

A New View of Life-History Evolution

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## A new view of life-history evolution

Stephen C. Stearns

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In this paper I explore two lines of thought. First, do life-history tactics exist at the intra-specific level? Four arguments are examined: (1) biological constraints violate the assumptions of the Euler-Lotka equation; (2) experimental evidence on mosquito fish indicates that physiological problems can overwhelm the expected coadaptations of life-history traits; (3) the pattern of heritabilities of life-history traits indicates that they have not responded to the same selection forces; (4) authors of review articles perceive tactics more readily at higher taxonomic levels than within species. Tactics may not exist in the expected form.

Second, when might optimality models work, and why? (1) Some optimality models contain a hidden genetic component; (2) polygenic traits are not as tightly constrained as few-locus systems; and (3) the evolution of the developmental system should uncouple the phenotype from the constraints of the genetic mechanism.

Implicit in these thoughts is a more general point: training in quantitative genetics, development, and physiology is just as necessary for the study of life-history evolution as is training in demography and population genetics.

Finally, four new research programs are suggested as extensions and criticisms of the arguments raised here.

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В данной статье я развиваю мысль в двух направлениях. Во-первых, существует ли тактика жизненного цикла на интравидовом уровне? Проведены 4 аргумента: 1. биологическая напряженность нарушает взаимосвязи, описанные уравнением Эйлера-Лотки; 2. эксперименты, проведенные на гамбузии, показали, что физиологические проблемы могут перекрывать предполагаемые коадаптации онтогенеза; 3. характер наследственных особенностей онтогенеза показывает, что они не связаны с такими же направлениями отбора; 4. авторы обзорных статей чаще рассматривали тактические особенности на высших таксономических уровнях, чем внутри вида. Тактические особенности имеют неожиданную форму.

Во-вторых, когда должны действовать оптимальные модели и почему?

1. некоторые оптимальные модели имеют скрытый генетический компонент; 2. полигенные особенности не так сильно появляются, как малолучусные системы; и 3. эволюция развивающейся системы отключает фенотип от прессы генетического механизма.

Неясно выражено в этих рассуждениях более общее положение: привлечение данных по количественной генетике, развитию и физиологии также необходимы для изучения эволюции онтогенеза, как и исследования демографии и генетики популяции. В конце рассматриваются 4 новые исследовательские программы как продолжение и критика приводимых здесь аргументов.

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## 1. Introduction

In this paper I question the existence of life-history tactics as traditionally defined at the intraspecific level. Then I comment on some of the recent criticisms of optimality theory, and suggest why optimization may work under certain circumstances. While working through those problems, I realized that the general framework in which I view life-history evolution has changed over the last few years. Previously a background in demography and population genetics was sufficient. Now the subject has broadened, its focus has shifted, and re-education in development, physiology, quantitative genetics, and macroevolutionary theory is appropriate. Documenting that shift in general emphasis is a major, but largely implicit, goal of this paper.

I have addressed the suggestions of the symposium organizers, to “review and speculate on points of current interest” with the intent of answering such questions as: “Is the bridge between ‘theory’ and ‘reality’ crumbling? If so, is it serious? And if it is serious, can we do anything about it?” From my point of view, it is not that old bridges are crumbling – perhaps they never really existed – but that new bridges are being built into unfamiliar territory with foundations set on unexamined substrate. The situation is interesting, not perilous. I use the last section of the paper to suggest what we might do about it in the form of outlines of several research programs. In an Appendix, I provide an indexed entry to the life-history work published from 1975 through 1979.

## 2. Do life-history tactics exist?

A life-history tactic is “a set of coadapted traits designed, by natural selection, to solve particular ecological problems” (Stearns 1976: 4). On the surface, that is a plausible definition of what appears to be a real object that can be recognized by three characteristics: (a) coadaptation of traits achieved (b) by natural selection as the solution to (c) particular ecological problems. We have no difficulty defining natural selection (differential reproduction and survival correlated with heritably variable traits), but it is not so easy to specify how we are to recognize that several traits are coadapted among themselves, or what the ecological problem is or was. I shall approach these problems from four points of view: a mathematical model, an experiment I recently completed, some meditations on results from quantitative genetics, and a comment on the taxonomic levels at which trends are perceived.

### 2.1. The Euler-Lotka equation

The familiar Euler-Lotka equation, which can be written:

$$1 = \int_0^{\infty} e^{-rx} l_x b_x dx,$$

is seductive precisely because it compactly states the interrelations among age at maturity ( $\alpha$ ), age specific survival ( $l_x$ ) and fecundity ( $b_x$ ), age ( $x$ ) and one measure of fitness, population growth rate ( $r$ ). However, it is one thing to note that certain traits are mathematically interrelated in a plausible model, and quite another to assert that they are coadapted. The coadaptation of these traits is an assumption of this model, not a conclusion that can be drawn from it.

One implicit assumption of the Euler-Lotka model is that age at maturity, survival, and fecundity are not constrained by other factors and are free to coevolve under the influence of purely demographic forces. Whenever these traits show strong allometric relations with a lineage, as is the case in two primate taxa (Fig. 1: Leutenegger 1979), the ungulates and subungulates (Robbins and Robbins 1979), the salamanders (Kaplan and Salthe 1979), some frogs (Kuramoto 1978), and in other groups cited in those papers, that assumption does not hold because life-histories are evolving under developmental constraints. For example, in the entire order Procellariiformes (albatrosses, petrels, fulmars) the clutch size is one and the birds are morphologically “prepared” with one brood patch to incubate only a single egg (Ashmole 1971). A change in clutch size in any procellariiform would require concurrent changes in

