

THE EVOLUTION OF LIFE HISTORIES

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THE EVOLUTION OF LIFE HISTORIES

Theory and Analysis

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For Daphne, Graham, and Robin

He that would seriously set upon the search for truth ought, in the first place, to prepare his mind with a love of it. For he that loves it not, will not take much pains to get it; nor be much concerned when he misses it. There is nobody in the commonwealth of learning who does not profess himself a lover of truth; and there is not a rational creature that would not take it amiss to be thought otherwise of. And yet, for all this, one may truly say, there are very few lovers of truth for truth's sake, even among those who persuade themselves that they are so. How a man may know whether he be so in earnest is worth enquiry: and I think that there is one unerring mark of it, viz, the not entertaining any proposition with greater assurance than the proofs it is built upon will warrant. Whoever goes beyond this measure of assent, it is plain, receives not truth in the love of it; loves not truth for truth's sake, but for some other by-end.

Locke

Essay Concerning Human Understanding (1691)

Preface

There are many different types of organisms in the world: they differ in size, physiology, appearance, and life history. The challenge for evolutionary biology is to explain how such diversity arises. This book is concerned with the diversity of life histories and in particular with the ways in which variation can be analyzed and predicted. The central thesis is that natural selection is the principle underlying force molding life history variation. This is not to say that organisms are perfectly adapted to their environments—only that this assumption will generate predictions that are acceptably close in most instances. This book is both an exposition of ways in which to view the world and an account of what we have learned about the evolution of life histories.

Chapter 1 examines two different approaches to analysis, the genetic approach and the optimization approach. Though genetic aspects are discussed throughout the book the principal method of analysis is optimization. The second half of chapter 1 discusses the broad scope of constraints within which life histories can vary. Though much can be achieved without explicit recourse to genetic argument, a proper understanding of the evolution of life histories necessitates an appreciation of the implicit genetic assumptions. These are discussed in chapter 2. Chapter 3 presents the general framework of life history theory, primarily the concept of fitness and trade-offs. The mathematical tools by which predictions can be made and tested are described in chapter 4. Fundamental to life history theory is the characteristic equation that describes how the age schedules of birth and death determine the rate of increase. Equally important is the hypothesis that reproduction carries a cost in terms of survival and/or future reproduction. Factors affecting the age schedule of birth and death are described in chapter 5 and costs of reproduction in chapter 6. Chapters 7 through 10 each cover a particular aspect of the life history: age and size at maturity, reproductive effort, clutch size, offspring size. These categories do not exhaust the possibilities but do represent the major components of a life history.

Three topics not covered in depth are senescence, comparative methods, and parental care. Organisms in the wild do not generally live long enough to grow old, and thus, though the topic is of great interest with respect to the evolution of trade-offs, it is not particularly relevant to the analysis of variation in nature. (It is indeed possible that evolution has acted to post-

pone senescence beyond the age normally reached in the wild state, but this makes it of historical rather than topical interest in the analysis of variation in the wild.) An exhaustive coverage of the topic is given by Rose (1991). Variation within a taxon may represent independent evolutionary events or be the result of a single event in the common ancestor. The statistical problems introduced by this possibility are noted and addressed in particular instances in this book but the reader is referred to the recent review by Harvey and Pagel (1991) for a detailed account of the comparative method. The evolution of parental care is examined in several sections where particular aspects are relevant but a full account is beyond the scope of the present book. A thorough survey of this topic is given by Clutton-Brock (1991).

In selecting analyses I have concentrated on those theoretical developments that have been tested experimentally. Mathematical analysis is an important component of life history theory and analysis, and as a consequence this book contains numerous equations. I have attempted to ease the burden of equations by providing, in addition, both verbal and pictorial arguments. Covering a large number of papers I have not been able to follow the symbolism of each individual paper. Rather than use numerous greek symbols for constants I have used c subscripted appropriately to distinguish it from other constants within an equation; in some cases specific symbols have been used for particular values where I wish to emphasize their importance or where they have a conventional symbol.

