THE EVOLUTION OF LIFE HISTORY TRAITS: A Critique of the Theory and a Review of the Data

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INTRODUCTION

In 1976, I reviewed (84) two models which give alternative explanations for the adaptation of life history traits to stable and fluctuating environments. Deterministic models (*r*- and *K*-selection) predict that organisms exposed to high levels of density-independent mortality, wide fluctuations in population density, or repeated episodes of colonization will evolve towards a combination of earlier maturity, larger broods, higher reproductive effort, and shorter lifespans than will organisms exposed to density-dependent mortality or constant population density (48, 65). Stochastic models (58, 77) predict the evolution of the same combinations of life history traits, but for different reasons: when fluctuations in the environment result in highly variable juvenile mortality, then a syndrome of delayed maturity, smaller reproductive effort, and greater longevity should evolve.

Several years ago I set out to test these predictions by measuring the reproductive traits of two species of small fish that had been introduced to Hawaiian reservoirs in 1907 and 1922. Ambiguities appeared in the interpretation of the results, some of them inherent in the theory, others in the observations. I could not decide which of several possible causal systems had produced the pattern I observed. To determine what my results meant, I first tried to understand what life history data could mean in general, given the present state of our knowledge. In brief, the theory is not yet refined enough to be tested by crucial experiments that can pinpoint flaws. Under these circumstances, observation and experiment cannot falsify predictions definitively, but they can profitably arbitrate among the various simplifying assumptions that theorists may want to try out in their pursuit of unambiguous predictions that cleanly touch reality.

In this paper, I hope to demonstrate that the interpretation of data is ambiguous because the theory is incomplete. Theory can form the empiricists' search image, which then contains just as many unarticulated assumptions as does the theory. That is the subject of the first section of this essay. I then briefly list some of the obstacles to empirical work in the second section. In the third section, I review a representative sample of life history data, for two reasons. First, although there are difficulties relating theory and observation, the data show clearly that the number of types of life histories is limited. Thus hope for a general explanation of life history diversity is justified. Second, a review of life history diversity can itself challenge theorists by revealing the complex nature of the phenomena.

SOURCES OF AMBIGUITY IN THE THEORY

Students of life history evolution seek to explain variation in age at maturity, number of young, reproductive effort, size of young, and interbrood interval. Empiricists take one of two general approaches. On the one hand, they compare existing forms, assume that the conditions under which these forms are living represent the conditions under which they evolved, and test possible explanations against field observations. This, the comparative approach, often makes use of those interspecific or intergeneric comparisons that are subject to the pitfalls ably summarized by Lack (42). Empiricists taking a direct approach, on the other hand, measure the selective difference between habitats and predict how life history traits should change if a population is introduced into one from the other. If the traits do not change as predicted, new theories are required. Placing evolutionary predictions at risk has not been popular. Evolution moves slowly and biologists are impatient. I believe that the logic of comparison is weaker than the logic of prediction, which should be used wherever feasible. The foundations of both will be strengthened by making explicit seven sources of ambiguity in the theory.

These ambiguities all share a general form. Each represents an unanalyzed complexity or subtlety, and for each we do not know whether explicit consideration of the problem would make any difference to our predictions. So long as we can accumulate confirmations of predictions that take real risks, we can continue on the assumption that these ambiguities make no difference. However, when falsifications force us to reconsider the assumptions, a skeptic could argue that the model failed to fit reality because it ignored or misrepresented one or more of these sources of ambiguity, and not because of the other features in the model with which we are usually concerned. Without relaxing his assumptions and examining the behavior of models that incorporate none of these complexities, without, in other words, showing that these ambiguities had no influence upon his predictions, one could not answer this objection. I call this the Dilemma of the Faustian Empiricist, who pursues the basis of his knowledge perhaps a bit too far for his own comfort.

These considerations should not inhibit theorists or empiricists, precisely because we do not yet know if they make any difference, and the only way we are going to find out is by testing energetically the interaction of theory and experiment.

1 Diploid Genetics and Ontogeny

What are the consequences of ignoring the complexities of diploid genetics and ontogeny? I will begin with one classical model of genetic fitness. My purpose is not to criticize this particular model, but to use the discussion of the ambiguities associated with it to illustrate a more general problem. In population genetics, fitness is sometimes measured as the malthusian parameter, m, defined as the fitness of a *genotype*. Lotka's (46) equation defines m:

$$1 = \int_{A}^{W} e^{-mx} l_x b_x \, dx,$$

where m is the rate at which that genotype is increasing, x is age, l_x is the probability of survival to age x, b_x is age-specific fecundity, A is age at maturity, and W is age at last reproduction. Whereas m is a property of a genotype, l_x and b_x can only be measured on a population. That population is made up of a single, stable genotype only if it is an asexually produced clone (27). As Kempthorne & Pollak (37) state, ". . . there is deep obscurity in the malthusian formulation. It is fundamental that a diploid individual contributes genes and not individuals to the next generation." By making the assumption that the complexities of sex and ontogeny do not matter, life history theorists are ignoring the essence of selection in a mendelian population: the coadaptation of the gene complex (51). The usual *Gedanken* experiment consists of endowing a series of clones with certain reproductive traits, putting them in competition, and seeing which one wins (e.g. 58).

You may object that some models have successfully tied genetics to life history evolution. In fact, commendable efforts have been made, but no one has avoided these objections. Murphy (58), MacArthur (47), and Roughgarden (74) attempted to account for sex. They assumed that age at maturity and fecundity, or r and K, are so tightly associated genetically that they can be productively modelled as alleles at a single locus. Implicit in that approach is the necessity of assuming what one is trying to explain: the association of early maturity and high fecundity, or low r's and high K's. Charlesworth (13) generalized the one-locus-two-allele case to an age-structured population, thus considerably extending the realism attained by population genetics. The remaining difficulties appear intractable. For three reasons, we cannot generalize the one locus case to life history traits, most of which are influenced by many genes. First, as Wright (102) showed for pelage color of guinea pigs, the interaction of two or more loci can be wildly nonlinear. Second, the selective value of an allele at one locus can depend on the frequency of alleles at other loci, and always depends on whether the trait influenced by that allele is currently above or below the optimum value in the population at large (102). Third, evidence of two sorts indicates that changes in a few regulatory genes with large effects, rather than many structural genes with small, additive effects, and rearrangements of large blocks of genes determine large differences between species: (*a*) chimpanzees differ strongly from man in morphology, behavior, ecology, and life history traits, but are

so nearly identical at electrophoretically detectable loci that the difference between chimpanzee and man for structural loci is less than the equivalent difference between pairs of sibling species of fruit flies or mammals (39); (b) differences in rates of anatomical, molecular, and chromosomal evolution between frogs and placental mammals indicate that there are two kinds of evolution: serum albumins in frogs and mammals have evolved at about the same rate, but chromosome number has changed 20 times faster in mammals than in frogs, paralleling the much greater anatomical diversity of placental mammals (100). These kinds of evidence convince me that detailed genetical models of life history evolution will have a strong flavor of unreality for some time to come, perhaps forever. If regulatory genes are preeminently important, if loci in general interact nonlinearly, and if linkage rearrangements result in more rapid evolution than changes in structural loci, then the assumptions of classical populations genetics are profoundly violated, and its generality is limited to the single locus case. Traits determined by single loci are rarely important to ecologists.