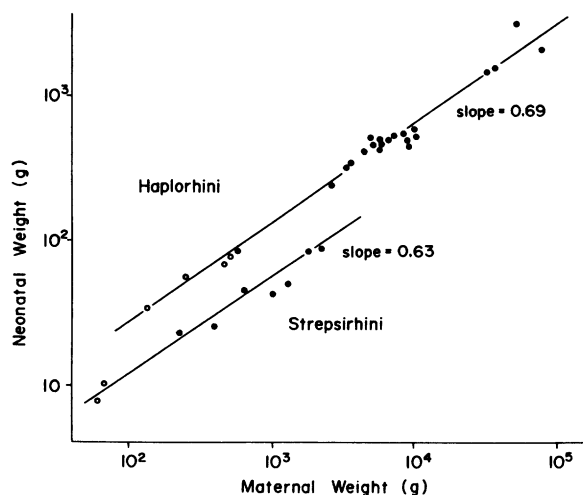


Fig. 1. Adapted from Leutenegger (1979) to illustrate allometric constraints on a life-history trait: birth weight in primates. The open circles indicate species with multiple births; solid circles indicate species with single births. The Strepsirhini include galagos, pottos, and lemurs; the Haplorhini include monkeys, baboons, apes, and man. In both lineages, birth weight is a tight function of maternal weight, with remarkably little variance. The largest deviation from expected birth weight is in man, the second point from the top right. Allometric constraints violate an implicit assumption of life-history theory: that life-history traits are free to evolve under purely demographic forces.

the developmental mechanisms that produce the brood patch. We should not be surprised if Euler-Lotka models make unsuccessful predictions of adaptive variations in life-history tactics within lineages, like the *Procellariiformes*, constrained by allometry and development. Inter-lineage comparisons may be more successful. This point shall become important in a different context later in the paper.

Individual life-history traits may also have stronger evolutionary interactions with physiological traits than with other life-history traits. This appears to be the case in comparisons of precocial and altricial birds (Ricklefs 1979), of cotton rats and wood rats (McClure and Randolph 1980), and in flatworms (Calow and Woollhead 1977, Woollhead and Calow 1979). Some of these interactions may be classed as costs of reproduction affecting parental survival. This class of physiological interactions does not violate the implicit assumption of the Euler-Lotka equation, but in fact provides the mechanical basis for understanding the coadaptations of reproductive effort, survival, interparity and longevity, the goal of a number of interacting models that incorporate the cost of reproduction into the Euler-Lotka equation (e.g., Goodman 1979, Michod 1979, Caswell 1980a, b, Bell 1980, Law 1979b, Charlesworth and Leon 1976, Pianka and Parker 1975, and many others – see references). However, many interactions of life-history traits with physiological traits do not involve the costs of reproduction; they constrain demographic traits but cannot be easily incorporated in demographic models. Examples are found in Ricklefs (1979), in McClure and Randolph (1980), and in the next section.

2.2. An experiment on intraspecific variation in life-history traits

I recently completed a series of experiments designed to shed light on what was causing microgeographic variation in the life-history traits of mosquito fish in Texas. The mosquito fish, *Gambusia affinis*, is a small, sexually dimorphic, poeciliid fish, primarily an inhabitant of fresh water, native to the Gulf Coast, Mississippi basin, and Atlantic lowlands of the United States and Mexico. Since 1905 it has been spread around the world for mosquito control. Males stop growing when they mature; females have indeterminate growth (Fig. 2). Fertilization is internal; females can retain viable sperm for several months; and young are born as yolkless,

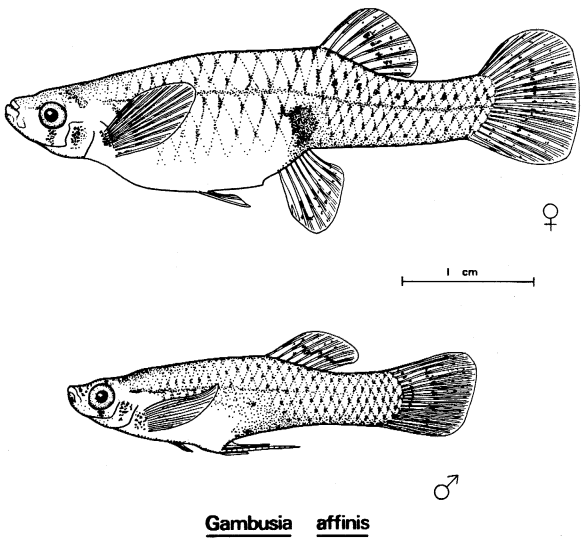


Fig. 2. Female and male mosquito fish, *Gambusia affinis*. Note the striking sexual dimorphism: the male's anal fin is modified into an intromittent organ, the gonopodium. Males stop growing when they mature; females do not. The flattened dorsal surface and upturned mouth are probably adaptations for feeding on insects trapped in the surface film.

swimming fry. Most populations studied have broad salinity and thermal tolerances (cf. Stearns and Sage 1980 for references).

In the field, I collected fish from a small fresh-water stream and from a brackish (10‰) estuary 200 m away. In both 1975 and 1976 the fish living in freshwater contained fewer, larger embryos than those living in brackish water, and had a slightly smaller ratio of reproductive to somatic biomass (Tab. 1). This is a classic life-history difference, and if accompanied by the appropriate differences in age at maturity and longevity, which I could not assess from the field data, it would fit neatly onto the tables published in Pianka (1970) and Stearns (1976) of the correlates of r- and K-selection.

These data fit at least three hypotheses which were not mutually exclusive: (1) the fish in brackish water did not differ genetically or ontogenetically from the fish in fresh water, but they were getting more food to eat; (2) the difference between the two populations had a genetic basis resulting from local adaptation; (3) the two populations were genetically identical, but the fish were developmentally sensitive to salinity, producing different phenotypes in different environments. The experi-

Tab. 1. Summary of field data: Comparisons of fresh and brackish populations of *Gambusia affinis* at Armand Bayou, Texas, in April, 1975 and 1976.

Trait	1975			1976		
	Fresh	Brackish	p	Fresh	Brackish	p
Mean number of young in 75 mg females	16.0	25.4	0.001	13.3	19.6	0.001
Dry wt of all embryos/dry wt of mother for 75 mg females	0.27	0.31	0.001	0.22	0.25	0.001
Mean weight (mg) of early-eyed eggs	1.34	1.16	0.001	1.20	1.03	0.001

ments reported below were designed to test the hypotheses of local adaptation (2) and developmental sensitivity (3); food levels were controlled in the experiments.

