparation) has analysed both an explicit two-locus model and a polygenic model and concludes that 'the change in sign of genetic covariance is much easier to obtain than to avoid' when genes have unstructured pleiotropic effects on growth rates and reaction norms.

Crossing reaction norms are a particularly strong case of genotype x environment interactions. Such interactions are expected to be pervasive for components of fitness, for when reaction norms do not cross, when one always lies above the other, then that reaction norm is superior across all environments and will be fixed. This process should continue until the only reaction norms left in the population are those that cross, i.e. where genotypes reverse ranking across environments. When reaction norms cross, genetic correlations are likely to reverse sign.

Reproductive investment vs survival. A similar analysis can be constructed for any other trade-off among traits that are phenotypically plastic. Reaction norms can also be predicted for the trade-off between reproductive investment and survival, one of the two classical costs of reproduction (Uchmanski & Stearns, in preparation). Where genetic variation exists for such reaction norms, one expects only the crossing norms to be maintained. In Fig. 3, the overall phenotypic trade-off, measured across a range of environmental conditions and for many genotypes, is negative: an ellipse drawn around all points observed would have a major axis running from the upper left to the lower right. However, within that phenotypic variation are important hidden details that make all the difference. Genetic variation in reaction norms, simplified here as linear norms for only three genotypes, is expressed in crossing genotype x environment interactions.

In the left-hand portion of the diagram, with low survival and high investment, the genetic correlation between reproductive investment and

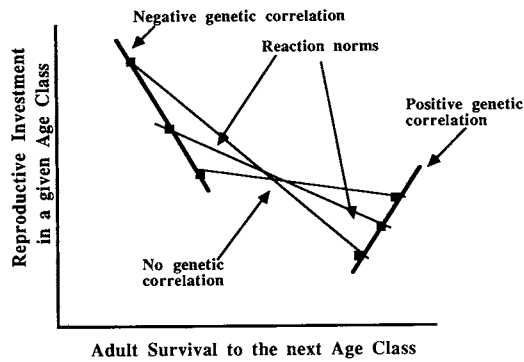


Fig. 3. If one measures a trade-off between reproductive investment at a certain age and survival to the next age across a range of environmental conditions, the overall phenotypic correlation may be negative but within that phenotypic variation the expression of genetic correlations may be negative in some environments, zero or non-significant in some and positive in others.

survival is negative. In the right-hand portion of the diagram, with high survival and low investment the genetic correlation is positive. In the middle, there is no genetic correlation between the two traits. Although that portion of the diagram lies in the centre of a phenotypic correlation that is negative, no genetic correlation is expressed under those environmental conditions and there will be no response to selection in environments corresponding to the middle of the diagram.

People who are trying to measure trade-offs through experimental manipulations may want to ask themselves whether the variation in the environment created by the manipulation takes place entirely on the left or the right of Fig. 3 or whether the manipulations create a mixture of the two extremes. In the latter case, the results will be difficult to analyse unless an unusual amount is known about both genetic and environmental sources of variation.

Fig. 3 depicts one of the simplest possible types of genotype \times environment interactions. In real data sets, reaction norms may cross and recross each other several times and genetic correlations between traits may change back and forth from positive to negative repeatedly as an environmental factor changes continuously across its normal range. In some species, genetic correlations will be negative in well fed and positive in poorly fed populations. In other species with different physiologies, genetic correlations will be positive in well fed and negative in poorly fed populations. Fig. 3 depicts only one of these possibilities; they are not exhaustive and can only be distinguished by experiment.

To that it should be added that energetic investment must be measured but almost never has. Exemplary attempts have been made by Calow & Woollhead (1977), Hirshfield (1980) and Rekkie & Bazzaz (1988a, b). The most commonly used measures of 'reproductive effort,' 'reproductive allocation' and 'reproductive allotment' are indirect and hard to interpret.

Figs 1–3 depict a type of interaction between genetic and phenotypic variation and covariation in which physiological mechanisms make a big difference, for they embody the constraints that force the reaction norms or growth curves to cross, that cause changes in rank of genotypes across environments. We have almost no information on the mechanisms that lead to those changes in rank; if such changes in rank are common, that information will become crucial.