Another approach should clarify the point. Consider the way a population geneticist, who tries to deal with the complexities of diploid genetics, and a life history theorist, who usually does not, view the structure of evolutionary theory. One population geneticist (44) has posed as the general problem of evolution the understanding of four transformations within and between genotype space and phenotype space (Figure 1). The initial distribution of genotypes in the population, G_1, is transformed by the (as yet unknown) laws of ontogeny, T_1, into the initial distribution of phenotypes, P_1. These phenotypes are not all equally fit, and T_2 consists of the laws of ecology (as yet unknown) that determine the relative survival of phenotypes, resulting in the set of selected phenotypes, P_2. T_3, inverse epigenetic laws (as yet unknown), permit the inference of genotypes from phenotypes, giving us G_2, the distribution of genotypes that underlies the P_2 set of phenotypes. The partially understood rules of Mendel and Morgan, T_4, produce the next generation of genotypes: the subject of theoretical population genetics.

Lewontin's model poses the problem of evolutionary ecology with striking clarity: T_1, T_2, and T_3 are not understood, and without them, knowing a bit about T_4 is of little help. Life history theorists (and most other evolutionary ecologists) approach the problem a different way. They see associated with each transformation a surface structure of observables and a deep structure (the relationships embodied in the transformation rules) in terms of which they seek to explain the surface structure (85). In life history work (Figure 2), the surface structure consists of individual organisms, their demographic and physiological characteristics, and a set of environmental measures that describe the conditions they encounter. Statistical inference connects the surface structure to an intermediate structure consisting of estimates of age at maturity, age-specific survivorship and fertility, growth rates, size of young, the time course of resource availability and weather, and so forth. The deep structure relates parameters that measure fitness, such as r, K, or the probability of leaving no young at all; these connect to the intermediate structure by such models as Lotka's demographic equation, the Lotka-Volterra equations, or analogous difference equations.
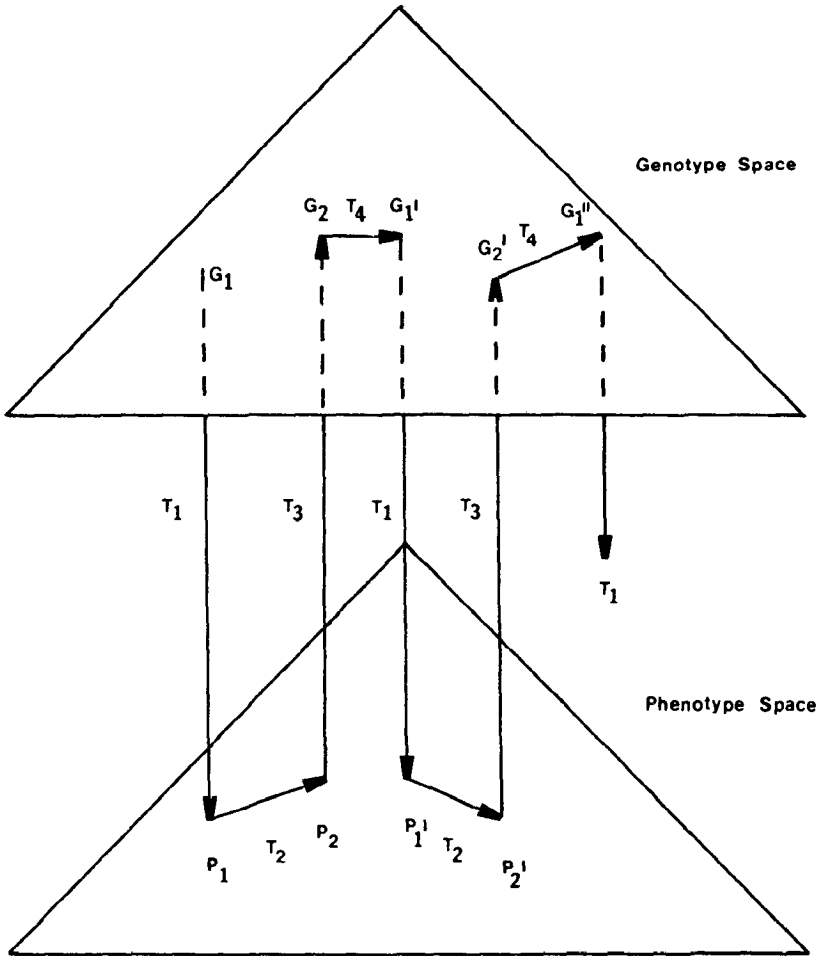
Figure 1 A population geneticist's view of evolution. A generational cycle starts with an initial distribution of genotypes, G_1, proceeds through a series of epigenetic and selective transformations, and finishes with a new distribution of genotypes, G_1'. This initial conceptualization implies that both dynamics and statics are part of the problem statement. After (44).

Life history theorists do not isolate any of Lewontin's transformation sets cleanly. Life history theory is a set of optimality models; theoretical population genetics is a set of mechanistic models. They approach the problem of evolution in profoundly different ways. To make predictions about the relative survival of phenotypes, life history theorists ignore ontogeny (T_1) and genetics (T_4). This method is attractive because genotypes are not being continuously destroyed and reshuffled by sex, and because the complications of developmental plasticity and canalization can be ig-
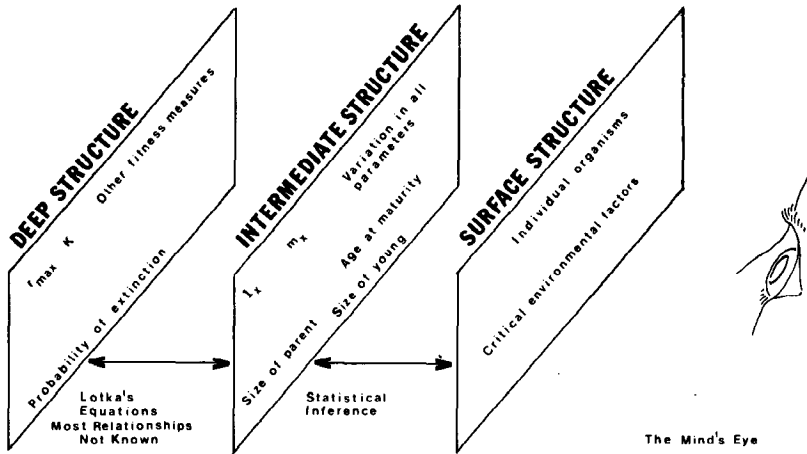
Figure 2 An evolutionary ecologist's view of evolution. The surface structure of observables is related by statistical inference to an intermediate structure of demographic parameters. These are in turn shaped by the deep structure of relationships implied by fitness and optimization assumptions. Statics are emphasized; dynamics are not. Compare with Figure 1.

nored. But they buy their ability to make statements about the relative fitness of phenotypes at a considerable cost in realism, and by compressing Lewontin's sequence,

$$G_1 \xrightarrow{T_1} P_1 \xrightarrow{T_2} P_2 \xrightarrow{T_3} G_2 \xrightarrow{T_4} G_1 \xrightarrow{T_1} P_1',$$

into the much shorter sequence,

$$P_1 \xrightarrow{T_{LH}} P_1',$$

where T_{LH} are the transformation rules defining the relative fitness of life history phenotypes.

Thus life history theory may suffer from a lack of realism, whereas the theory of population genetics founders on too much realism as soon as the mechanisms are pursued beyond one locus. In order to drive that point home, I mention a problem explored by Rocklin & Oster (73): The dimensionality of the phenotype space in Figure 1 is much lower than the dimensionality of the genotype space. For each generation the possible genotypes greatly exceed the realized genotypes; and to the extent that canalization is important, the realized genotypes greatly exceed the phenotypes produced. This difference in dimensionality seems to make impossible genetical models that predict phenotypic traits, such as life histories.