I brought live fish from both fresh and brackish water back to the laboratory, maintained them in the type of water in which they had been caught, and on the day a female gave birth I put half her brood into fresh water and the other half into brackish water. After one week, I again split the broods, putting half into fresh and half into brackish water. Then I combined the broods to get 20 fish per 19 liter aquarium; in any one aquarium the fish varied in age over a four day range. Thus there were 8 treatments defined by the origin of the parents and the salinity of the water in which the first week of life and the rest of life were spent: FFF, FFB, FBF, . . . , BBB. There were 1 to 4 replicates per treatment, and a total of 480 fish in the experiment. I weighed and measured all fish when they were 86 d old, and reared all surviving females to maturity.

The major result of this experiment, validated by subsequent experiments that demonstrated that the effect was not a laboratory artifact, was that no matter what their origin or early environment, these fish grew poorly and had low survival rates in fresh water (Stearns and Sage 1980). The freshwater population was physiologically maladapted to life in fresh water for osmoregulatory reasons, either because it was swamped by gene flow from brackish water or because it was the product of a recent colonization event (there was road construction around the stream in 1967 and in 1969). Thus the fish in freshwater in the field may have been producing fewer young and making smaller reproductive efforts because they had to divert energy into osmoregulation, violating the implicit Euler-Lotka as-

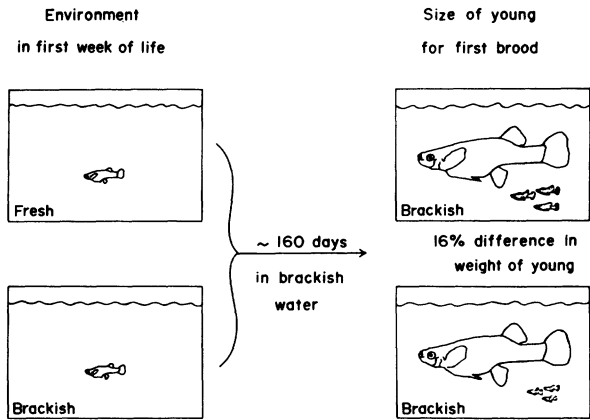


Fig. 3. *Gambusia* has a developmental sensitivity to early environment. No matter what environment their ancestors came from – fresh or brackish – fish that spent their first week of life in fresh water, but lived the rest of their lives in brackish water, gave birth about 160 d later to offspring that were 16% heavier than the offspring of fish who spent their first week of life in brackish water. This closely matches the difference in size of embryos in the field: 16–17% larger in fresh water.

sumption (Sect. 2.1.). However, that would not explain why they were producing larger offspring.

This brings us to the most intriguing result of this experiment. No matter what their parent’s origin, fish that spent the first week of their life in fresh water gave birth 160–170 d later to offspring that were 8–15% heavier than the offspring of females that had spent the first week of their life in brackish water (Tab. 2). Differences in birth weights were affected by early environment and by the order in which females matured within an aquarium, but not by whether the previous

Tab. 2. Dry weights of newborn fry.

A. Means				
Mother	Conditions experienced by Week 1	Rest of Life	n	Means ± 2 SE (mg)
Fresh	Fresh	Brackish	177	0.85±0.05
Fresh	Brackish	Brackish	175	0.79±0.04
Brackish	Fresh	Brackish	78	0.87±0.07
Brackish	Brackish	Brackish	97	0.76±0.04
B. Analysis of variance				
Source of Variation	Degrees of Freedom	Mean Square	F	Significance of F
Main Effects				
Mother's Origin	1	0.164	2.041	0.154
Week 1	1	1.431	17.847	0.001
Maturation order	8	0.354	4.414	0.001
Residual	516	0.080		
Total	526	0.085		

generation came from fresh or brackish water (Tab. 2B). Females that matured later had larger young. An analysis of the residuals revealed that the offspring of fish that had spent their first week of life in fresh water were 0.06 mg heavier than the grand mean of 0.82 mg, and that the offspring of fish that had spent the first week of their life in brackish water were 0.06 mg lighter. Recall that in the field, fish living in fresh water carry embryos that are 16–17% heavier than fish living in brackish water; this is precisely the direction and the magnitude (16%) of the difference of the *residuals* measured in the laboratory (Fig. 3). In contrast to the significant effect of early environment on weight of young, neither early environment ( $p = 0.67$ ) nor place of mother's origin ( $p = 0.385$ ) had a significant impact on fecundity (number of young corrected for weight of mother).

Whether the data on weight of young indicate the existence of a developmental "threshold" or represent some more continuous function of the environment remains to be seen. The nature of the physiological and developmental mechanisms necessary to produce the effect are under investigation. The relevant point for this discussion of life-history tactics is that growth and survival were influenced by osmoregulatory problems, that weight of young displayed a sensitivity to the mother's early environment that precisely matched the direction and magnitude of the difference observed in the field, and that fecundity did not respond as did weight of young.

For these reasons, I question the appropriateness of citing the differences observed in the field as evidence for the existence of life-history tactics, specifically as evidence for a trade-off between many, small young and a few, large young. Fecundity and size of young did not display sensitivity to the same factors in this experiment, nor were any significant differences in fecundity observed in the laboratory among fish reared in brackish water, suggesting that the differences seen in the field were a by-product of physiological stress.

One can still use the whole pattern as evidence for the existence of evolutionary tactics in which physiological and developmental traits interact with life-history traits. One cannot use this pattern as evidence for the existence of narrowly defined life-history tactics in which life-history traits interact among themselves more strongly than with any other traits.

### 2.3. Some implications of the quantitative genetics of life-history traits

Because some life-history traits – size of young, number of young, age and size at maturity, and fecundity – are economically important, they have been a central interest of animal and plant breeders. Because life-history traits are more strongly correlated with fitness than are many other traits, one expects their heritabilities to be relatively low, for directional selection on fitness will

have eliminated from the wild population much of the additive genetic variance of characters correlated with fitness. These expectations are in large part fulfilled (Lerner 1954, Nordskog 1977), especially when the experiments are done on recently founded stocks and not on organisms that have been in the laboratory for many generations (Dawson 1977).