The measurement of trade-offs

Genetic methods

In their thorough review of trade-offs, Bell & Koufopanou (1986) noted a pattern with important implications. When people have tried to measure genetic correlations with breeding designs, usually variations on full-sib/half-sib crosses or di-allele crosses, the results have been mixed. Sometimes the genetic correlations are negative, sometimes positive, sometimes insignificant. However, when the sign of the correlations has been measured through the correlated response of one trait to selection on another, negative correlations, genetic trade-offs, have been measured much more frequently. The results of breeding designs and selection experiments carried out on the same traits and often the same species have not been consistent with each other.

Given the statistical problems inherent in breeding designs, this may not be surprising. It is usually difficult in practice to raise enough families to avoid sampling problems, to which the estimates of covariances are especially sensitive. In selection experiments, it may be easier to start with and to maintain a larger effective population size. This could explain why the results of a large number of such experiments are more consistent.

Many people are now attempting to measure genetic trade-offs. The pattern noted by Bell & Koufopanou (1986) suggests that approaches using correlated responses to selection could be preferred to breeding designs because they produce more consistent, replicable results. Selection

experiments also have an inherent logical advantage: they predict correlated responses to natural selection directly through correlated responses to artificial selection rather than indirectly through breeding design. However, if Figs 1–3 are correct it will also be necessary to measure correlated responses to selection under at least two and preferably three environmental conditions representing the range naturally encountered.

Another response to the inconsistency of results from breeding designs can also be justified. The results mentioned might not be due to sampling variation but an accurate reflection of real patterns. If so, then some inherent advantage of breeding designs over selection experiments should not be forgotten: the information extracted per individual is higher; it is easier to control environmental conditions for the duration of the experiment; and some breeding designs can be completed more rapidly than some selection experiments.

Physiological mechanisms

Whether one perceives a physiological trade-off or not depends on the type of organism examined. That successive reproductive attempts share the same resource pool is unlikely in small birds and mammals, in which high metabolic rates leave no room for storage. A shrew or a hummingbird must use what it has eaten in the last few hours to suckle its offspring or produce its eggs. They are ‘income breeders’, using current income for reproductive investment (Thomas, 1986). Income breeders have a very short-term ‘physiological memory’. The suctorian *Tokophrya* is a particularly clear example of an income breeder. It feeds on *Paramecium* and produces one offspring for each *Paramecium* eaten. Kent (1981) could construct a wide range of fecundity schedules by varying the amount of food offered.

Great tits may be income breeders in one sense but not in another. Pettifor, Perrins & McCleery (1988) found no evidence for a trade-off between clutch size and adult survival in great tits, but Tinbergen (1987), Smith, Källander & Nilsson (1987) and Linden (1988) all found a trade-off between clutch size and success of second broods. While Tinbergen (1987) and Linden (1988) found no effect of increased clutch size on adult survival, Nur (1984) found such evidence in blue tits. One might define tits, where short-term costs within seasons are clear but longer-term costs are not at all clear, as capital breeders within seasons but income breeders between seasons. Sibly & Calow (1984, 1986) refer to income breeders as having

‘direct costing’ — the cost of reproduction being drawn out of current revenue.

On the other hand, ‘capital breeders’ store energy that can be mobilized later for reproduction. This creates a mechanical linkage between current and future and reproduction. Good examples of capital breeders include red deer (Clutton-Brock, Guinness & Albon, 1983) and *Daphnia* (Goulden & Hornig, 1980).

Sibly & Calow (1984, 1986) refer to capital breeders as having ‘absorption costing’ — the cost of reproduction is drawn against physiological savings previously made. The mathematics of direct and absorption costing differ; most life-history theory assumes absorption costing, which involves primarily physiological mechanisms. The direct costing used by income breeders is more easily related to behavioural mechanisms, such as decisions on how long to forage each day, than it is to costs of reproduction.

Income and capital breeders represent the extreme points on a continuum. It would be interesting to know whether disruptive selection tends to shape any given species towards specialization for one type or the other but not some intermediate mixture. Some data bear on this point. If kestrels are allowed through manipulations to increase their income, they start breeding earlier, lay the larger clutches that are normally found earlier in the year, and also get fatter (Meijer, Daan & Dijkstra, 1989). They appear to mix the two alternatives. The poeciliid fishes are a family that contains the full spectrum from ‘capital breeders’, such as guppies (*Poecilia*) and swordtails (*Xiphophorus*), to ‘income breeders’, such as *Heterandria formosa* Agassiz (Turner, 1937). Comparative studies among species within this family could get at the reasons for the evolution of the difference between capital and income breeding (J. Travis, personal communication).

