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Evolutionary physiology of the cost of reproduction

Michael R. Rose and Timothy J. Bradley

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The concept of a cost of reproduction has associations with a variety of other ideas in population biology, among them trade-offs and antagonistic pleiotropy. Within the concept of a cost of reproduction, a variety of components can be distinguished, such as physiological and ecological costs of reproduction. This article concentrates on the former type of cost. Empirically, a variety of approaches can be, and have been, used to analyze the cost of reproduction. Three are distinguished: genetic, environmental, and physiological. These are discussed first in general terms and second with specific reference to research on laboratory evolution in *Drosophila*. The latter discussion serves to focus and to instantiate the general analysis of the field. Emerging themes from this area of research include the environmental plasticity of costs of reproduction, the difficulties facing simple trade-off theories, and the critical role of physiological integration in determining costs at the organismal level.

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The cost of reproduction is a protean theme of population biology, appearing in different guises throughout a range of academic fields, from behavioral ecology to population ecology to evolutionary ecology to population genetics. Its terminology varies as it is played out across these keys, from “trade-offs” to “developmental constraints” to “antagonistic pleiotropy”. Depending on the focus of research, one or another of these terms may be favored, but we believe that there is a fundamental unity to all these variations, and we hope to bring that unity to the forefront in this article. At the outset, when we refer to “the cost of reproduction” we mean no more, and no less, than the presence of an antagonistic interaction between processes related to reproduction, at whatever level of function, and processes related to survival. Naturally, we hope to elaborate on, and explore, this initial definition in the course of this article.

Despite the unitary features of the cost of reproduction, it does nonetheless take on disparate forms in the lives of actual organisms. It is not always the case that the cost of reproduction necessarily involves an en-

ergetic allocation between survival and reproduction, once a conventional assumption (e.g. Gadgil and Bossert 1970), as will be argued below. Moreover, organisms may modulate the relationships between these different cost-features using a variety of evolved controls, most importantly hormonal controls (Finch and Rose 1995). Such modulation suggests some unity to the cost of reproduction, but a clear perception of the diverse forms of the cost is still valuable for empirical and theoretical penetration.

Another major point for us is the diversity of empirical approaches that can be taken to the problem. There have, for example, been some testy exchanges about the relative validities of genetic and manipulative experiments (e.g. Partridge and Harvey 1985, Reznick 1992). We will distinguish three major approaches, and argue that none of them are notably useful if pursued reflexively, while their interaction and indeed integration are perhaps the most valuable experimental strategy of all.

Central to our research has been the intensive exploration of a system that has been constructed for its ease of experimental investigation: selected laboratory stocks

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of *Drosophila*. This type of system has been studied extensively and intensively over the last 50 years, though it is by no means the only good system for research on laboratory evolution (vid. Bell 1996). However, it is particularly good for the study of the cost of reproduction compared to the alternative microbial systems, partly because it is easier to study individual organisms and to differentiate the phases of the life-cycle. In any case, we claim the privilege of the specialist, and use *Drosophila* research performed by ourselves and our colleagues as a foundation for resolving the general issues raised by the cost of reproduction hypothesis.

But we begin with an attempt to sharpen the general terms of our discussion, from the conceptual underpinnings of the cost of reproduction to its empirical exploration. Only then will we turn to the specifics of the *Drosophila* system to ground our analysis.

Experimental approaches

We crudely differentiate two basic approaches to experimental research on the cost of reproduction: genetics and selection, on the one hand, and environmental manipulation and physiological analysis, on the other. However, these approaches have a number of important points of intersection and interaction, which we will try to indicate. Above all, the use of this conceptual dichotomy does not imply our advocacy of its practical implementation. Indeed, in our own work, we lean heavily on the combination of elements from both sides of the split. We use the two categories only for clarity of exposition.

Quantitative genetics and laboratory selection

Two common approaches to the study of the cost of reproduction are based on evolutionary genetic methods: quantitative genetics and laboratory selection. The former approach, quantitative genetics, has a well-developed methodology (vid. Falconer and Mackay 1996). Experiments involving correlations between the phenotypes of relatives, such as parents and offspring or sibs, are standard means of estimating genetic variation of characters and genetic covariation between characters. On the other hand, selection experiments in evolutionary biology have no fixed methodology. Quantitative genetic techniques are sometimes used in "artificial selection" experiments, which of course are not to be confused with laboratory selection, but there is a much broader range of selection studies that have been used (cf. Bell 1996, Rose et al. 1996).