Animal breeders are also interested in the genetic correlations among traits (the additive genetic component of the phenotypic covariances), for these will determine the rate of overall progress of selection for several traits at once. For example, if age at maturity and fecundity have a negative genetic correlation, then selection to increase fecundity in earlier-maturing organisms should be successful; if the correlation is positive, then any progress made in one trait will be at the expense of any progress that might be achieved in the other.

One could argue that the structure of the genome should have been moulded by natural selection to produce appropriate genetic correlations for the coadapted traits thought to make up tactics. Sets of traits with such genetic structure would then move smoothly as a unit under changes in selection pressure. To put it another way, if demographic tactics are real, and entire sets of characters coevolve to solve an ecological problem, and if the rankings of these characters are strongly concordant along a selection gradient, as was once suggested for the tactics tentatively identified as *r*- and *K*-selected (Pianka 1970), then to move smoothly along that selection gradient in a process of microgeographic local adaptation would require genetic correlations that mirrored the demographic tactics.

I can think of numerous *a priori* objections to this argument, but it is interesting to treat it as a working hypothesis and to ask for the verdict of the data. In chickens, age at maturity has a negative genetic correlation with fecundity and a positive genetic correlation with egg weight, and fecundity and egg weight are negatively correlated (Lerner 1954: 151). In other words, there does seem to be a genetic basis for a tactic of early maturity, high fecundity, and small young in this domestic strain. The same negative genetic correlation of age at maturity with fecundity is found in fruitflies (Robertson 1957), whereas there is no genetic correlation of egg size with egg number in domestic rainbow trout (Gall 1975). The verdict of the data is not unanimous, but it suggests a genetic correlation between age at maturity and fecundity.

Ambiguity enters the interpretation of such results on several levels. On the one hand, any character strongly correlated with fitness will have low heritability when first brought into the laboratory, and will display low genetic correlations with all other traits simply because it does not vary very much. In nature, the genetic correlations may have been strong immediately following a shift in selection pressure, but so long as selection is directional both the heritabilities and the genetic corre-

lations should be driven to low values. Thus weakly positive or negative genetic correlation coefficients tell us nothing about the forces that produced them (cf. Lewontin 1974). Strongly positive or strongly negative correlations imply high heritabilities inconsistent with strong correlations with fitness. In other words this technique gives us the genetic correlation of “uninteresting” traits, tells us nothing about the correlation of “interesting” traits, but at least the heritability results tell us which are the traits that do not correlate strongly with fitness.

On the other hand, recall that heritabilities are functions of the environments in which the traits are expressed. If one finds organisms in a laboratory population, some of which mature early and have many young, others of which mature late and have few young, and if the genetic correlations are strong and mirror the phenotypic correlations, one may very well be observing a trend that has nothing to do with life-history tactics in the field and everything to do with the fact that some genotypes are well adapted and others poorly adapted to the laboratory environment.

For both these reasons, genetic correlations will tell us little about the existence or nonexistence of sets of coadapted traits. However, if one trait has a low heritability and another has a high heritability, they are probably not coadapted, at least not within that population, because one has been under strong directional selection and the other has not. In *Drosophila serrata* (Birch et al. 1963), *D. pseudo-obscura* (Dobzhansky et al. 1964), poultry (Lerner 1954), and wild *Tribolium* (Dawson 1977) the heritability of fecundity is higher than the heritability of age at maturity. This result indicates that fecundity and age at maturity are not strongly coadapted within populations, and questions the reality of tactics as patterns that can be recognized within species.

#### 2.4. Implications of the taxonomic level at which tactics are perceived

People doing broad surveys of life-history traits across genera, families, even phyla (Tinkle et al. 1970, Pianka 1970, Cody 1971) have been more likely to perceive broader life-history “tactics” than people studying intraspecific variability (e.g., Stearns and Sage 1980, Birch et al. 1963, Dobzhansky et al. 1964, Lerner 1954, Dawson 1977, but see Leggett and Carscadden 1978). For example, it is much more likely that a worker will notice covariance among *two* traits, e.g., size of young and number of young, among populations of a single species, than it is that he will notice covariance among *three* traits, e.g., size of young, number of young, and age at maturity. Comparisons among species within a genus might detect covariance of three traits; comparisons of genera within a family, or of families within an order, might detect covariance among four traits, and so forth. Lack (1968: 9) noticed the same pattern in com-

menting on the relative power of comparisons made at various taxonomic levels:

“First, differences in breeding adaptations are easier to interpret between closely than distantly related species, because closely related species differ in relatively few ways, with one (or more) of which the differences in breeding biology are probably linked. On the other hand, in distantly related species a complex of associated adaptations may confuse interpretation. Unfortunately from this viewpoint, closely related species usually agree in their main breeding adaptations, so comparisons have to be made between higher taxonomic units, and it is not easy for this purpose to decide on the most suitable unit.” This pattern is not firmly established by a study in which taxonomic levels were rigidly controlled, but I think it will hold up under new results, and I want to examine its implications.

I see two processes generating the increase in the number of covarying life-history traits as one ascends the taxonomic hierarchy. One, allometrical constraints within lineages, is well-known and may not be controversial. As long as life-history traits are constrained by allometry within a lineage, intra-lineage comparisons will not reveal the broader tactics recognizable at higher levels. Only comparisons within a large sample of lineages will reveal demographic forces operating relatively unconstrained by allometry, and then only if life-history constraints differ considerably among lineages. The other process, punctuated equilibria, has no unequivocal empirical support and calls into question the gradualism and microevolutionary emphasis of the neo-Darwinian synthesis, yet it neatly explains the pattern.

Suppose, following Eldredge and Gould (1972), that all adaptive change takes place rapidly during the genetic revolutions that characterize speciation events. Further suppose that once formed, species consist of stable, coadapted gene complexes with strong resistance to change (Mayr 1963). Then major reorganizations of relationships of whole sets of traits are not likely to occur during the lifetime of a species, nor are major trends, tactics, likely to be perceived with intraspecific comparisons. Speciation events become the source of evolutionary novelty, extinction events become the major agent of natural selection, and we expect to see major patterns existing only above the species level, which is where we find them, and not within species, where we in fact do not find them.