Most physiological decisions on growth, storage and reproduction are mediated by hormones. Hormones affect many processes simultaneously, creating patterns of correlations among many responses. Of course, these patterns depend both on the concentration of hormones in the body and on the sensitivity of the different cell types to those hormones. Both can be changed in evolution. That sex hormones mediate trade-offs is strongly suggested by evidence from the human reproductive system: female sex hormones that promote reproduction early in life are also involved in disturbances to calcium metabolism later in life. Could this be an example of how antagonistic pleiotropy shapes the evolution of senescence? Endocrine

regulation is an obvious aspect of intermediate structure with impact on phenotypic correlations that has received almost no attention in life-history research. Work in this area should become a higher priority. Endocrine mechanisms may prove to be only the tip of an iceberg of physiological mechanisms that modulate the expression of genetic covariance.

Why might we get positive correlations when we expect negative ones?

Life-history theory predicts negative correlations among certain traits; however, observations indicate that these traits are often positively correlated, especially when the measurements are made on individuals within populations (Bell & Koufopanou, 1986). van Noordwijk & de Jong (1986) have pointed out a simple interaction that can lead to positive, zero or negative correlations between two traits that are nevertheless involved in a classical physiological trade-off. Suppose that the energy acquired in food, A , is strictly allocated within each individual either to reproduction, R or to survival, S :

$$A = R + S.$$

This is just the Principle of Allocation asserted by Levins (1968) and Sibly & Calow (1986). However, as stated it does not make explicit the variation among individual organisms that always occurs. In this context, individuals vary in the amount of energy acquired, A , and in the fraction of the energy acquired that is allocated to reproduction, B . If we indicate each individual by a subscript i , then we have

$$R_i = B_i A_i,$$

$$S_i = (1 - B_i) A_i$$

The point that van Noordwijk & de Jong noticed is that the sign of the correlation between R and S will depend on the relative degree to which each varies among individuals. This is most easily seen in a graph (Fig. 4). van Noordwijk & de Jong (1986, p. 141) explain this result with an analogy to economics: 'if the budget is fixed, people spending more on housing should spend less on cars. In fact, the amount of expendable income is variable, and in many situations positive correlations are observed between the per-family expenses on housing and on cars. There is little problem in identifying rich and poor families on this basis. . . Where biologists have observed positive correlations between life-history traits, they have often also identified individuals that perform well or poorly.'

If we observe a positive correlation where theory tells us to expect a negative one, this analysis suggests the critical empirical questions that should be asked. Do the organisms vary more in the amount of energy acquired than in the fraction of energy allocated to each function? How do those two variances (in A and B) change across environments in nature? The answers to those two questions will help us to decide whether the trade-off is important in natural populations or not.

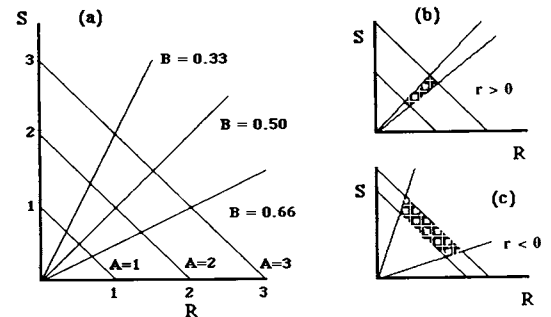


Fig. 4. Consider a trade-off between reproduction (R) and survival (S). The total amount of energy acquired is set by A , where $A = R + S$. The fraction of energy allocated to reproduction is determined by B , so $R_i = B_i A_i$. In (a), the general possibilities are sketched. In (b), the variation among individuals in energy acquired (A) is large but the variation in fraction allocated to reproduction (B) is small. The result is a positive correlation between reproduction and survival. In (c), the variation in A is small but the variation in B is large. The result is a negative correlation between reproduction and survival.

Characterizing trade-offs

Intraindividual and intergenerational

Not all trade-offs have received attention commensurate with their probable importance. Intraindividual trade-offs have played a much larger role to date than intergenerational trade-offs. However, to take just one example, any change in a female's allocation strategy is likely to have implications for juvenile mortality in those organisms, like birds, many fish, insects and mammals, where parental care or provisioning is important. Such intergenerational effects can be quite real. In the poeciliid fish *Heterandria formosa*, there is a trade-off between number of broods and offspring size, and larger offspring have better survival (Henrich, 1988). Similar effects can be found in wild radishes (Stanton, 1984). Here an intraindividual trade-off between brood number and offspring size becomes an intergenerational trade-off between brood interval and juvenile survival.

what produced the patterns we see today? Measurement of genetic trade-offs certainly illuminates the first but may not be as relevant for the second as might be hoped (J. Travis, personal communication).