Quantitative genetics of life-history characters

If the cost of reproduction is being studied as a factor in the evolution of life histories, which it often is (cf.

Roff 1992, Stearns 1992), then the seemingly obvious place to start is genetic covariation between reproductive characters and survival characters. For example, one point of great interest has been the existence of a negative additive genetic correlation between early fecundity and longevity. The available estimates for parameters like these generally are not negative (vid. Rose 1991, Roff 1992, Stearns 1992), which at first sight casts doubt on the cost of reproduction concept in the evolutionary setting.

There are several reasons, however, for doubting the salience of many of these results, if not the approach in general. The first is that experimental populations that have been inbred in the laboratory, which is commonplace, are expected to give additive genetic correlations that are biased toward positive values. This arises because genotypes that are artificially made more homozygous will be generally depressed for components of fitness, compared to genotypes that are less homozygous, given the widespread occurrence of generally deleterious and recessive alleles maintained by mutation-selection balance. Inbreeding thus shifts additive genetic correlations toward positive values (Rose 1991).

The second cause for doubt about many genetic correlations is genotype-by-environment interaction. The laboratory will usually be a novel environment for experimental organisms that have recently been sampled from nature, such that some genotypes will be generally better suited to that environment compared to others. This has been proposed as a factor biasing genetic correlations toward positive values (e.g. Rose 1991), and the principle has been experimentally demonstrated (Service and Rose 1985).

A third problem is that quantitative genetic experiments measure only the initially preponderant patterns of genetic variation and covariation. That is, they do not necessarily produce reliable inferences as to the long-term constraints on evolution. Thus, for example, it could be the case that a particular population at a particular time in a particular environment has genetic covariation between reproduction and survival that is generally positive, but selection in that same environment could produce selection responses in which survival trades-off against reproduction over the course of many generations. If it is the constraints on evolution that are the point of interest, then quantitative genetic studies may mislead.

Laboratory selection experiments

For the above reasons, laboratory research on life-history evolution has turned to selection experiments. A common avenue for such experimental work has been *Drosophila* selection regimes in which the decline in the force of natural selection has been changed by experimental intervention (Luckinbill et al. 1984, Rose 1984, Partridge and Fowler 1992, inter alia). Irrespective of the particular results of these experiments, they too are

generally afflicted with major problems of experimental design analogous to those that impact quantitative genetics experiments. Inbreeding in the course of selection can halt or reverse gains made by selection, affecting the inferred patterns of genetic covariation (e.g. Roper et al. 1993, Chippindale et al. 1994). Genotype-by-environment interaction can also lead to erroneous inferences about patterns of genetic covariation, with spurious reversal of the sign of genetic covariation a possibility (e.g. Leroi et al. 1994). Unintended selection can also cause erroneous inferences of genetic covariation between reproductive and survival characters (cf. Chippindale et al. 1994). For all of these reasons, we have characterized laboratory selection experiments as interesting and productive, but perhaps treacherous (Rose et al. 1996).

It should be noted that one of the key problems for laboratory genetic and selective approaches to the study of the cost of reproduction is the effect of environmental factors on patterns of genetic variation and covariation. Not only does environmental change, intended or not, alter phenotypic values of characters by direct impact on the non-genetic basis for character expression, such environmental change also may *interact* with gene expression to produce artifactual scientific conclusions. Any such interaction depends on the evolutionary history of the population under study relative to the environmental regimes imposed experimentally. This problem undermines or qualifies a great deal of laboratory genetic research on the cost of reproduction.

Environmental manipulation and physiological analysis

Gross environmental manipulation

It has been argued that manipulation of the organism's life-history by environmental means offers a reliable guide to the constraints affecting the evolution of life-history, particularly such factors as the cost of reproduction (e.g. Partridge and Harvey 1985, Sinervo and Basolo 1996). This assertion has been strongly disputed, however, on theoretical grounds (e.g. Reznick 1992).