This argument is highly speculative. One could extend it by stating that the reason major changes occur in speciation events is this: Only in small peripheral populations racked by genetic drift and strong selection pressures can one fix the rare functional recombinants – regulatory mutants – that produce major ontogenetic shifts. If this argument is correct, it means that the kinds of detailed intraspecific studies that I called for in 1976 could be irrelevant, and that traditionally designed selection experiments will tell us nothing. If punctuated

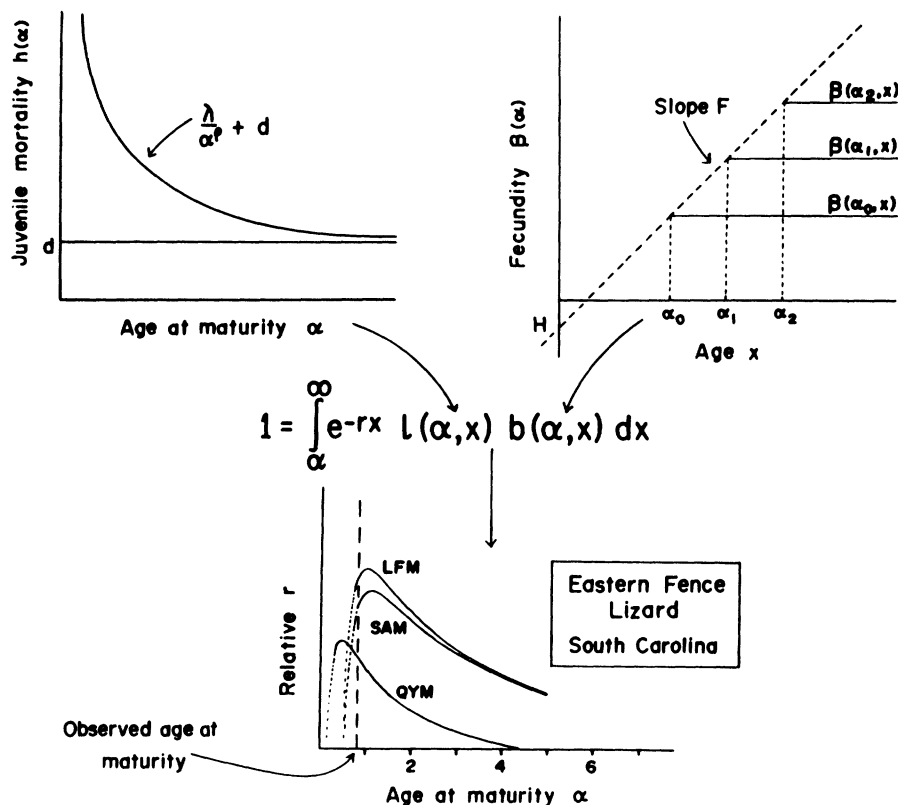


Fig. 4. These are the assumptions behind an optimality model that is troublesome because it seems to work. We tried to predict optimal age at maturity. Our first assumption was that organisms that delay maturity produced offspring that have lower juvenile mortality rates; this is represented by the declining curve in the graph on the upper left. Our second assumption was that organisms that delay maturity gain fecundity linearly; this is represented by the family of straight lines depicted in the graph on the upper right. We embedded these relationships in the Euler-Lotka equation (center), thus making the assumptions of stable age distribution and exponential population growth, then solved for the age at maturity that maximized population growth rate. The bottom graph shows the relationship of age at maturity and population growth rate for the South Carolina population of Eastern Fence Lizards Studied by Tinkle and Ballinger (1972). QYM indicates the Quality-of-Young-Model, which incorporates only the first assumption. LFM indicates the Linear-Fecundity-Model, which incorporates only the second assumption. SAM indicates the Salamander-Model, which incorporates both assumptions. The dashed line indicates the age at maturity that Tinkle and Ballinger observed in the field.

equilibria and interspecific selection generate the observed patterns of life-history tactics, then the appropriate experimental model is a laboratory speciation experiment of the sort recently carried out by Templeton (1979), but modified so that different lineages encounter different demographic demands.

To summarize, tactics may or may not exist. At this point it appears less likely that they can be recognized within species than among species or even higher taxa.

### 3. When might optimality models work well?

There has recently been a flurry of criticism (Stearns 1976, Oster and Wilson 1978, Lewontin 1979, Levin 1980) and defense (Maynard Smith 1978, McCleery 1978) of optimality models. One major criticism is that genetic mechanisms may imply a genetic equilibrium that does not match the optimum predicted for the

phenotype. I take these criticisms seriously. Because I do, some success I have recently had with an optimality model is troublesome. Let me first outline the model and the test whose successful result troubles me, then share with you three thoughts on why the model may have "worked."

#### 3.1. An optimality model for delayed maturity

There are four or five hypotheses in the literature on why delayed maturity evolves (see papers coded B1 in the References). Richard Crandall, a physicist at Reed College, and I chose to work with the two we found most plausible: (a) that organisms that delay maturity produce higher-quality offspring, offspring that have higher survival to maturity, and (b) that organisms that delay maturity gain fecundity. We built models that started with the Euler-Lotka equation and that assumed either the first hypothesis, the second hypothesis, or



both. In other words, we assumed a stable age distribution, an exponentially expanding population, that  $r$  defined fitness, and that optimizing  $r$  was an appropriate procedure. We then estimated some parameters of the models from data on nine populations drawn from five species of lizards and salamanders. There was some arbitrariness in the estimation procedure, but I do not think it was a circular procedure, and we used the same estimation procedure for all species. We made nine predictions of the ages at which these lizards and salamanders should mature (Fig. 4); the correlation of the predicted age at maturity with the observed age at maturity was 0.93 for the quality-of-young hypothesis, 0.90 for the fecundity-gain hypothesis, and 0.96 for the model combining both hypotheses (Stearns and Crandall 1980). These are the first quantitative, rather than relative, predictions of age at maturity, and they were remarkably accurate.