This book would not have been possible without the continuing support and encouragement of my wife and colleague, Dr. Daphne Fairbairn. I should also like to thank Dr. Greg Payne for suggesting that I attempt this enterprise. Sharon David provided invaluable logistical support, and the following colleagues patiently read and commented on various chapters: Drs. D. Berrigan, M. Bradford, E. Charnov, J. Gittleman, R. Huey, I. McLaren, L. Mueller, J. Myers, D. Reznick, B. Sinervo, J. Smith, and S. Stearns.

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Life History Variation: A First Look

The natural world is composed of a vast array of organisms displaying an enormous diversity of life histories. Plants and animals show profound variation in all aspects of their life histories: age at maturity, age-specific fecundity, survival rate, size at birth, etc. This variation is evident at both the inter- and intraspecific levels. For example, at the interspecific level, species of flatfish range in size from 2-cm long tropical species that reproduce within their first year of life to behemoths such as the Pacific halibut (*Hippoglossus hippoglossus*) which exceed 200 cm and take over 10 years to mature. Though the range in variation within a species is not as dramatic as between species, it is still impressive, as illustrated by variation in the flatfish, *Hippoglossoides platessoides*. In this species maturation occurs at age 3 years at a length of 20 cm in populations off the coast of Scotland while the same species requires 15 years to reach maturity at a length of 40 cm on the Grand Banks of Newfoundland. Longevity and maximum size are equally different in the two populations, Scottish fish reaching a maximum length of 25 cm and an age of 6 years, compared to 60 cm and 20+ years on the Grand Banks (Bagenal 1955a,b; Pitt 1966; Roff 1982). Similar observations on variation in life history characteristics could be made in most taxa. But though the diversity of life histories is readily apparent, attempts to understand its origin and maintenance are still in their infancy. The evolution of diversity in life histories is the subject of this book.

The basic hypothesis underlying most analyses of the evolution of life history traits is that variation is constrained in large measure by trade-offs between traits. These trade-offs can be defined and the evolution of the traits can be predicted either by a genetic model or by one which assumes that selection maximizes some measurable metric that defines fitness. The latter approach, frequently referred to as the optimality approach, has been much used in the last three decades and has, or so I shall attempt to

demonstrate, been highly successful in advancing our understanding of the observed patterns of life history variation. Evolution cannot proceed without genetic variation, and thus an important topic of study is the genetic basis of life history traits. The incorporation of genetic models into life history analysis is still in its infancy and present approaches are not entirely satisfactory. The elements of genetic modeling are described in chapter 2, and the theoretical bases of the two approaches in chapter 3. Thereafter, I concentrate upon the optimality approach, discussing, where appropriate or data permit, implications of genetic considerations. Chapter 4 provides a review of the mathematical tools appropriate for the analysis of life history variation, and the remainder of the book uses these tools and the general framework elucidated in chapter 3 to analyze the evolution of life history traits.

The primary goal of any organism is to reproduce. A central aim of life history analysis is thus the understanding of how the age schedule of reproduction evolves. An important component in this evolution is the age schedule of mortality since this both shapes and is shaped by the age-specific expenditure of reproductive effort. Chapter 5 looks at how these two age-specific functions are described and the general factors that should be taken into consideration in an analysis of how they vary. Chapter 6 expands on the themes introduced in chapter 5, dealing in depth with the cost of reproduction with respect to both survival and fecundity.