Experimentally, there are often significant disanalogies between the results of genetic manipulation and manipulations of the surrounding environment (light, temperature, available nutrients, and so on; e.g. Chippindale et al. 1993). Nonetheless, even if gross environmental manipulation is not a highway to reliable inferences concerning such evolutionary constraints as the cost of reproduction, it may still be a useful source of information concerning the existence or basis for any such cost. We do not wish to preclude some role for experiments of this kind *ab initio*.

Phenotypic manipulation

In addition to non-genetic manipulations that involve a change in the extra-somatic environment of the organism, there are those that involve a manipulation of the body itself: castration, egg ablation, painting, the addition of artificial structures, such as hats or tail extensions, and so on. This distinction has been particularly emphasized by Sinervo and Basolo (1996), who argue that the latter type of manipulation is a more legitimate test of the endogenous evolutionary constraints facing organisms. Their argument is a powerful one, but it is not necessary to have a firm conclusion about the relative merits of the two variants of environmental manipulation in order to benefit from the clarity that the dichotomy provides.

There is a long history of environmental manipulation of reproductive activities in nesting birds. Beginning with David Lack, many behavioral ecologists have increased or decreased the number of offspring in the nests of various bird species, and then observed the total reproductive output and the survival of the nesting parent(s) (Roff 1992, Stearns 1992). It has been common-place in these studies to find some reduction in later survival after increases in the number of offspring.

The most common type of surgical manipulation pertaining to the cost of reproduction has been animal castration and analogous ablations of reproductive structures in plants. These experiments have generally indicated an increase in survival following such manipulation, particularly in semelparous organisms. [See reviews of Finch (1990) and Finch and Rose (1995).] Indeed, these experiments are undoubtedly the best evidence for a general cost of reproduction, as a trade-off between survival and reproduction has been more reliably found in these experiments than any other kind.

Physiological analysis

We use the term physiological to indicate costs that are internal to the organism, such as the energetic costs of courting or gamete production, or the use of possibly limiting factors such as protein. Costs which involve other organisms (e.g. competition or predation) can be thought of as ecological costs and will be dealt with in other papers in these proceedings.

Physiological costs are a particularly interesting area for study because the costs can be quantified and compared between disparate activities and functions (cf. Sibly and Calow 1989). For example, the cost of egg production can be estimated in terms of joules expended per egg, and compared with the cost of flight or thermoregulation (Ware 1982, Pandian and Verberg 1987, Masman et al. 1989, Schmidt-Nielsen 1990). This capacity not only to seek and possibly demonstrate trade-offs, but also to quantify them over the disparate activities of the organism, has led a number of researchers to explore physiological approaches to

estimating the cost of reproduction in a variety of organisms (reviewed by Roff 1992, Stearns 1992, Sinervo and Basolo 1996).

Energetic costs: One cost which has been extensively investigated is the energetic basis of trade-offs. Both direct and indirect calorimetry have been used to estimate the increase in metabolic output required for many of the activities associated with reproduction (MacNally 1984). Even the costs of behavior carried out by animals in the wild can be estimated using time/activity analysis or doubled labeled water studies (Nagy 1975, Bennett 1986, Masman et al. 1989).

An additional approach is to determine the energy content of the egg or sperm produced by an individual. For small birds, for example, the total energy content of a clutch of eggs may exceed the total energy content of the body of the female, although not necessarily the total energy output of the female during the egg-laying period (Drent and Daan 1980, Rahn et al. 1985).

For males, the energy content of the sperm is generally small compared to the energy content of the body or the energy output associated with mating. Ancillary bodily secretions, including seminal fluid, can in some species be a substantial energetic drain, however (Pitnick and Markow 1994).

Material costs: Organisms are limited in their growth and output not only by energy, but also by materials present in limiting quantities (vid. Roff 1992). These can be sources of nitrogenous compounds (principally amino acids in animals), vitamins, minerals such as calcium or iron, etc. While all of these are ecologically and physiologically important in a variety of situations, protein limitation has been investigated most thoroughly in terms of its effects on reproductive output. One way of approaching the problem of which factors might be limiting to reproduction is the use of diet supplementation. Under circumstances where calories are limiting, a diet supplemented with fats or carbohydrates would be expected to increase reproductive effort, either in the current or in subsequent bouts of reproductive effort. In conditions in which protein is limiting, protein supplementation would be expected to increase reproduction more than an energetically equivalent supplement of lipid. Numerous examples of either caloric or protein limitation have been observed for female reproduction (Widdowson 1981). In males, protein limitation is rare, and caloric supplementation is generally more effective in boosting reproductive effort and success.