I do not claim that, because these predictions were successful, we now understand why these salamanders and lizards delay maturity. I do think this line of work looks promising. However, I am troubled by the success of the predictions: if these species are constrained to evolve according to the genetic mechanism, how could they have optimized age at maturity, especially in a model that ignores genetics? For the purpose of this discussion, let us grant only that this test was successful enough to make it worth our time to worry about how any such model would be successful.

### 3.2. Are some life-history models also automatically genetical models?

We used the Euler-Lotka equation for phenotypes:

$$1 = \int_{\alpha}^{\infty} e^{-r x} l(\alpha, x) b(\alpha, x) dx.$$

This is the same equation Fisher (1930) used to define the fitness an accele substituted at a locus with  $m$ , the malthusian parameter, substituted for  $r$ :

$$1 = \int_{\alpha}^{\infty} e^{-r x} l(x) b(x) dx.$$

Although the formal similarity is exact, the differences in interpretation are profound. In the first version,  $r$  is population growth rate, and  $l$  and  $b$  are the actually observed values of the expectations of survival and fecundity of *organisms*. In the second version,  $m$  is the rate at which a new allele grows in a population, and all the parameters represent the marginal effect on survival, fecundity, and age at maturity of the new *allele* in combination with all the various genotypes produced in the population.

I now claim that the model may have been successful because it was a genetical model all along, and that we were looking at the marginal effect of a modifier introduced to the population on the assumption that modifi-

cations of age at maturity had certain consequences for fecundity and juvenile survival. Note that the salamander populations in particular are probably fairly stable in the long run, so that they could in no sense be considered  $r$ -selected. However, even in a stable population a new mutant can grow exponentially while displacing the other alleles at its locus. Thus if we view this process as occurring at the level of the gene, then this selection is  $m$ -selection, not  $r$ -selection, and selection for exponential gene growth can produce phenotypes that were previously rationalized as  $K$ -selected, i.e., delayed maturity.

These comments do not get around all the criticisms of optimality, especially not those in Oster and Wilson (1978), which are deep and general. They do emphasize that work on the interface of genetics and life-history evolution is crucial (e.g., Charlesworth and Williamson 1975, Michod 1979, others coded as A3 in the References). We are left with such problems as these: (a) linkage disequilibrium implies a genetic equilibrium that may not match the phenotypic optimum (Moran 1964), (b) if the heterozygotes are most fit, then independent assortment will destroy the optimal phenotypes every generation (Lewontin 1979), and (c) frequency dependent selection may favor just such heterozygotes (Levin 1980).

### 3.3. Are the constraints relaxed for polygenic traits?

The first point I wish to raise is that we might expect some of these criticisms to have less force if the trait in question is determined by many genes with small, additive effects. If a trait is determined by 20 or 30 genes scattered over 10 to 20 chromosomes, then linkage effects are not likely to be significant. Moreover, intermediate phenotypes can be produced by combinations of homozygotes at different loci, as well as by heterozygotes at all loci (e.g.,  $\frac{+}{+} \frac{+}{+} \frac{+}{+} \frac{+}{+}$  can produce the same phenotypic effect as  $\frac{+}{+} \frac{+}{+} \frac{+}{+} \frac{+}{+}$ ). Thus a polygenically determined trait can be stably fixed at an intermediate value by homozygotes. This answer does not get around the criticism that epistasis and pleiotropy make it unlikely that a polygenic system *can* be optimized for one trait at a time. The next section attempts a reply to this point.

### 3.4. Can we expect canalization for the components of fitness?

A canalized trait is developmentally buffered in the sense that the phenotype produced in different environments or in organisms with different genotypes varies relatively little. To the degree that a trait is canalized it will develop into a phenotype that is not affected by genetic substitutions. If a certain phenotype is optimal, then directional selection for canalization of the trait should operate to eventually produce a reorganization of the epigenetic machinery that makes the phenotype

independent, to a certain degree, of the genotype. This will only work for a given optimal phenotype if the optimum is not continually shifting around in space and time. Given the heterogeneous and fluctuating nature of environments, that is a strong objection. However, let us suppose that canalization does evolve within a lineage, perhaps during a long period of stable conditions, and that the canalized traits are life-history traits. This should occur when there is selection for the mean value, rather than for the variance, of a trait (cf. Slatkin 1974, Gillespie 1977), unless we are to postulate canalization of the variance itself, which would seem to require subtle but not unthinkable (cf. Wourms 1972) developmental mechanisms.

Once a trait is canalized, then modifier genes acting on the developmental system (and arising at loci not originally involved in the canalization event) should produce gradual shifts in the phenotypic mean value towards an optimum without running into all the difficulties raised for uncanalized traits determined by one or a few loci. In other words, I suggest that if we consider polygenically determined traits under complex developmental control – and these are the kinds of traits that are usually ecologically important – we find that some of the criticisms of optimality models lose their force. In fact, many of the arguments against optimality can be taken as arguments for the very canalization that might permit optimal phenotypes to be realized. However, not all such criticisms have been blunted (cf. Oster and Wilson 1978) and Lewontin's (1979) dictum that the "price of optimality arguments is eternal vigilance" remains in force.

### 3.5. Age at maturity: a special case

Recall that this discussion of optimality models arose because I found surprising the success of some predictions concerning a particular trait, age at maturity, that were based on just such models. One of the arguments I made is that ontogenetic processes, specifically canalization, may free traits from genetic constraints and permit them to evolve towards optimal phenotypes. However, age at maturity appears to be a key trait that controls several major ontogenetic pathways involving size and shape (Gould 1977, Alberch et al. 1979). In other words, changes in age at maturity have major implications for other important traits, and those implications have a mechanical basis in ontogenetic processes. Thus the level of focus has shifted from genetics to epigenetics, but the original criticisms of optimality may hold just as strongly in altered form: developmental mechanisms may imply developmental equilibria that do not match the phenotypes predicted by life-history models that ignore those developmental mechanisms.