Some have suggested that the analysis of evolutionarily stable strategies (ESS's) is practically assumption-free and gets around all these difficulties. Smith & Price

(79) defined an ESS as "... a strategy such that, if most of the members of a population adopt it, there is no 'mutant' strategy that would give higher reproductive fitness." At least two difficulties make the analysis of ESS's, promising as it is, less than the solution to all our problems. First, nothing guarantees that the analyst can conceive of all the adaptive options; second, nothing guarantees that the options conceived will be genetically attainable, particularly if the options consist of combinations of complex traits, like life histories.

2 Design Constraints

Design constraints may keep populations from reaching predicted optima. To visualize this source of ambiguity, consider Figure 3a, which represents in three dimensions the relationships among the elements of the deep structure. The independent variables, P_1, P_2, ... P_n are the elements of a life history that can evolve. Their interaction determines the values of the dependent variable, fitness, which in this three-dimensional representation is a surface with peaks and valleys. A and B represent local optima on the fitness surface determined by P_1 and P_2 (e.g. age at maturity and clutch size) in an unspecified environment and with other life history traits held constant in some particular combination. These points are located either through the analysis of the maxima of equations relating fitness measures to life history traits, or through graphical analysis where the assumptions are embodied as the shapes of curves rather than as equations. Then the theorist asserts that because those are the combinations of traits that are maximally fit in the model, those should be the combinations found in nature. Here a problem characteristic of all optimality models surfaces.

Nothing guarantees that the optimum point will be located in an accessible portion of phase space. For example, first, the chitinous exoskeleton of insects restricts growth and limits the number of eggs that can be carried at one time. Second, the water vascular system of echinoderms prevents colonization of land and, through osmotic constraints, of fresh water. Third, the complex interrelationships and multiple functions of mammalian hormones make the evolution of reversed sex roles in mammals difficult. None of these examples represent trade-offs between opposing selection forces. They are design barriers, limits beyond which organisms cannot operate. Design constraints should not be confused with trade-offs or costs, all of which share the characteristic that if the opposing selection force were removed, the phenotype would be free to move beyond the point already attained.

In the language of our model, this means that the fitness surface is dissected by barriers implicit in the design of particular groups of organisms. These barriers will be located in different places, and have different shapes, for different groups. What are the consequences? Consider Figure 3b. Here B is the optimum point, but the population started at A. The population cannot get from A to B because it runs into the barrier implied by design constraints. As the population evolves, it should travel upward along the fitness surface, following the high ground, as far as it can go, stopping at the barrier. If our theory were flawless, we could predict that a population should be at B; if we observed not-B, we could then state that its evolution had encountered a design constraint, and we could check for that. But our
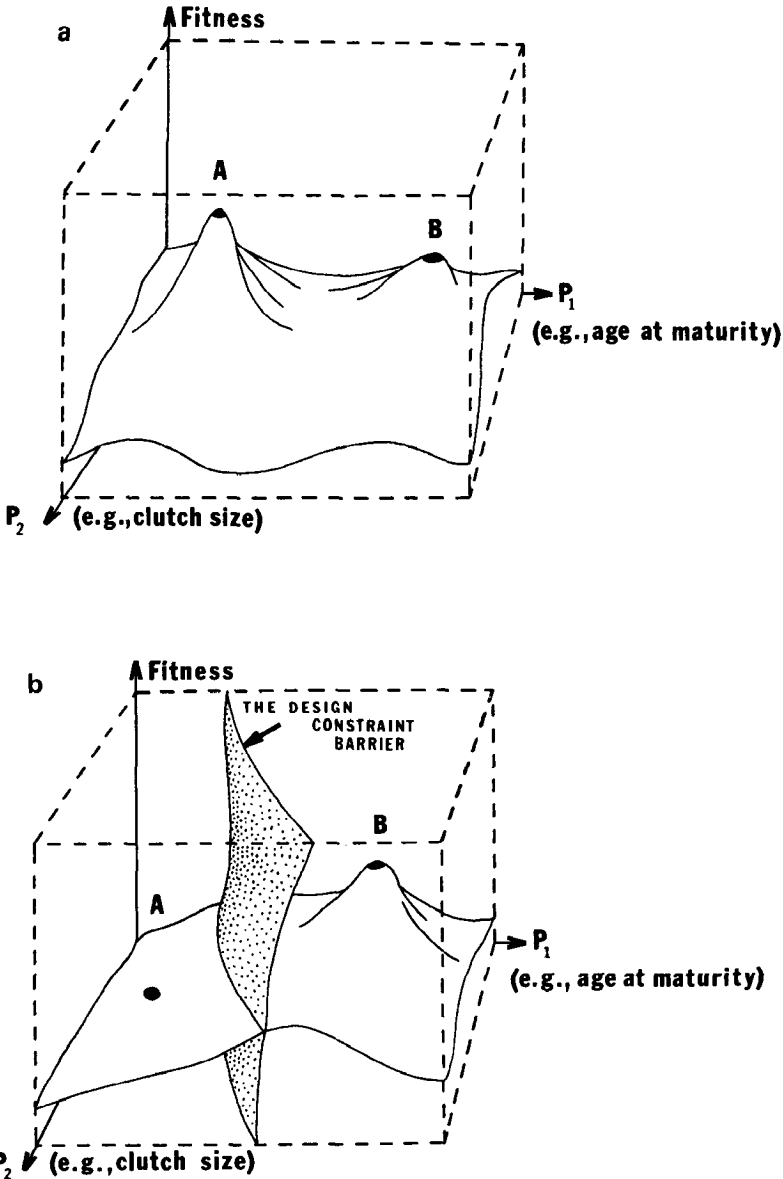
Figure 3   The optimization-design constraint ambiguity. (*a*) Life history theory may predict optimum combinations of traits, e.g. points *A* (a global optimum) and *B* (a local optimum); but (*b*) a design constraint may keep the population from attaining the optimum (point *B* in this case) if it started on the wrong side of the design constraint barrier. See text for the epistemological consequences.

theory cannot be trusted. We do not know where the design barriers are located; and when we observe not-B, we can only say that (a) the population is up against the limits of an unknown design constraint, or (b) not enough time has elapsed for the optimum to be attained (i.e. the constraint is dynamic, not static), or (c) there is something wrong with the theory.

I should insert a *caveat* here. Figures 3a and 3b seriously misrepresent the actual state of affairs. We are accustomed to thinking of smooth Wrightean (101) fitness surfaces. In fact, the fitness surfaces generated by simple models are non-picturable—so convoluted and discontinuous that, like four dimensions, the human imagination cannot grasp them (Oster, personal communication). We cannot actually trace the possible paths between two points in fitness space to determine if access is possible. This limits further the conclusions that may be drawn from optimality models.

3   Multiple Causation

Alternative explanations of life history diversity, all dealing with evolutionary rather than proximate causes, are possible and are rarely mutually exclusive. Multiple causation frequently operates on life histories.

Two *leitmotifs* dominate the development of life history theory: the deterministic view (19, 26, 43, 48, 83) and the stochastic view (17, 55, 56, 58, 77). The consequences of the deterministic view are relatively well understood, at least for r-selection. Although not as thoroughly explored as the deterministic approach, the stochastic viewpoint offers a plausible alternative explanation for the trends "explained" by r- and K-selection. Murphy (58) showed, with a simulation model of an age-structured population, that where juvenile mortality fluctuates, organisms with delayed reproduction, small reproductive efforts, and a few young are favored. Thus he predicted that where fluctuations in population densities result primarily from fluctuations in recruitment, a syndrome of traits should evolve that would appear to be K-selected, not r-selected. Schaffer (77) confirmed Murphy's conclusion from a simple analytical model of a population without age structure. In considering the contrasting case where adult mortality fluctuates, Schaffer predicted the evolution of a syndrome of traits similar to those predicted by r-selection: early maturation and large reproductive efforts. Table 1 compares the predictions of the two viewpoints.