The laboratory *Drosophila* model

Introduction to *Drosophila* life-history evolution

There are many possible ways to address the hypothesis of a cost to reproduction, as we hope we have made clear

to this point. One of the simplest and easiest is to force the evolution of increased adult survival by manipulating the force of natural selection. This is so easy to do that the first *Drosophila* experiments of this kind were inadvertent (Rose 1991). If you culture with discrete generations, as most *Drosophila* workers do, then the force of natural selection can be manipulated simply by changing the age at which adults are allowed to contribute eggs for the next generation. Typically, this age is quite early, from a few days to a few weeks of adult life. But it can be postponed to much later ages. Routine culture of eight weeks of adult life or more has been achieved with *D. melanogaster* kept at 25°C. Under these conditions, significantly increased lifespan can be produced in ten generations or so (Rose 1991). This experiment has been deliberately performed a number of times now with success.

The interest of these experiments for the present purposes lies in the relationship between improved adult survival and reproduction. It is a corollary of the cost of reproduction hypothesis that reproduction should be decreased with selection for increased adult survival. This result is indeed often observed (e.g. Luckinbill et al. 1984, Rose 1984), but not always (e.g., Partridge and Fowler 1992, Leroi et al. 1994). However, it should be pointed out that major qualifications arising from experimental artifact have been offered for these negative results (Roper et al. 1993, Chippindale et al. 1994, Leroi et al. 1994). For this reason, we do not conclude that the cost of reproduction hypothesis has been refuted by the *Drosophila* laboratory selection results. In any case, our main goal here is to outline research with our present *Drosophila* system, in which increased adult survival is associated with decreased early reproduction under the evolutionarily appropriate conditions.

Genetics and selection

Our research in this area has primarily used *D. melanogaster* populations descended from a sample collected in 1975 near Amherst, Massachusetts, by the late Philip Ives (1970). Before any type of experimentation began, the Ives laboratory population was taken through about 40 generations of outbred culture. However, the main populations to be discussed here were not created until more than 100 generations of laboratory culture had been achieved. Most research with the Ives population has concentrated on derivatives of it obtained by laboratory evolution with altered demography or with the addition of lethal stresses. This array of populations has constituted a kind of synthetic taxonomic unit, all deriving from a common ancestor.

The canonical form that laboratory evolution has taken in this system is varying adult ages of culture reproduction. At present, there are stocks with a range of ages of adult egg-laying from 2 days to about 9 weeks,

with a total of 25 populations. Generally speaking, there is a strong positive correlation between the age of culture reproduction and the longevity of the population. This is in accord with the evolutionary theory of aging (Rose 1991), but that is not of primary interest here. The major question here is whether or not this variation in longevity is inversely associated with early reproduction, revealing a cost to this early reproduction for adult survival. In many experimental assays, this type of cost has been borne out (e.g. Rose 1984). But in the early 1990's, this cost appeared to disappear, longer-lived populations having no deficit in early reproduction (Chippindale et al. 1993).

This posed the question of whether evolution had found a way to circumvent the cost of reproduction, giving increased adult survival with no reduction in early reproduction. This problem was studied extensively by Leroi et al. (1994), particularly with a view to testing whether or not genotype-by-environment might be causing artifactual variation in the apparent cost to reproduction in stocks selected for increased adult survival for more than ten years. After many experiments, they concluded that there was no cost to reproduction when the flies were handled under conditions of abundant nutrition and low crowding. But when flies were handled with crowding, accumulating waste products, and poor nutrition, there was a strong cost to early reproduction, about six-fold, arising from enhanced adult survival. In other words, natural selection under the original conditions of the Ives population, which has been kept with two-week generations for more than 20 years – over 500 generations, apparently sacrificed later adult survival for the sake of early reproduction.