In the life of any organism the first "decision" that it must make with respect to reproduction is when to start reproducing. The age at first reproduction is therefore a convenient starting place for analysis (chapter 7). Maturity may involve little commitment by the individual, but in others the decision may profoundly influence future alternatives. Pterygote insects, for example, essentially cease to grow upon eclosion into the adult form (there are no more molts and the only growth that can occur is a relatively small change in weight); therefore, the commitment to become mature may limit future possible gains in fecundity or male attractiveness that accrue by virtue of increased size. On the other hand, indeterminate growers such as most fish species can mature and divert just a small fraction of energy into reproduction and hence not sacrifice significant future growth. This brings us to the second aspect of reproduction, age-specific reproductive effort, a topic dealt with in chapter 8. For females this will typically mean the amount of energy invested directly into offspring in terms of biomass and perhaps parental care, while for males it is the amount of energy invested into securing a mate plus, if relevant, the amount invested in parental care. Reproductive effort is clearly quantitative: an organism can expend very little or so much as to cause death after reproduction. Demographically, reproductive effort can be divided into two functional relationships: that between reproductive effort and survival and that be-

tween reproductive effort and number of offspring. Reproductive effort can be treated as a fairly abstract quantity, but operationally it must be translated into the number of offspring produced at each age. These offspring may be produced in one or several clutches. Increases in clutch size represent increased reproductive effort which may or may not have significant effects on survival and future reproduction. As a consequence of these impacts on demography clutch size will evolve: this is the subject of chapter 9. The same reproductive effort can be divided in a variety of ways, one of the most important of which is the division between the number and size of propagules. Small propagules permit an increased number but their mortality and time to maturity may be increased. Further, the optimal combination may vary with both the environment and the conditions of the mother. Chapter 10 completes the life cycle by examining the evolution of propagule size.

In this chapter I present a brief overview of the mathematical analysis of life history variation (a discussion expanded upon in chapters 2–4) and then a brief review of constraints, specific examples of which are discussed in greater detail elsewhere in the book when describing the analysis of particular life histories.

1.1. Mathematical Analysis of Life History Variation

Mathematical analysis is a primary tool in the study of the pattern and evolution of life histories. This is to most population biologists now a self-evident fact; but the use of mathematics in ecological investigations has had a much rockier road than its use in genetic analysis, and its general acceptance as an important tool dates only from the 1960s. Kingsland (1985) provides an excellent historical survey of the rise of mathematical approaches in ecology from the work of Lotka in the 1920s to the studies of MacArthur up to 1970. The importance of the mathematical approach to the understanding of genetic variation is amply illustrated by Provine's review of the history of population genetics (Provine 1971) and by the biographies of three of the most influential geneticists of this century: Fisher (Box 1978), Haldane (Clark 1984), and Wright (Provine 1986).

Even by the latter half of the 1940s mathematical thinking had still not made a significant impact on ecological theory; Allee et al. (1949, p. 271) observed that "theoretical population ecology has not advanced to a great degree in terms of its impact on ecological thinking." An early antipathy to the use of mathematical analysis may account in part for the delay in the merging of the ecological and evolutionary perspectives in what is now commonly known as "life history analysis." An influential factor encouraging the use of mathematical investigation into life history variation was

Lamont Cole's 1954 paper, "The Population Consequences of Life History Phenomena," which set out the basic mathematical framework by which the consequences of variation in life history traits can be analyzed. Cole's paper ushered in an era of research predicated on the integration of mathematics and biology in the study of the evolution of life history patterns. The success of this approach can be gauged from the enormous increase in publications on life history evolution: citations for life history studies for the years 1960 to 1980 indicate a doubling time of 4.7 years, a rate that is two to three times the rate for science as a whole (Stearns 1980).

In his review, Cole analyzed how changes in demographic attributes, such as the age at first reproduction, influenced the rate of increase of a population. Except for citations of its historical importance, Cole's paper seems to have gained widespread notice because of an apparent paradox with respect to the value of semelparity versus iteroparity: "*For an annual species, the absolute gain in intrinsic population growth which could be achieved by changing to the perennial reproductive habit would be exactly equivalent to adding one individual to the average litter size*" (Cole, 1954, p. 118, Cole's italics). The resolution to this paradox is very simple (see chapter 8, section 8.1), but its importance lay in drawing attention to the value of mathematical analysis of life history phenomena. Cole's paper enunciated two important principles that are the basis of life history analysis:

The birth rate, the death rate, and the age composition of the population, as well as its ability to grow, are consequences of the life-history features of the individual organisms. These population phenomena may be related in numerous ways to the ability of the species to survive in a changing physical environment or in competition with other species. Hence it is to be expected that natural selection will be influential in shaping life-history patterns to correspond to efficient populations.