One could argue that the deterministic and stochastic approaches make the same predictions for the same environments. In a stationary population where resources are limiting and competition is fierce, variation in juvenile survival may be greater than variation in adult survival (32). Similarly, in a population moving through a series of colonizing episodes, adult survival must vary considerably, perhaps much more than juvenile survival. One can suggest that the two approaches are dealing with the same phenomena at two different levels, as though there were two levels of deep structure in Figure 2. This is essentially the point made by (99): "Because neither the carrying capacity nor the mechanism of population regulation is known for most natural populations, data on life history parameters are often consistent with more than a single hypothesis." I add that even if such knowledge were available, the data could still be consistent with more than a single hypothesis.

Table 1 A Summary of the theory

Model	Assumptions	Predictions
Deterministic		

r-selection	exponential population growth
	stable age distributions
	repeated colonizations or
	  fluctuations in population
	  density
		earlier maturity
		more, smaller young
		larger reproductive
		  effort
		shorter life

K-selection	environment stable
	population near equilibrium
	  density
	logistic population growth
	competition important
		later maturity
		fewer, larger young
		smaller reproductive
		  effort
		longer life

Stochastic	environment fluctuates population near equilibrium	
	(*a*) juvenile mortality or birth rate fluctuates, adult mortality does not	later maturity smaller reproductive effort fewer young
	(*b*) adult mortality fluctuates, juvenile mortality or birth rate does not	earlier maturity larger reproductive effort more young

A priori criteria can aid the choice among models that are empirically indistinguishable. Models couched in terms of the means and variances of adult and juvenile mortality rates would make more readily falsifiable predictions than models couched in terms of population regulation because their assumptions can be checked. [It may not be possible to distinguish density-dependent mortality from density-independent mortality; see (72)]. This approach would avoid the indefinable relationship between K and life history traits, and by making explicit the variability in juvenile and adult mortality, would make possible the examination of other fitness measures, such as the minimization of the probability of leaving no young at all. I find these advantages persuasive. Such a theory does not exist; its development should challenge us all.

The first three theoretical ambiguities afflict all models in evolutionary ecology. The remaining four are peculiar to life history theory.

4   The Assumption of a Stable Age Distribution

One must assume fixed age schedules of survivorship and fecundity to write an equation relating the elements of a life history to one measure of fitness, r. Because this is equivalent to assuming a temporally constant, spatially homogeneous

environment, most graphical models make an analogous assumption. Although the stability of an age distribution is rarely checked (12), it is reasonable to assume that few, if any, natural populations have achieved it. Again, the dilemma is that of the Faustian Empiricist: A skeptic could always claim that the failure of the model to fit reality lay in its assumption of a stable age distribution, and not in any of its other features.

This criticism could be blunted by showing that the departures from stable age distribution were small [e.g. perhaps (97)], but where the mortality schedule has been shown to vary wildly (e.g. 57), the criticism retains considerable force. The only detailed theoretical analysis of populations not in stable age distribution (62) supports this point. In that model, population densities varied in a very surprising way, leading to unanticipated selection forces on life histories.

5 K *as a Function of Life History Traits*

Unlike r, K cannot be realistically expressed as a function of life history traits. Some of the most stimulating life history work has taken the following pattern. Let r be the measure of fitness, and examine its sensitivity to changes in age at maturity, fecundity, etc. Then predict that the trait to which r is most sensitive should be under the strongest selection pressure, should be found closest to its theoretical optimum (or against a design barrier), and should exhibit the least additive genetic variance of any of the traits (e.g. age at eclosion in *Drosophila melanogaster*). This process reduces life history traits to a common currency, units of r, and permits direct comparisons. For example, Lewontin (43) could say that at certain values of other life history traits, the increase in lifetime fertility necessary to increase r from 0.30 to 0.33 was a change from 780 to 1350 eggs, and that a decrease in age at maturity from 12 to 9.8 days, with no change in fecundity, made the same impact on r. Thus an additional 570 eggs were equivalent to 2.2 fewer days maturation time; both added 0.03 units of r.

This analysis is possible only because we can express r as a function of A, l_x, and b_x. No one could possibly write an equivalent expression for K because the general relationship between the sensitivity of a species to changes in its population density on the one hand, and its age at maturity, reproductive effort, and so forth on the other, is not clear. K is not a population parameter, but a composite of a population, its resources, and their interaction. Calling K a population trait is an artifact of logistic thinking, an example of Whitehead's Fallacy of Misplaced Concreteness. Thus r and K cannot be reduced to units of common currency. If they do trade off, so that higher r's imply lower K's, then the mechanisms by which that trade-off is accomplished are not demographic, but are bound up in physiology and social behavior, and as such could be expected to change from taxon to taxon.

In short, the theory of r- and K-selection contains a serious, and to my way of thinking fatal, flaw: A population that has a life history thought to result from r-selection is called "r-selected"; a population with the opposite traits is called "K-selected" in the absence of either evidence or deductive logic indicating that such traits have been molded by density-dependent effects. Such traits may eventually be shown to result from density-dependence, but the connection has yet to be demonstrated.

6   Post-Reproductive Survival: Alternative Equilibria

Certain classes of trade-offs between reproductive effort and subsequent adult survival can lead to any of several stable equilibria, depending on initial conditions.

Few have tried to model explicitly the effect that the act of reproduction has in decreasing subsequent survival [but see (67)]. Schaffer (75, 76) and Schaffer & Rosenzweig (78) have used graphs to analyze such trade-offs. When the relationships are purely concave, iteroparity, or repeated reproduction, is favored; when they are convex, semelparity, or "big-bang" reproduction is favored. The ambiguities enter when more complex, but biologically plausible, curves are analyzed. Sigmoid trade-offs lead to multiple stable equilibrium points, even in a simple, three-stage life history, and the number of possible equilibrium points can be expected to rise rapidly with the number of stages in the life history. Even simple stochastic models also show history dependence, as Cohen (18) has pointed out. The results obtained from any particular experiment that appears to settle down to "good" behavior may stem from a series of random events converging on a unique endpoint. Each repetition of the experiment will give a different result. In such cases, order and generality only emerge when one deals with the distribution of results from a large number of replicates.

These results lend plausibility to the idea that patterns of life history diversity have been influenced by chance historical events. In comparative work, the existence of either multiple stable endpoints or a broad distribution of possible outcomes results in terrible ambiguities. To make a precise and testable prediction in the first case, we would need to know not only the nature of the trade-off, which could be measured, but also the initial conditions, which can only be specified in manipulative experiments. In the second case, we would need a large number of well controlled replicates to discern the possibility of a strong stochastic effect.

7   Choice of Time Scale

Should we use a relative (generation time) or absolute (solar time) scale? This question becomes pressing as we try to extend the generality of the field to accommodate comparisons of higher taxa in a productive way. Choosing one time scale or the other leads to differing interpretations of just what we are trying to explain. Consider the life histories of two barnacles on the California coast (31).

The life histories of *Chthamalus fissus* and *Tetraclita squamosa* differ in absolute time (Figure 4a). *Chthamalus* is smaller, shorter-lived, matures earlier, and may be making a larger reproductive effort than *Tetraclita* (it appears to spawn as frequently as it can acquire the energy to do so). Because it lives in the relatively unstable upper intertidal where physical factors are limiting, *Chthamalus* could be called r-selected. In contrast, *Tetraclita,* living in the relatively stable subtidal zone, where biotic factors are limiting, could be called K-selected.