Overall, the genetic and selection experiments with these *Drosophila* stocks have underscored the general importance of the cost of reproduction. At the same time, they have shown that costs of reproduction may depend strongly on the environment, such that these costs may be entirely eliminated in a sufficiently different environment, particularly a benign one.

Environment and physiology

Because of the substantial differences in the reproductive contributions made by male and female *Drosophila*, it is useful to examine the costs of reproduction separately in the two sexes.

Costs of reproduction in female Drosophila melanogaster – energetic costs

Even in the absence of substantial yeast supplementation of the diet, female *Drosophila* can produce a quantity of eggs in one day equal to 50% of the dry mass of the female's body (Djawdan et al. 1996). In the presence of yeast, this production can increase 10-fold

(Chippindale et al. 1993). It is plausible to assume that this tremendous rate of egg production might pose energetic limitations on other functions, including somatic maintenance. *Drosophila* differ from other organisms in that adult size is determined and fixed at ecdysis, before the initiation of reproduction. Energy storage in the adults in the form of lipids and carbohydrates can and does vary greatly, however, and has been shown to be highly responsive both to selection and environment.

Service (1987) examined metabolic rate and energy storage in the soma of B flies, which have been selected for early reproduction, and compared them to the O flies, which have been selected for late reproduction. He found that the young B flies had higher metabolic rates and lower storage of lipid. Djawdan et al. (1996) examined these same populations and found no differences in metabolic rate despite a five-fold difference in the rate of egg production.

This failure by Djawdan et al. (1996) to observe a difference in metabolic rate is very surprising, given the increase in early reproductive effort in the B flies. These flies were fed on the normal maintenance food without the addition of live yeast, so it could be argued that the rate of egg production was too low to show a maximal response. Simmons and Bradley (1997) addressed this issue, examining B and O flies which were stimulated to produce eggs by the addition of up to 7 mg of additional live brewer's yeast per vial. This level of yeast stimulates egg production about 10-fold versus a non-supplemented diet. Under these conditions, the B flies did have a somewhat higher metabolic rate than the O flies (i.e. there was a genetically determined difference in metabolic rate), but the rate was unaffected by yeast supplementation or levels of fecundity.

To date, therefore, three studies have examined the issue of differences in metabolic rate between the B and O flies. Service (1987) and Simmons and Bradley (1997) found significant differences in metabolic rate, with the B flies having a higher rate, while Djawdan et al. (1996) found no differences in metabolic rate. Service and Simmons measured the metabolic rates of a small number of flies in a vial environment while Djawdan et al. (1996) measured rates in cage environment with a large number of flies.

In a separate study, Djawdan et al. (1997) examined the metabolic rates of flies which had been selected for postponed reproduction, starvation resistance, or desiccation resistance, along with their control populations. They found that the flies selected for late reproduction or stress resistance had lower metabolic rates per mg of body weight. When the weight of water, lipid and carbohydrate was removed, however, the metabolic rates of the flies were statistically indistinguishable. The authors pointed out that the metabolic adaptation in these flies was therefore not a modification of the metabolic rate but rather a change in the storage of

compounds (including energy storage compounds) which can be used to resist various forms of stress.

If energy is the basis for a trade-off between reproduction and somatic maintenance, then stored nutrients clearly must drop to cover the cost of reproduction. One can assume that the accumulation of energy stores is vital both to reproduction and somatic health. These stores might be the common currency in which the trade-off between reproduction and survival is paid. A logical corollary, and indeed possible experimental verification, of these ideas would be the demonstration that the energy used in reproduction should be equal to that which is thereby made unavailable for storage. As discussed above, physiological techniques permit one to be quantitative in assessing this trade-off.

Djawdan et al. (1996) tested this model by quantifying the energy content of eggs produced by B and O females and comparing this to the energy stored by the females as lipid and fat. The energy which B flies place in eggs in the first 20 days of adult life is more than 50 J while the O flies produce eggs containing about 6 J. The B flies show no change in somatic energy storage during this time period, while the O flies show an increase in only 1 J in energy storage. One would expect the O flies to be able to conserve not only the energy which might be placed in the eggs, but also the cost of nutrient transport and egg synthesis. The above 54 J is therefore a minimum estimate of the energy saved by foregoing reproduction, yet only 1 J shows up as somatic storage. These studies were conducted on groups of 500 flies of mixed gender in large flight cages under conditions identical to the fly culture conditions. All the costs of feeding, flight, egg production, mating, etc., are encompassed in these measurements. It is quite surprising, therefore, that increased egg production does not lead to increased metabolic costs.