This comment is not so much a council of despair as an indication of a research program. Genetic covariances could be measured in a set of closely related species. If the structure of the correlation matrices were similar, it would count for the long-term stability of trade-off structures within populations and against the cautionary comment above. If they differed in closely related species that had originated recently, it would count for this interpretation. The speciation events in the study group should be recent and datable and breeding or selection experiments would have to be possible on a scale that would yield reliable estimates of differences.

Signs and shapes of trade-off functions

A negative relationship between two traits can be linear, convex, or concave, to mention the simplest possibilities. Schaffer's (1974a) theoretical work demonstrates that such differences in shape can strongly influence the predicted evolutionary responses. Thus we always have three important questions to ask about the relationship between two traits: (1) is it positive or negative?; (2) what is its shape?; (3) what are its interactions with other traits and environmental factors?

The first two questions would be answered if we knew the signs of the first and second partial derivatives of the second trait with respect to the first. The matrix of first partial derivatives defines the *first-order trade-off structure*, the matrix of second partial derivatives defines the *second-order trade-off structure* and the matrix containing a graph in each cell defines the *complete two-way trade-off structure*. Any trade-offs that are non-linear in a complex fashion can only be properly described by the third matrix, the complete trade-off structure. Interaction effects among trade-offs would go beyond that (Pease & Bull, 1988). The graph in each cell for the complete trade-off structure might have to describe a complex surface in three or more dimensions, rather than a line in two dimensions, to show interaction effects among two or more trade-offs.

These matrices represent the manner in which the organism is integrated with respect to life-history traits. They abstract the developmental physiological and ecological implications that each trait has for the others. Schaffer's (1974a) and

Bell's (1980) analyses of the trade-offs between reproduction and survival and between current and future reproduction suggested that the curvature of some trade-offs is a critical piece of information. Whether an organism should invest everything in current reproduction, to the detriment of growth and survival, or choose an intermediate level of reproductive investment, reserving something for the future, depends on whether those trade-offs are convex or concave. This is a qualitative condition — we just want to know whether the lines bend up or down — but it has proven to be quite elusive. Bell & Koufopanou (1986) summarized the few attempts to measure that curvature (e.g. rotifers, annual meadow grass) and in every case concluded that the pattern was not detectably different from a straight line.

Trade-offs or dynamic linkages?

If genotype \times environment interactions are pervasive and if they have the sorts of effects depicted in Figs 1–4, then it is natural to ask whether we should continue to use the word 'trade-offs' at all. Trade-offs are usually conceived of as static, dependable relationships: more of this, less of that. They certainly apply to energetic relations within individuals. When we move from the individual to the population, things become more complex. If interactions there are as dynamic and flexible as Figs 1–4 would suggest, and the relationship between two traits could easily change from positive to negative over the normally encountered environmental range, then the more general phrase 'dynamic linkage' might be preferable to 'trade-off' as a descriptor of the underlying mechanisms. Population-level trade-offs differ qualitatively from trade-offs among functions within individuals.

Conclusion

Measuring the cost of reproduction has proven to be difficult. The perspective advanced here will not make it any easier. Both phenotypic and genetic correlations among traits must be measured across the range of environments naturally encountered before one can claim that costs and selection gradients have been estimated. Genetic correlations are more reliably measured in selection experiments than with breeding designs. Correlated responses to selection must also be measured across a range of environmental conditions to estimate reliably the impact of genetic correlations on evolutionary change. Much more

attention needs to be given to the mechanical basis of trade-offs in aspects of intermediate structure. The relationship between endocrine action and genetic and phenotypic correlation in particular deserves more attention.

Acknowledgments

This work was supported by the Swiss Nationalfonds. Comments by Jacqui Shykoff, Martin Gebhardt, Bruno Baur, Elke Hillesheim, Arie van Noordwijk, Joost Tinbergen, David Reznick, Peter Calow, Joe Travis and Paul Harvey improved the presentation. The ideas in Figs 1 and 2 were developed in cooperation with Jacob Koella and Martin Gebhardt.

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Received 23 November 1988; revised 19 January 1989; accepted 19 January 1989.