On the other hand, the life histories of the two barnacles recalculated in generation time appear quite similar (Figure 4b). Our problem is to explain the similarity, rather than the difference. By reproducing many times within a season, *Chthamalus* appears to be dealing with intraseasonal unpredictability, which could be more
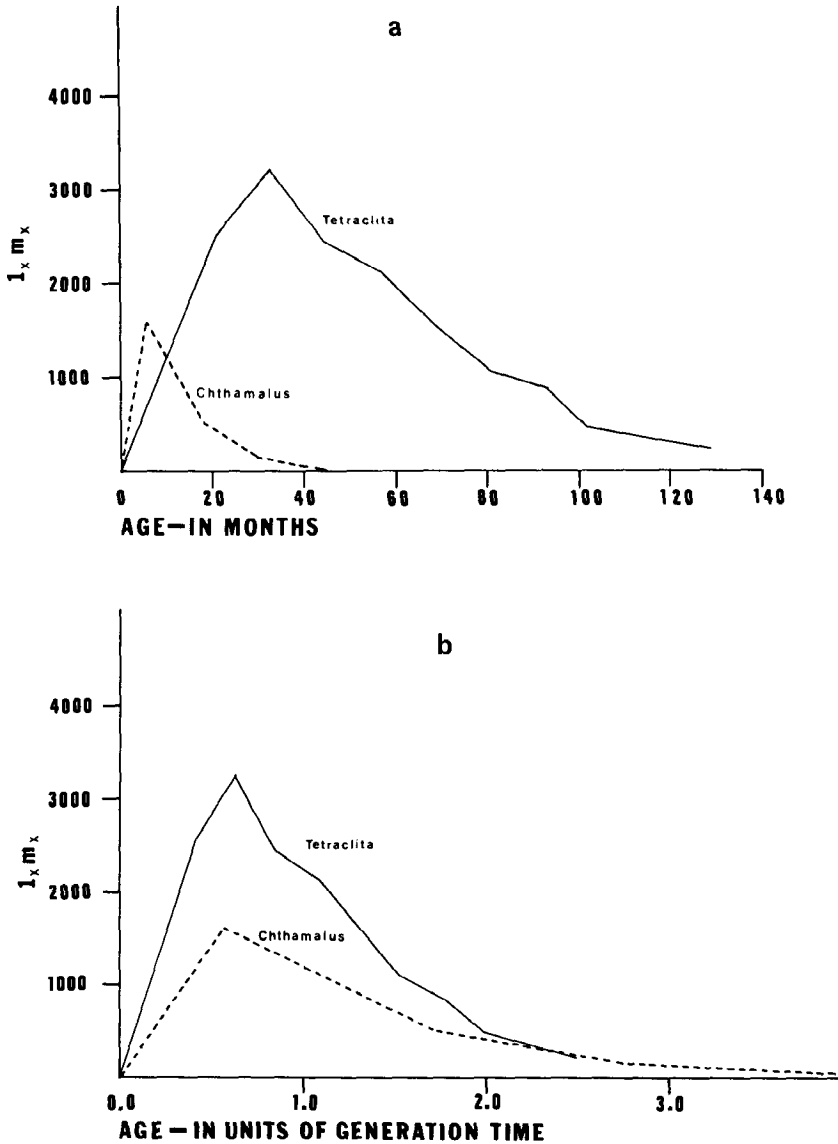
Figure 4   The ambiguity arising from the choice of time scales. Should we use generation time or absolute time? (*a*) The life histories of two intertidal barnacles graphed in absolute time [From (31)]. (*b*) The same life histories graphed in generation time. Figure 4*a* emphasizes the differences between the two species, Figure 4*b*, the similarities. Which should we be trying to explain?

important in the upper intertidal. By spreading its reproduction out over many years, *Tetraclita* appears to be dealing with inter-year variability, which could be more important in the subtidal. In both cases, the variable factor is probably the survival and settling of planktonic larvae.

Which of the two measures should we choose? One could argue either way on a priori grounds. The relativistic measure, generation time, has the strong advantage of placing the scientist in the organism's frame of reference. The absolute measure, solar time, corresponds much more generally to the natural periodicities of the environment. Note that posing the question as a dichotomy may itself be misleading, because we may not have to choose between them. The issue is whether population growth shall be modelled as a function of age, $n(a)$, as a function of time, $n(t)$, or as a function of both, $n(a,t)$ (Oster, personal communication). Leslie matrix models use $n(a)$, Lotka-Volterra models use $n(t)$, and the von Foerster equations use $n(a,t)$ (61).

SOURCES OF DIFFICULTY IN OBSERVATION AND EXPERIMENT

In the foregoing I want to have suggested enough of the difficulties that afflict life-historical empiricists to convince you that published life history data are not reliable enough to justify any great faith in the generality of conclusions drawn from them. The review of published data in the next section will extend this point. Consider first, however, five problems which further compound our difficulties.

1. We often cannot identify the unit of evolution in the field. The spatial structure of most populations is almost impossible to observe, making it hard to measure the rate and direction of gene flow in nature.

For life history traits, on which selection is almost certainly operating, the degree of correspondence between the genetic component of the trait observed in the field and local environmental conditions will depend on the magnitude of local selection pressures, the rate of gene flow, and the nature of the average global selection pressure encountered by the whole interbreeding unit (Spieth, personal communication). When migration rate exceeds selection pressure, the local group must frequently be adapted to the entire spatiotemporal mosaic encountered by the panmictic unit, and any correlation between local environmental conditions and reproductive traits could be spurious.

2. There are severe technical problems with getting reliable life tables (12).

3. The criteria used for selecting organisms for meaningful measures of reproductive effort necessarily conflict.

Energy budgets require two measurements, the time spent by an organism in various activities, measured in the field, and the energy expended on those activities per unit time, measured in the lab. Time budgets are most easily measured on large, long-lived species, sessile species, or species living in open habitats. Energy expenditures are most easily measured on small, short-lived organisms that will grow, mate, and reproduce under laboratory conditions. Clearly, time budgets cannot usually be estimated with the same accuracy as energy budgets for the same species. [See (32) for a thoughtful discussion of the second and third empirical difficulties.]

4. Laboratory work requires organisms with short generations (thus ruling out comparisons with long-lived species) for two reasons: First, differences observed in the field may contain a strong element of developmental plasticity. To check this, one must rear the organisms through two generations in the laboratory to eliminate, in the first generation, first-order developmental plasticity, and in the second generation, maternal effects. Second, to carry out a program that tests evolutionary predictions with selection experiments, one needs organisms with short generation times. Because most animals are immediately excluded, rigorous empirical generalizations are impossible. Charlesworth (personal communication) has suggested an additional difficulty inherent in any laboratory approach: "A species which is simply better adapted to standard lab conditions would have a greater longevity *and* fecundity than one which is not so well adapted."

5. To measure the reduction in survival rates caused by reproduction, one must keep the organisms from reproducing and monitor subsequent survival, preferably in the field. But in any organism with no parental care, one cannot stop the commitment of essentially full reproductive effort by withholding mates.

SUMMARY OF SOURCES OF AMBIGUITY

Table 2 summarizes the theoretical and empirical sources of ambiguity just discussed. Each of the twelve items presents a worthy challenge. Overcoming or clarifying any would be significant. In certain cases, it would be profound.

The ideal organism for a complete life history study would have the following attributes. It should be possible (*a*) to define the boundaries of the field populations and to measure emigration and immigration rates; (*b*) to construct, by marking or aging, cohort life tables from field data with confidence limits on the mortality and fertility columns, and to measure the temporal component of the coefficient of variation in adult and juvenile mortalities, exclusive of measurement error; (*c*) to measure activity budgets in the field and energy budgets in the laboratory; (*d*) to achieve a relatively short ($\leqslant$ 8 weeks) generation time in the laboratory; and (*e*) to make the organism forego reproduction (preferably in the field) and then to follow its subsequent survival.