Thus natural selection is seen as maximizing some quantity, here termed "efficient populations," but elsewhere in the paper identified as the rate of population growth. This is not to be taken as indicating that Cole favored the idea of group selection: the tenor of his paper makes it clear that his use of population can be understood in modern terms to be equivalent to genotype. Thus Cole is making the point that selection favors those genotypes that have the highest rates of increase. The second important principle put forward by Cole is that natural selection favors those patterns of birth, death, and reproduction that maximize the rate of increase. This observation was certainly not unique to Cole and can be traced back to Fisher (1930) and in verbal form to Darwin and Wallace. Andrewartha and Birch (1954) emphasized the importance of the potential for increase, devoting a whole chapter to the concept in their book, *The Distribution*

and Abundance of Animals. Birch later stressed the relationship between the genotype and its rate of increase, r :

Natural selection will tend to maximize r for the environment in which the species lives, for any mutation or gene combination which increases the chance of genotypes possessing them contributing more individuals to the next generation (that is, of increasing r) will be selected over genotypes contributing fewer of their kind to successive generations. (Birch 1960, p. 10).

Mathematical modeling has been, and continues to be, an important component of the analysis of life history variation (Stearns 1976, 1977; Parker and Maynard Smith 1990). No model is constructed to capture all the intricacies of the real world, for if it did so it would be as difficult to understand as the real world itself and little would be gained. The purpose of model construction is to address a particular aspect of the real world, ranging from a very detailed analysis of a very specific circumstance to an assessment of a general proposition. All models necessarily are simplifications of reality, and to ensure that the results are robust relative to the assumptions, Levins (1966, p. 423) recommended the use of several different models incorporating different assumptions: "Then, if these models, despite their different assumptions, lead to similar results we have what we can call a robust theorem which is relatively free of the details of the model. Hence our truth is the intersection of independent lies."

There are two basic approaches to the analysis of life history variation, which I shall call "the genetic approach" and "the optimization approach." These methods are neither entirely distinct, nor do they address *exactly* the same questions. The genetic approach is, in large measure, concerned with local events in the sense of describing and predicting variation at small scales of time. The optimization approach addresses the issue of what combination of traits is most favorable in the long run. But there is overlap: quantitative genetic methods have been employed to predict allometric relationships between morphological traits (Lande 1979), and optimization has been used to predict changes in the age schedules of reproduction and growth in response to environmental fluctuations that occur within the life of an organism (Stearns and Koella 1986).

1.1.1. Genetic Approach

Consider a trait whose expression is governed by a single locus with two alleles. A selection coefficient representing their relative contribution to the next generation can be assigned for each of the three genotypes. From this it is a trivial matter to predict the frequencies of the three genotypes at equilibrium (e.g., Hartl 1980). This example encapsulates the genetic approach: define the genetic mechanism determining the phenotypic trait

and then simply crank the model through the appropriate mathematical machinery to obtain the equilibrium frequencies. Given a proper knowledge of the genetic architecture of a trait this is obviously a more satisfactory procedure than assuming that some quantity is being maximized as is required for the optimality approach. But the critical problem is the correct definition of the genetic architecture.