### 3.6. Summary of comments on optimality models

My comments on optimization can be summarized in

four points: (a) some optimality models may contain an unsuspected genetic component; (b) polygenic traits do not evolve under the genetic constraints postulated to hold phenotypes away from the optimum value in few-locus systems; and (c) canalization, and the evolution of the developmental system in general, should uncouple the phenotype from many of the genetic constraints suggested by the kind of thinking that visualizes one gene producing one character. However, (d) by bringing in the developmental system, I have raised the possibility that developmental, rather than genetic, mechanisms keep phenotypes from attaining optimum points. That possibility needs exploration.

These are merely suggestions, and they imply *not* comfortable acceptance of optimality arguments but careful work to discover whether these counter-arguments have any force.

## 4. Some open problems for research

The remainder of this paper is devoted to a list of some research problems suggested both by the topics just discussed and by a look at the recent literature. The list is of course not exhaustive and represents my personal bias; it does articulate some questions whose answers I currently want to know.

### 4.1. Is the perception of a tactic a function of the taxonomic units used?

If most evolutionary change occurs during speciation events, if intraspecific differentiation is relatively unimportant, and if allometric constraints are stronger within lineages than between lineages, then one expects to see tactics most clearly in comparisons of genera, families, or orders. It would be extremely interesting to take that as a working hypothesis, then test it by carefully observing (with appropriate statistical procedures, such as factor analysis) the clustering of traits in phenotype space when the unit of observation was, first, individual organisms, then populations, then subspecies, then species, then genera, then families. The amount of work implied is enormous, and it would be wise to do it on a very well-studied lineage to minimize duplications of effort. If one found stronger clustering at higher taxonomic levels, the *existence* of the trend would be confirmed, but the reasons for the trend would remain controversial.

### 4.2. Does polygenic determination in fact avoid some of the optimality criticisms?

We need a careful analytical dissection of the properties of three different kinds of models for the evolution of the same traits: one-locus/two alleles, polygenic, and optimality. The ideal analysis would be general enough so that we could state with some assurance that certain

general types of genetic determination of traits do, or do not, keep the phenotype from attaining an optimum value.

#### **4.3. What is the content of a new specialty, developmental evolutionary ecology?**

There is an evolutionary tension between phenotypic plasticity and canalization, and we must understand why some traits are plastic and others are not in certain lineages and in certain habitats. These problems require solution before we can successfully attack the general problem of evolutionary ecology: how can we predict the direction and magnitude of changes in phenotypic traits when specified changes are made in the environment? Gould (1977) and Alberch et al. (1979) have recently published intriguing suggestions on the evolutionary significance of relative shifts in rates of growth and maturation. Other hints come from sources like Levins (1968), from the extensive work on phenotypic plasticity in plants (e.g. Bradshaw 1965), from Wourms (1972), from observations on the developmental sensitivity to early environment in mosquito fish (Sect. 2.2 above), from Waddington (1978) and from Lande (1979). Just as canalization uncouples the phenotype from the constraints of the genetic mechanism, developmental plasticity uncouples the gene pool from the short-term selection pressures imposed by spatial and temporal heterogeneity. When are these uncouplings advantageous, and when are they not?

#### **4.4. To what extent does the evolution of demography constrain the evolution of behavior?**

In a finite population, the particular details of an age distribution set limits on the possible social interactions. For example, in a set of small groups constructed by random sampling of a large, exponentially growing population, parent-offspring, sib-sib, and cousin-cousin interactions are likely to predominate. Is a similar set of small groups drawn from a stationary population, grandchild-grandparent interactions are more likely than in the first set. If the limits on group size are strongly constrained by the productivity of food resources, and if life-history traits evolve more slowly than behavioral traits (or if they are allometrically constrained within a lineage), then demography constrains the evolution of behavior.

Few seem to be working in this area, but the questions are ripe for attack. Cohen's (1971) lucid book on stochastic models of monkey troops suggests a way to represent group size dynamics and distributions. Leutenegger (1979) suggests some of the allometric constraints on primates. The life-history models used must be rich enough to represent the differing mortalities and mating probabilities of both sexes. The behavioral models must have convenient connections to

the life-history models, so that the costs and benefits of alternative behavioral acts are mirrored in survival and fecundity schedules. The objects of the exploration include these: Does the evolution of certain life-histories entirely rule out certain classes of behavioral interactions? If so, what are the consequences, i.e., must compensating adaptations evolve? Can behavioral adaptations compensate for allometric constraints? If so, how? Which combinations of life-history traits, evolved as adaptations to certain environmental conditions, raise the probability that a behavioral interaction will be with a close relative? Can we combine Cohen's (1971) models of group dynamics (or their successors), Hamilton's (1972) models of inclusive fitness (or their successors), and models of life-history evolution to map out the probabilities of altruism and local mate competition in a phase space defined by group size and demography?

Two examples may strengthen the case for pursuing this research program. Parent-offspring conflict only occurs in iteroparous organisms, and it may explain why some organisms intermittently skip reproduction. This offers an alternative to several recently published explanations (Bull and Shine 1979, Ross 1979, Waller 1979, Downhower and Brown 1975, Thibault and Schultz 1978). In an unpredictable environment selection may (we do not yet know this) favor reduced reproductive efforts, increased longevity, and a longer reproductive life span, essentially because such a life-history permits the organism to sample many environments in time. It could evolve for the same reasons that sex may have evolved: to scatter offspring (genes) among many situations (genotypes) to increase the likelihood that a subset of the offspring (genes) produced will encounter exceptionally good conditions (genotypes). Such environments, unpredictable from season to season and from generation to generation, are precisely the environments that favor having a few old animals around who had experienced and learned from rare catastrophes long ago. Stuart Altmann has called this the "grandmother effect" (pers. comm.). Is this a case in which life-history adaptation and behavioral adaptation interact to promote the evolution of increased longevity and reduced reproductive effort?

Clearly these questions need precise mathematical formulation. They only hint at the richness of the unexplored interface between life-history evolution and sociobiology.