These criteria, taken together, are quite restrictive, and adhering to them rigidly would preclude most of the interesting work that could be done. I do recommend against working on species for which none of the criteria could be satisfied. Investigators should focus on those questions for which most of the criteria can be met in a tractable species.

PUBLISHED EVIDENCE ON LIFE HISTORY DIVERSITY

This section evaluates present knowledge of diversity in life history traits for many taxa. In judging these papers by the criteria developed here and in the previous section, I am not implying that their authors have in some way failed; rather, I am trying to establish, on a uniform basis, what we do and do not know. Much of the work examined here was done before the field attained its current state of sophistication; and it would be unreasonable to criticize someone for not checking a point

Table 2 Summary of sources of ambiguity

Ambiguity	Difficulty it leads to
Theoretical	
1. Experimenter assumes that the complexities of diploid genetics and ontogeny are irrelevant.	epistemological and general
2. Design constraints restrict optimality arguments.	epistemological and general
3. Several alternative explanations which are not necessarily mutually exclusive are usually possible for any adaptation.	epistemological and general
4. Experimenter assumes a stable age distribution.	epistemological and peculiar to life history work
5. K cannot be expressed as a function of life history traits.	technical and peculiar to life history work
6. Sigmoid trade-offs between the cost of repro-duction and subsequent adult survival lead to multiple stable equilibria.	epistemological and peculiar to life history work
7. What is the appropriate time scale?	epistemological and peculiar to life history work
Empirical	
1. What is the unit of evolution?	technical and general
2. Reliable life tables are hard to get.	technical and particular
3. Measurement of reproductive effort restricts the choice of organisms and thus of com-parisons.	technical and particular
4. Need for short generation times restricts choice of organisms.	technical and particular
5. Measurement of cost of reproduction restricts choice of organisms.	technical and particular

that had not yet been raised, or to criticize data gathered as a byproduct of a study with other objectives. I have used papers frequently cited and readily accessible. While I have not exhausted the literature, I believe my review conveys an accurate impression of the reliability of the better papers. I relied most heavily on papers that discuss intra- or interspecific comparisons.

Both r- and K-selection and the stochastic models can be applied in three ways: as *systems of classification,* as *explanations*, and as *predictions*. Thus many workers have used the r- and K-selection dichotomy as a convenient shorthand, referring to the combination of early maturity, large clutches, large reproductive effort, small young, and a short life as r-selected, perhaps without meaning to imply the evolutionary origin of that suite of traits by their use of the term. The stochastic models predict the association of the same traits for different reasons. I refer to that syndrome as fitting the *accepted scheme,* because as yet no predictions of alternative associations of traits have been made. Reproductive traits may covary according to the accepted scheme without distinguishing between deterministic and stochastic

models as *explanations,* or even guaranteeing that either model is involved. But if reproductive traits do not covary according to the accepted scheme, we can be sure that neither model provides a sufficient explanation. Therefore, if the data were adequate, I determined whether each comparison fit the accepted scheme.

I used six criteria of reliability: (*a*) Did the author rear the organisms under constant conditions to isolate the genetic component of the variability observed in the field? [Where enough field data are available, laboratory work may not be necessary, e.g. the analysis of heritability of clutch size in the Great Tit (64).] (*b*) Did the author attempt to measure the environmental factors later invoked to explain differences in reproductive traits? (*c*) Did the author attempt to measure the degree of density-dependent or density-independent regulation? (*d*) Did the author attempt to measure the year-to-year variability in the mortality schedule? (*e*) Were the statistics convincing? For intraspecific comparisons, were analyses of variance or covariance done? For interspecific comparisons, did the author demonstrate that interspecific differences were still significant when intraspecific variation was taken into account? (*f*) Was an attempt made to measure reproductive effort? If so, at what level of sophistication? Was the rate calculated as the calories diverted to reproduction per unit time as a proportion of total calories passing through the organism? For each of the six criteria, one could make a commendable effort with less than convincing results. Therefore, in the Tables I have indicated satisfaction of the criteria at three levels: "no" indicates that no attempt was made; "maybe" signals a good try whose data remain unconvincing; "yes" signifies a criterion completely satisfied. The review is organized by taxa.

Salamanders

Table 3 summarizes the quality of data on salamander life history adaptation. This literature is strong in large field samples (criterion *e*) that demonstrate intra- and interspecific differences, but weak in measuring the factors on which explanations of life history diversity have been based (criteria *b, c,* and *d*) or on documenting the genetic basis of the diversity (criterion *a*). Only one of five salamander comparisons fits the accepted scheme. Five species of *Desmognathus* show unusual resistance to change, while *Batrachoseps attenuatus* has unusual developmental flexibility.

Table 3 Reliability of life history data on salamanders

Ref.	Comparison[a]	Taxon	Criterion a	b	c	d	e	f	Fit scheme?	Number of criteria met
(60)	inter	*Desmognathus*	no	no	no	no	yes	maybe	no	2
(87)	inter	*Desmognathus*	no	no	no	yes	yes	no	no	2
(11)	intra	*Gyrinophilus*	no	no	no	no	yes	no	yes	1
(88)	intra	*Desmognathus*	no	no	no	no	yes	no	no	1
(29)	intra	*Notophthalmus*	no	no	no	no	yes	no	?	1
(50)	inter	*Batrachoseps*	no	maybe	no	maybe	maybe	no	no	3

[a] Inter = interspecific; intra = intraspecific.

Lizards

Table 4 summarizes lizard life history data. Reproductive effort is more frequently measured on lizards than on most taxa; the field statistics are good and there is much comparative life table information. Broad, intergeneric comparisons of many species reveal a set of syndromes that resemble the accepted scheme (95), but detailed studies break the trend (3, 92–94, 97). Although no study satisfied all criteria, the best work published in 1974–75 represented a considerable advance over 1969–70. The lizard data emphasize that rigorous definitions of reproductive effort can be made in the presence of year-to-year variability in mortality schedules and should be included in future studies.

In a very thorough study, Tinkle & Hadley (94) measured the calories in reproductive effort per season for ten species, estimated the annual energy budgets for three species, and examined correlations of the reproductive data with age at maturity, with adult and juvenile survival rates, and with generation time. Only one correlation was significant: the ratio of clutch calories to body calories (a rough measure of reproductive effort) was negatively correlated with mean annual adult survivorship. The authors recognized that, had they been able to measure annual energy budgets for all ten species, there might have been less noise in their correlations. Of the three species for which they had estimates of the annual energy budgets, the one with delayed maturity and long life, *Sceloporus graciosus,* had the highest per season reproductive effort (0.23), while an essentially annual species, *Uta stansburiana,* made an intermediate effort (0.19). Sample sizes were small, and from too few populations to make the interspecific comparisons airtight. Nevertheless, these data, which are among the best available, force the conclusion that lizards do not neatly fit the accepted scheme.