Most traits of ecological interest—fecundity, age at maturity, clutch size, egg size, etc.—are continuous in character. Even traits that appear dichotomous, such as liability to disease (Cavalli-Sforza and Bodmer 1971; Curnow and Smith 1975), wing dimorphism (Roff 1986a), diapause (Mousseau and Roff 1987), and sex ratio (Bull et al. 1982; Trehan et al. 1983), are best understood as being the result of some underlying, continuously varying factor exceeding or not attaining a threshold for the expression of the trait. The expression of traits that show continuous variation is not, in general, the result of a single gene, nor two genes, but of a large number of genes that, acting additively, produce a continuous spectrum of phenotypes. The analysis of such traits is the domain of quantitative genetics. This is largely a statistical approach to genetic variation and is founded upon a mathematical analysis of variation rather than an understanding of how groups of genes interact to determine a particular trait. The delineation of the parameters describing quantitative genetic variation—additive, dominance, and epistatic effects—requires breeding data which for many organisms are not available, and may represent formidable technical difficulties.

A second difficulty is that the expression of a trait changes with the environment in which the organism is raised. Such variation is termed “phenotypic plasticity.” If an organism produces a phenotype that varies as a continuous function of the variation in the environment then the phenotypic plasticity is termed a “norm of reaction” (Stearns 1989). However, such a distinction is not really tenable since the definition of continuous variation is largely a matter of opinion, and because threshold traits produce discrete morphs but the underlying factors may vary in a continuous manner with the environment (i.e., show norms of reaction). Therefore, I shall refer to any change in phenotype across a gradient a norm of reaction even if the changes are abrupt. There are very few traits that do not vary with their environment, and hence phenotypic plasticity is an integral part of life history variation (Birch 1960; Levins 1963; Bradshaw 1965; West-Eberhard 1989). An additional complication is that reaction norms are themselves functions of the environment, and frequently the reaction norms of different genotypes cross, a phenomenon known as genotype-by-environment interaction ($G \times E$). Incorporating the concept of reaction norms and genotype-by-environment interactions into quantitative genetic theory is not in principle difficult but considerably compli-

cates the theory (for $G \times E$ see James 1961; Yamada 1962; Freeman 1973; Hill 1975; Zuberi and Gale 1976; Via and Lande 1985; Westcott 1986; Jong 1990a; and for phenotypic plasticity see Scheiner and Lyman 1989; Jong 1990a,b), and the technical difficulties of experimentally measuring the relevant parameters in a realistic setting are not to be taken lightly (Schlichting 1986; Noordwijk 1989).

Thus far, the discussion has centered upon single traits; but fitness is a composite trait resulting from the integration of age at maturity, reproductive effort, egg size, etc. Therefore, to understand how life histories evolve we must understand how the components of the life history interact. In a genetic setting we must measure the genetic and phenotypic covariance between all traits of interest. Providing we assume that this variance-covariance matrix remains stable over time we can use quantitative genetic theory to predict the outcome of selection acting on a composite trait such as fitness.

The use of quantitative genetic methods to analyze life history variation is not a simple task. If we can ignore, at least as a first approximation, the genetic architecture of the traits under study and approach the study from the perspectives of maximization of fitness within a set of constraints and trade-offs, a solution can be obtained relatively easily. The important issue is whether the two approaches lead to the same result, simply by different avenues of analysis. In the next section I present an overview of the second approach—optimization theory. In chapter 2 some necessary background on quantitative genetic theory is given and in chapter 3 I present a more detailed discussion of optimization theory and its relationship to quantitative genetic theory, showing that current research does indeed indicate that in general the solutions obtained by the two methods will be the same.

1.1.2. Optimization Approach

The concept of trade-offs is central to present theories of how life history traits evolve, for it is such trade-offs that limit the scope of variation. Within the set of possible combinations there will be at least one combination that exceeds all others in fitness. Optimality analysis assumes that natural selection will drive the organism to that particular set. This represents an adaptationist program carried out within a holistic framework. (“Holism” is used here in the sense of multifactorial—see Wilson [1988] for alternate ways in which the term has been used in biology.) Gould and Lewontin (1979, p. 581) more narrowly defined the adaptationist program as one that “proceeds by breaking an organism into unitary ‘traits’ and proposing an adaptive story for each considered separately.” Mayr (1983) criticized this definition as being a caricature of the method as properly applied, noting (p. 327) that “selection does not produce perfect genotypes, but it