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Appendix

From 1975 through 1979, there were 182 papers published (in my sample – see caption to Fig. A1). In the previous history of the field (1760–1975), 135 papers had been published. The publication rate is no longer nearly as variable as it was from 1960–1974 (Fig. A1); it appears to have entered steady exponential growth, with 52 papers published in 1979: 1 per week. At this rate, the number of papers published will be 88 in 1985 and 192 in 1990 [ $\ln(\text{papers/year}) = 0.58 + 0.156(\text{year}-1959)$ , by least-squares]. Limits set by the number of workers entering the field will probably keep the actual figures below those projections.

Two comparisons place these comments in context. Price (1963) estimated the long term doubling time of all scientific publications at 10 to 14 years, and Schoener (1974) estimated the doubling time of publications on resource partitioning in communities at 2.8 years, or 4 times the overall rate. In the life-history work represented by my 1975–1979 sample, the doubling time is 4.7 years (exponential growth rate = 0.15/year), slower than the growth of resource partitioning studies from 1959 to 1974, but still two to three times the rate for science as a whole.

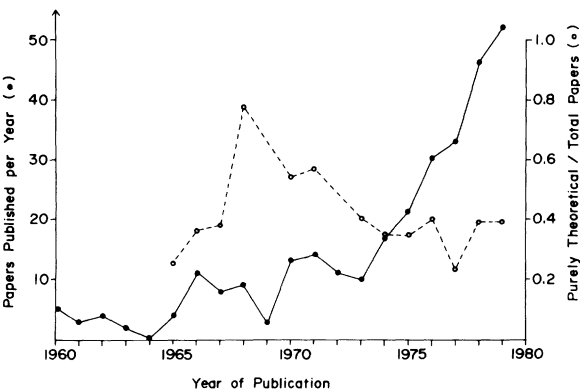


Fig. A1. Papers published per year, and the percentage of papers published that were purely theoretical, in life-history work from 1960 through 1979. The sample includes papers referenced in Stearns (1976, 1977), and papers published from 1975 through 1979 in *American Journal of Botany*, *American Naturalist*, *Bioscience*, *Biological Bulletin*, *Biological Reviews*, *Canadian Journal of Zoology*, *Copeia*, *Ecology*, *Evolution*, *Genetics*, *Journal of Animal Ecology*, *Journal of Experimental Marine Biology*, *Journal of the Fisheries Research Board of Canada*, *Journal of Theoretical Biology*, *Marine Biology*, *Nature*, *Oecologia*, *Oikos*, *Physiological Zoology*, *Proceedings of the National Academy of Science, USA*, *Quarterly Review of Biology*, *Science*, *Theoretical Population Biology*. Because of some late additions to the references, the figures given here may not correspond exactly with the References. Moreover, the decision as to what does, and what does not, constitute a paper on life-histories inevitably reflects my personal bias. However, the trends shown should be robust to increased sample size. The field is growing exponentially at 15% per year, and the proportion of all papers that are purely theoretical seems to be stabilizing at about 30%.

Tab. A1. Distribution of life-history work across subfields.

	No. of papers 1975–80
A. Interfaces with other disciplines	
1. Physiology: Cost of reproduction, reproductive effort	39
2. Behavior	1
3. Genetics	13
4. Development: Developmental plasticity, canalization	15
5. Management: Fisheries, Agriculture	4
B. Major theoretical questions (why or why not, in each case)	
1. Why delay maturity?	17
2. Why reduce reproductive effort? (Clutch size)	10
3. Why decrease lifespan?	1
4. Why reproduce more than once?	7
5. Why reproduce infrequently?	5
6. Why produce smaller offspring?	6
C. Special issues	
1. Tactics, r & K-selection	47
2. Fitness, optimality	22
3. Design constraints: allometry	11
4. Populations not in stable age distribution	10
5. The use and abuse of the comparative method	14

The proportion of purely theoretical papers rose to a peak in 1968 (Fig. A1: 78%), then declined to about 30% in the late 1970's. Only in 1970–1972 did the cumulative total of all purely theoretical papers published in the field equal or exceed the cumulative total of empirical papers and papers combining data and theory. By 1979, the cumulative total of theoretical papers was 35% of all papers, and should soon reach 30% if current trends continue. Thus the field seems to be in healthy balance. My previous comments (Stearns 1976) – to the effect that the field had too much theory and not enough data – resulted from an historical view that was too local. Moreover, I cannot take any credit for the change because the trend was reversed before my paper was published.

A brief examination of the distribution of papers classified by journal and by subject matter suggests two points: We may need a new journal, and some interesting questions have been neglected. For 1975–1979, the leading life-history journals were *American Naturalist* (49 articles), *Ecology* (24), *Oecologia* (20), *Evolution* (16), *Journal of Theoretical Biology* (8), *Theoretical Population Biology* (7), *Genetics* (7), and *Journal of Animal Ecology* (7), with 44 other articles distributed among 16 journals. The exponential growth of the field may justify the creation of a new *Journal of Life History Evolution*. One effect of that move would be to provide a single forum for both theoretical and empirical papers on life-history evolution; a by-product would be the

reduction of the publication queues at *American Naturalist*, *Ecology*, *Oecologia*, and *Evolution*.

The second point is that the distribution of life-history studies by subject matter (Tab. A1) is uneven. The neglected areas are *not* ones in which all the problems have been solved. Three times as much work has been done on the interface with physiology as has been done on the interfaces with genetics and development, and very little has been done on the interface with behavior or applied problems. Further, for convenience, one can define a short list of paradigmatic life-history problems by noting that the "ideal" organism matures immediately, produces an infinite number of offspring, lives forever, reproduces frequently, and has very large offspring, then asking why real organisms are not like that. Not all these questions have been equally attractive: there have been more papers on delaying maturity and on reducing reproductive effort than on lengthening life, reproducing less frequently, or producing smaller young. These issues need more attention. The dominant issue in the field is the evolution of reproductive tactics, closely followed by work on reproductive effort and the cost of reproduction, then by discussions of fitness definitions and optimality. To aid the reader in entering the literature, I have coded the references by the major issues addressed in each paper, according to the subject headings in Tab. A1 (cf. References).

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