All long-term studies of lizard populations have shown year-to-year variation in reproductive success (9, 22, 23, 89, 90, 96, 97, 103), and certainly not all lizards that encounter such variability are late-maturing, with one clutch per season as Murphy's model would predict, e.g. *Uta stansburiana* (90, 96). Some of the variation in reproductive success stems from changes in fecundity, some from changes in mortality, and the relative contribution of each is hard to measure because of the

Table 4   Reliability of life history data on lizards

Ref.	Comparison	Taxon	Criterion a	b	c	d	e	f	Fit scheme?	Number of criteria met
(91)	inter	112 species	no	no	no	no	yes	no	yes	1
(95)	inter	37 species	no	no	no	no	yes	no	yes	1
(66)	intra	*Cnemidophorus*	no	yes	no	no	maybe	no	?	2
(92, 93)	intra	*Sceloporus*	no	maybe	no	maybe	yes	wt	no	4
(5)	inter	*Sceloporus*	no	no	no	no	yes	no	yes	1
(33)	inter	*Typhlosaurus*	no	no	no	no	maybe	no	yes	1
(3)	inter	*Anolis*	no	no	no	no	maybe	wt	no	2
(94)	inter	10 species	no	no	no	yes	maybe	cal/ rate	no	3
(97)	inter	*Sceloporus*	no	yes	no	yes	yes	wt	no	4

difficulty in counting the number of clutches per season. It is possible, by judicious selection, to find series of both intra- and interspecific comparisons of lizards that fit the accepted scheme, but any attempt to fit all possible comparisons into the accepted scheme founders when the best-studied populations are examined.

Birds

Table 5 summarizes the quality of avian data. I have relied heavily on review articles (4, 16, 42) and included Hussell's (34) study as an example of one of the better pieces of detailed work. No one has reared large numbers of wild birds under constant conditions; therefore the genetic basis of observed diversity is unknown (criterion a). Hussell (34), Ashmole (4), and Lack (42) all tried to measure relevant environmental factors and, while failing to exclude alternative explanations, did render more plausible the hypothesis that food places the proximate limit on clutch size in birds. Criteria c through f were rarely satisfied, which indicates that many types of data are hard to obtain for birds, not that ornithologists have not tried to get them. For example, Ashmole (4) reported estimates of adult and juvenile mortality in sea birds based on banding returns, and pointed out that the assumptions of band survival and bird movement required for making such calculations are so frequently violated that the estimates are not reliable. Acquiring such data takes great effort. Although the data on avian life histories are not reliable, they have triggered much productive speculation, particularly because the patterns emerging from broad comparisons among species (16) and subfamilies (42) offer alluring glimpses of generality.

Mammals

The data on mammalian life histories (Table 6) are less reliable than the avian data. Convincing statistics on age at maturity are entirely missing, except for extremely broad comparisons, and virtually no comparative data exist on reproductive effort. Information is generally limited to litter size. The work done on the snowshoe hare stands out (e.g 36). It demonstrated a genetic component to geographical variation in litter size. Other than that, we know almost nothing about the coadaptation of age at maturity, litter size, longevity, and reproductive efforts in mammals. When such information is gathered, I suspect social systems and behavioral peculiarities will be shown to interact strongly with reproductive traits.

Table 5 Reliability of life history data on birds

			Criterion						Fit	Number of
Ref.	Comparison	Taxon	a	b	c	d	e	f	scheme?	criteria met
(42)	subfamilies	most birds	no	yes	no	no	no	no	?	1
(4)	inter	many sea birds	no	yes	no	yes	no	no	yes	2
(16)	inter	many birds	no	no	no	no	no	no	yes	0
(34)	intra	*Calcarius, Plectrophenax*	no	yes	no	no	yes	wt	?	3

Table 6   Reliability of life history data on mammals

Ref.	Comparison	Taxon	Criterion						Fit scheme?	Number of criteria met
			a	b	c	d	e	f		
(21)	inter	*Peromyscus*	no	no	no	no	no	no	?	0
(45)	inter	many mammals	no	no	no	no	no	no	?	0
(54)	inter	many squirrels	no	no	no	no	maybe	no	?	1
(6)	intra	*Sylvilagus*	no	no	no	no	yes	no	?	1
(35)	intra	*Rattus*	no	no	no	no	no	no	?	0
(36)	intra	*Lepus*	yes	no	no	no	yes	no	?	2
(80)	inter	*Peromyscus*	no	no	no	no	no	no	?	0
(20)	intra	*Sylvilagus*	no	no	no	no	yes	no	?	1

Both technical problems and the confounding effects of complex behavior make it difficult to draw reliable conclusions about evolutionary causes from the avian and mammalian data. This largely descriptive work illustrates the strengths and weaknesses of the comparative method. Its strength lies in suggesting hypotheses; its weakness lies in testing them. It cannot exclude alternative explanations, nor can it evaluate the relative impact of multiple causes. When one makes broad comparisons across either class, the accepted scheme emerges: Delayed maturity, small clutches, and long lives seem to come as a unit, as do early maturity, large clutches, and short lives. Where there are data available on mortality patterns, as for some seabirds (4), they are consistent with both deterministic and stochastic models. When intraspecific and intrageneric comparisons are examined, generalizations seem to vanish.

Fish

Table 7 summarizes data on fish life histories. The fish literature is strong in field data with large sample sizes, but weak in attempts to measure explanatory environmental factors, degree of density-dependence, mortality rates, or reproductive efforts. It has suggested three points of broader significance. First, Murphy (58) arrived at his hypothesis (that the combination of delayed reproduction, low repro-

Table 7   Reliability of life history data on fishes

Ref.	Comparison	Taxon	Criterion						Fit scheme?	Number of criteria met
			a	b	c	d	e	f		
(40)	intra	*Gambusia*	no	no	no	no	yes	no	?	1
(2)	intra	*Salmo*, others	yes	no	no	no	yes	no	?	2
(41)	intra	*Gambusia*	no	no	no	no	yes	no	yes	1
(58)	inter	herring-like fish	no	no	no	maybe	maybe	no	yes	2
(84a)	intra	*Neoheterandria*	no	no	no	no	yes	wt	yes	2
Stearns, unpublished data	intra	*Gambusia, Poecilia*	yes	yes	no	no	yes	wt	no	4

ductive effort, and increased longevity adapts the organism to fluctuations in recruitment) through a consideration of fisheries data. That was the first alternative hypothesis suggested that deals with the same reproductive trend "explained" by r- and K-selection. Second, nowhere is the impact of developmental plasticity more obvious than in fish. Growth rate, age at maturity, and fecundity are all very sensitive to temperature and food. This makes interpretation of field data difficult, and laboratory work necessary. Third, because of their broad range in fecundity and egg size, it was in fish that the trade-off between a few large young and many small young was first noted (86).

Insects

The outstanding characteristics of insect life history data (Table 8) are the carefully controlled experimental studies of maturation, longevity, and fecundity, with fairly good attempts to measure the factors that might account for the differences in these traits, such as adult and juvenile mortality. But there are no attempts to measure reproductive effort. While none of the studies reviewed here involved field work, the model laboratory systems have considerable relevance to natural conditions, particularly for the grain beetles.

Mertz (53) performed an elegant experimental analysis of the coevolution of fecundity and senescence in *Tribolium castaneum,* a flour beetle. He subjected beetles to three treatments: (*a*) certain death after ten days as an adult, (*b*) certain death after 20 days as an adult, and (*c*) no imposed mortality, in which case some beetles lived more than 400 days. In treatments *a* and *b,* 11 to 12 generations elapsed during the selection phase of the experiment; in treatment *c* some of the founders probably survived to the end. *Tribolium* begin reproduction at 3 to 4 days of adult age, and by the fifth day of adult life females are producing eggs at a rate of 10 to 18 per day, a level which they maintain until senescent decline sets in at about 70 to 80 days of adult age.