The above study by Djawdan et al. (1996) examined the energetic trade-offs associated with genetically determined differences in reproductive rate. Simmons and Bradley (1997) examined the trade-off using yeast as an environmental factor to influence the levels of fecundity. Under these conditions as well, the amount of energy placed in the eggs by the more highly fecund flies greatly exceeded the energy stored in the soma by the less fecund flies. Therefore, although a trade-off between reproduction and somatic energy storage is seen, caloric analyses indicate that the trade-off is not quantitatively perfect.

The explanation for these perplexing results is, in hindsight, rather simple. The concept of a fixed energy trade-off between reproduction on the one hand and somatic growth and storage on the other implies that energy is limiting. Under conditions in which food is readily available, such as the conditions in most laboratory experiments, the flies adjust to increased reproductive activity by ingesting more food, thereby providing ample energy for covering the cost of egg production.

In addition, the energetic cost of egg production appears to be very low, sometimes unmeasurable in these flies. How can this be? Firstly, it may be that flies turn from one form of energy expenditure (e.g. locomotion) to egg production during periods of reproduction, so that the energy output remains identical but is shifted to new activities. Secondly, egg production may require relatively little aerobic expenditure. Egg production involves the ingestion of food, its transport across the gut, hemolymph and ovary to the egg. Although this transport cannot be energetically free, it may be quite inexpensive compared to the very high standard metabolic rate observed in these small insects. Since the food compounds are merely transported and not oxidized, the effects of egg production on metabolic rate may be surprisingly low. This question deserves further detailed physiological investigation.

Costs of reproduction in female Drosophila melanogaster – other limiting factors

It is now clear that a quantitative energetic trade-off cannot be invoked as a complete explanation for the trade-off between reproduction and survival in *Drosophila*. It may be, however, that some dietary factors other than energy are limiting and serve as the basis for the trade-offs observed. If a dietary limiting factor exists, it must occur in yeast in abundance since live dietary yeast is known to promote high levels of fecundity in *Drosophila*. Protein is a logical candidate for such a trade-off. To date, no one has examined the hypothesis that protein limits fecundity in *Drosophila* in an experimental setting. Although formidable technical difficulties remain to be overcome (such as the quantification of protein ingestion and metabolism) this would seem to be a valuable area for further study.

Yeast also contains abundant quantities of nutrients known to be vitamins in insects, the most prominent of these being the B vitamin complex (Dadd 1985). It is conceivable that these factors may be limiting in fruit flies which ingest principally carbohydrate-rich diets, and there may be a trade-off between the B vitamins required for reproduction and those required for somatic maintenance.

An additional compound which cannot be synthesized by insects, and therefore serves as a vitamin, is cholesterol (DuPont 1982, Dadd 1985). This lipid is essential for membrane and steroid hormone synthesis and is virtually absent from the laboratory *Drosophila* diet outside of yeast. It may be that this compound acts as a limiting factor in *Drosophila* reproduction and its use in the egg may contribute to the costs of reproduction.

Clearly, much remains unelucidated in the study of the dietary aspects of reproduction in *Drosophila*. Careful nutritional analysis of feeding, reproduction, and egg production might be very useful in elucidating

dietary aspects of the trade-off between reproduction and somatic needs in these insects.

Costs of reproduction in male Drosophila melanogaster
Although ample evidence exists for the deleterious effects of reproductive activity on survival in male *Drosophila melanogaster*, few studies have been conducted on the physiological basis of these costs. In part, this is due to the difficulty of quantifying the energetic or nutritional output associated with their reproductive efforts. Such studies have been carried out in other *Drosophila* species in which the male contribution in the semen is more extensive. In *D. melanogaster*, Service (1989) found a significant reduction in starvation resistance in mated males when compared to virgin males. This difference might be due to a reduction in either lipid or carbohydrate levels, since Djawdan et al. (in press) have found that both contribute to starvation resistance. Clearly, much additional work is needed on the physiology of reproductive costs in *D. melanogaster*. Differences between the sexes should be very informative with regard to life-history evolution and evolutionary trade-offs as well.