One would predict that the age distribution of fecundity should shift to an earlier peak in beetles from treatment *a* and *c,* with *b* intermediate, and that beetles from

Table 8 Reliability of life history data on insects

Ref.	Comparison	Taxon	Criterion a	b	c	d	e	f	Fit scheme?	Number of criteria met
(7)	inter	*Calandra, Rhizopertha*	yes	no	no	yes	yes	no	no	3
(63)	inter	*Tribolium*	yes	no	no	no	yes	no	yes	2
(8)	intra	*Drosophila*	yes	no	no	no	yes	no	no	2
(52)	intra	*Tribolium*	yes	yes	no	yes	yes	no	?	4
(38)	intra	*Tribolium*	no	yes	no	no	yes	no	no	2
(68)	inter	248 species of Ichneumonids	no	yes	no	no	yes	no	?	2
(69)	inter	10 species of Ichneumonids	no	yes	no	no	yes	no	?	2
(53)	intra	*Tribolium*	yes	yes	no	yes	yes	no	?	4

c should live longer than beetles from a, with b again intermediate. In fact, when he assayed for fertility and longevity after rearing them under constant conditions for two generations to eliminate maternal effects, Mertz observed a statistically significant shift only in fecundity: Beetles from treatment a had fecundities about 15% higher than beetles from treatments b or c during the first ten days of their adult lives. Later in life, the fecundity relationships reversed, so that beetles from all treatments gave birth to about the same number of young during their lifespans. Mertz's experiment provides rare, direct evidence that a change in adult mortality can shift the age distribution of fecundity.

At present, *T. confusum* is probably the only species for which one can answer the question, "Are r and K negatively correlated as most theory assumes?" The answer is, "Sometimes they are, and sometimes they aren't" (38). King & Dawson measured population growth rates and equilibrium densities of *T. confusum* exposed to all 16 possible combinations of four temperatures and four food treatments. Developmental plasticity resulted in quite different growth rates and equilibrium densities. The correlation between r and K was negative but not significant (−0.148) in one type of rearing chamber, positive and significant (+0.561, $p < 0.001$) in another. Such experiments cannot establish the genetic basis of a trade-off between r and K, but they can show that where differences are based on phenotypic plasticity, that trade-off need not exist.

In summary, the insect data do not support the generality of the accepted scheme. Of the well-studied cases, only the comparison between *T. castaneum* and *T. confusum* (63) fits the accepted scheme, and it is complicated by the developmental response to experimental conditions. Neither comparisons of geographical races of the fly, *Drosophila serrata* (8), nor comparisons of the grain beetles *Calandra oryzae* and *Rhizopertha dominica* (7), fit the scheme. Field evidence on ichneumonid wasps (68, 69) and the results of selection experiments on *Tribolium* (53) suggest that patterns of adult mortality can dominate life history evolution.

Herbaceous flowering plants

Table 9 summarizes data on herbaceous flowering plants. The consistently high quality of work on this group probably stems from the influence of Clausen, Keck & Hiesey (15), who emphasized the necessity of separating genetically based variation from developmental plasticity; and of Harper (28), who championed the analysis of reproductive adaptations in plants. Many plant ecologists raise individuals under equivalent conditions (six of ten studies reviewed) and attempt to measure reproductive effort (six of ten studies reviewed). However, there were few attempts to measure the relevant selective forces (four of ten studies), to measure age- or stage-specific mortality rates, or to measure degree of density-dependence (one of ten studies), even though the latter was frequently invoked as an explanation (1, 24, 25).

Solbrig's experiments on dandelions (24, 81, 82) equal the best on any organism. By growing four biotypes of parthenogenetic dandelions under constant conditions, he found that he could neatly arrange them into a series ranging from small leaves and high reproductive output (type A) to large leaves and low reproductive output

Table 9 Reliability of life history data on plants

Ref.	Comparison	Taxon	Criterion a	b	c	d	e	f	Fit scheme?	Number of criteria met
(70)	intra	*Echinochloa*	yes	no	no	no	yes	no	no	2
(71)	intra	*Euphorbia*	yes	no	no	no	yes	no	no	2
(14)	inter	*Lemna, Salvinia*	yes	no	yes	no	yes	no	no	3
(24)	inter	*Solidago*	no	no	no	no	yes	wt	yes	1
	intra	*Taraxacum*	yes	maybe	no	no	yes	wt	yes	4
(1)	inter	*Solidago*	no	no	no	no	yes	wt	yes	2
(25)	inter	*Helianthus*	no	no	no	no	yes	wt	yes	2
(30)	intra	*Polygonum*	yes	yes	no	no	yes	wt	?	4
(49)	inter	*Typha*	yes	yes	no	no	yes	wt	yes	4
(98)	inter	*Asclepias*	no	yes	no	no	yes	no	no	2
(59)	both	*Oryza*	yes	no	no	yes	yes	no	yes	3

(type D). In three plots varying from highly disturbed (frequently mowed and trampled) to relatively undisturbed (mowed once a year to a height 20 cm above the ground), the biotypes fell into a convincing cline, type D dominating the undisturbed site, type A the disturbed site, and types B and C sharing the intermediate site with type A. Type D always outcompeted type A. Solbrig's data fit neatly into the accepted scheme, but patterns emerging from recent work on dandelions from Montana (Solbrig, personal communication) break that trend.

McNaughton's (49) data on cattails (*Typha*) are also reliable. He raised them under constant conditions, tried to measure relevant environmental factors, and measured reproductive effort. Cattails also neatly fit the accepted scheme. Populations from North Dakota (*T. latifolia* and *T. angustifolia*) matured a month faster than populations from Texas (*T. latifolia* and *T. dominguensis*), produced more and smaller fruits per clone, more and smaller rhizomes per clone, and grew to a lower height.

In a provocative paper, Oka (59) examined inter- and intraspecific variability in the reproductive traits and phenotypic plasticity of wild (*Oryza perennis*) and domestic (*O. sativa*) rice. Under seminatural conditions annual forms had higher seed production, more soil-buried seeds, strong seed dormancy, less vegetative reproduction, and higher juvenile mortality than perennial forms. All annuals, of course, died after their first season of reproduction, but during that first reproductive period they experienced lower adult mortality rates than the perennials. These results roughly fit the accepted scheme, but go beyond it in emphasizing the broad range of reproductive adaptations in plants: Seed dormancy, vegetative reproduction, and developmental plasticity have to be considered.

In herbaceous plants the accepted scheme is not general, but does fit some cases. Sunflowers, goldenrods, dandelions (so far), and cattails seem to fit; grasses, milkweeds, and duckweeds do not. Wilbur (98) demonstrated that a more complex set of selective factors, accounting for predation, competition, and mortality, could explain more types of reproductive variability than r- and K-selection. Hickman (30) showed that all the reproductive variability observed among populations in the field could be due to developmental plasticity.

As a whole, the published life history data are moderately reliable as description, but are not reliable as tools for uncovering evolutionary causation. To what degree does this conclusion depend on the criteria used and the papers selected? I tried to select the best papers, which would make the conclusion conservative. The criteria arise naturally from the models being tested: criteria *a* to *d* were included to assay attempts to check assumptions and avoid circular reasoning; criterion *e*, to establish the statistical reliability of the data; and criterion *f*, to probe the degree of realism achieved. Additional criteria could have been used, but I would oppose the elimination of any of the six employed, with the possible exception of the requirement that degree of density-dependence be measured. That seems to have been asking too much. I doubt that adding criteria would change the conclusions.

How well do the data fit the accepted scheme? In about half the studies containing sufficient information, the organisms fit the accepted scheme ($n = 18$); in the other half, they did not ($n = 17$). Authors of a broad view (16, 95) were slightly more likely to perceive the accepted scheme than authors of a detailed study on intraspecific variability, but there are a number of counterexamples (24, 41). Studies fitting the scheme satisfied 1.5 of the 6 criteria, on average; those that did not satisfied 1.9. That slight difference in reliability is not significant. I am satisfied that neither the deterministic nor the stochastic models are empirically sufficient. Their predictions are not consistent with much of the evidence. We do not yet have a general and reliable theory of life history evolution, and the crux of the problem is: What will be an empirically sufficient set of parameters in which to couch the theory?

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CONTENTS