A possible role for hormones in the cost of reproduction
In some ways, our exploration of the physiological analysis of the cost of reproduction has been very unsatisfying. Rather than providing a single and quantifiable mechanistic explanation for the negative effects of reproductive activities on somatic function, these studies have pointed to multiple effects, environmental plasticity in response, and the interaction of multiple organ systems. Clear answers regarding the basis of trade-offs are still lacking and several elegant models have not stood up to quantitative analysis.

One conclusion we can draw from previous studies is the importance of integrative processes and functions that influence the entire organism: behavior, nutrient flux, tissue function, and somatic survival. An unanswered question for these studies is how environmental factors can have such crucial effects on organismal performance. We suggest that the effects of diet, environment, mating, etc., may be integrated through the actions of the reproductive hormones. Such interactions have been proposed in vertebrates, and have been the subject of a number of studies (Marler and Moore 1988, 1991, Ketterson and Nolan 1992, Sinervo and DeNardo 1996).

In insects, the reproductive hormones, juvenile hormone and ecdysone, circulate throughout the body and can influence virtually every tissue through their effects on gene expression and tissue growth (Rybczynski and Gilbert 1994, Riddiford 1996). It may be the case that the shifting of physiological activity from somatic to reproductive functions involves not a shift in energy allocation as had been previously proposed, but rather a shifting of nutrient allocation, transport and biosyn-

thesis. Orchestrated by the release of hormones which control the rate of egg production, the tissues in the body may wax or wane depending on their specific contributions to reproduction. Such effects have been proposed to occur in some vertebrates. Folstad and Karter (1992) proposed that elevated levels of testosterone, associated with enhanced secondary sexual characteristics in male birds, are causally linked with depression of the immune systems. Wedekind and Folstad (1994) further suggest that the actions of testosterone, though deleterious, can be maintained in the populations through selection for enhanced reproductive success.

A model involving trade-offs between reproductive and somatic function mediated by hormonal action in insects, suggests new experimental means for dissecting the details of the effects of reproduction. For example, the work of Partridge and coworkers (Partridge et al. 1986, Chapman et al. 1995, Chapman and Partridge 1996) has demonstrated a gradient of increasingly deleterious effects as female flies either remain virgin, come into contact with males whose reproductive organs are blocked, come into contact with males lacking sperm, or come into contact with fertile males. It might be that an analysis of the hormone levels in such females would also reveal an increasing titer of the reproductive hormones as sexual contact and reproductive activity increase. Similar analyses on lines of flies which are genetically differentiated with regard to reproductive strategies of energy allocation might give insights into the role of the reproductive hormones in these processes. Such studies would then provide a rationale for investigating hormonal effects in the absence of male contact, and would begin to pinpoint mechanisms by which female physiological systems are directed away from somatic tasks and toward reproductive ones.

Future studies must tackle the problem of global physiological changes, including the effects of environment, diet, and mating status. It may be useful to direct these studies at the control systems influencing whole body function in order to obtain a more complete picture of the physiological costs of reproduction.

Conclusion: costs, complexity, and hormones

Starting from cases in which the cost of reproduction seems self-evident, more exacting evolutionary, genetic, and physiological analysis reveals more and more complexities and ambiguities. "Energetic trade-offs" between survival and reproduction do not turn out to be based on simple allocative mechanisms, while limiting dietary factors are elusive.

There are at least two distinct responses that this situation might elicit. The first would be to say that real-world organisms do not read *The American Naturalist*: instead of following simple allocative functions,

actual organisms evolve according to more complex rules. This reflects their nature as feedback-laden, Darwinian, carbon-based forms of life, rather than simple formulas.

A second response to this situation would be to re-double efforts to find an elegant controlling mechanism for life-history, on the assumption that we have simply failed to find the critical mechanisms to this point.

Our own view is uneasily perched between these two extremes. Overall, we intuit that the complexities that we have inferred are real features of the cost of reproduction. But we still hold out hope that hormones may provide the missing integration that will fully explain how this cost evolves.

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