Mechanisms of Life History Evolution

The Genetics and Physiology of Life History Traits and Trade-Offs

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"…integrating an understanding of mechanisms into life history theory will be one of the most exciting tasks facing evolutionary biologists in the 21st century."

Barnes & Partridge (2003)

Foreword: Harvey's legacy

Graham Bell

"Ex ovo omnia" wrote Harvey (1651), and more than three centuries later his dictum still stands. Many examples of vegetative reproduction in animals have been described since Trembley (1744) astonished the world by describing the asexual budding of *Hydra*, but all lineages, so far as we know, pass through a single-cell stage sooner or later. The only more certain observation is that the individual that develops from the egg will eventually senesce and die. The journey between the two fixed points of egg and corpse has no prescribed route, however, and biologists have struggled to discover and interpret the lives of animals, plants, fungi, and seaweeds since the beginning of scientific biology in Harvey's time.

In very broad terms, two main approaches have been followed. The first is concerned largely with juvenile forms, and specifically with discrete developmental stages such as larvae. This is the older school, and its subject is usually called "life cycles." The second is concerned largely with adults, and specifically with the quantitative schedule of reproduction. This has developed over the last 50 years, and its subject is usually called "life histories." The two have been developed to a large extent independently of one another, and the linkages between them remain few and weak.

The study of life cycles is the older tradition, and dates back to the time when it was first demonstrated by Steenstrup (1845) that very dissimilar individuals could be produced, one from another, as a succession of forms belonging to the same lineage. The only example that is familiar to everyone (now that classical zoology has withered from the curriculum) is the succession of polyp and medusa in some cnidarians, but much more complex life cycles have evolved in groups such as digenean trematodes. It is often difficult to work out how and when one stage gives rise to another, especially when this involves reproduction by eggs. In other cases, however, the developmental sequence is clear even though it passes through larval stages that are very different from the adult, by virtue of the physical continuity of macroscopic individuals. There is no profound difference between the two, however. The juvenile starfish, for example, develops as a miniature version of the adult from a small patch of tissue within the body of a small ciliated-band animal living in the plankton. As the starfish animal enlarges, the ciliated-band animal shrinks, and its remnants are eventually discarded. This process is called "development" because the physical continuity of larva and adult is clear, but it is manifestly the same kind of process as the transition between polyp and medusa, a succession of morphologically distinct phases within a single lineage.

The study of life cycles has been predominantly descriptive, a tradition that has continued, in the form of discovering the regulatory genes responsible for the evolution of body plans, down to the present day. The possibility of a theoretical account of the life cycle was raised by Garstang (1928) nearly a century ago: given that an animal developing from an egg must grow steadily larger, it must be functional first as a small individual and subsequently as a large individual. A ciliary-band animal living at low Reynold's number in the plankton is one possible route to a large hydraulically powered animal living on the sea floor, whereas the reverse route is impracticable. Nevertheless, a systematic theoretical framework capable of interpreting the succession of phases in development has yet to be constructed.

The parallel effort to understand the sexual phases of life cycles is a similar but more complicated story, largely because of the great difficulty of establishing the site and timing of the crucial events of fusion and reduction, even after the advances of microscope design in the later nineteenth century. It was not until the closing decades of the century that the essential distinction between spore and gamete was unequivocally established, and by the end of the first decade of the twentieth century a correct account of the alternation of generations in the life cycle of seaweeds and land plants had been successfully accomplished (see the review by Farley 1982). A theoretical basis for understanding the alternation of generations in terms of the fundamentally different requirements of spores and gametes, and thus the different structure and behavior of spore-producing and gamete-producing individuals, was provided at the same time (Bower 1908). Before it could be extensively developed, however, the field was largely abandoned, swept away by the flood of research into transmission genetics, which had just been provided with the firm theoretical framework of Mendelism. The endlessly varied sexual cycles of eukaryotes have continued to provide rich material for extending our knowledge of natural history, but we cannot yet interpret them within a consistent theoretical framework. In recent years there has been a modest revival of interest in the theory of phenomena such as gamete dimorphism, but this has not yet become firmly coupled to field studies and experimentation.

The field of life histories has developed more recently and in a very different fashion, being highly theoretical from the outset. Simplifying history (as one must in a foreword) it was galvanized by Cole's paradox: a lineage in which females live forever and produce an infinite number of litters of whatever size has the same rate of increase as one in which all females die immediately after producing their first litter, but produce one more offspring (Cole 1954).

Working out the reasons for this counter-intuitive result led to a general interpretation of suicidal versus repeated reproduction that was subsequently elaborated into an account of the schedule of reproduction over the whole of the adult stage. Juvenile stages such as larvae are ignored; alternative adult stages such as sporophytes and gametophytes are not distinguished. Freed from zoology, botany, and genetics a highly abstract and general theory of the life history could be developed.

Much of this theory was based on a principle of optimality: quantities such as the rate of reproduction and the probability of survival are negatively correlated, such that intermediate values of both maximize the overall rate of increase of a lineage. This enabled the schedule of reproduction to be predicted from the costs of reproduction, in terms of reduced growth or survival. This approach has had some brilliant successes, beginning with David Lack's classical interpretation of clutch size in birds (see Lack 1966). It could also be extended to the puzzling phenomenon of senescence, which could now be interpreted as a non-adaptive side effect of selection for early reproductive maturity (Williams 1966a). Moreover, the generality of the predictive framework made it possible to contrive experimental tests in laboratory model systems, which had never been possible for life cycles.

The very generality that gave the theory such power was also a source of weakness, insofar as the sources of the costs of reproduction on which the theory was based did not need to be specified and therefore could not be investigated within the confines of the theory itself. For this reason, attention began to shift towards the nature of the costs themselves. This is not as straightforward as it might appear. It seems obvious that producing larger offspring will mean producing fewer, and almost equally obvious that allocating a greater share of resources to reproduction must deplete the stock available to support maintenance and defense. One function necessarily interferes with the other. It was soon found, however, that in practice the correlations between fitness components are usually positive rather than negative. This was quickly attributed to environmental variance of productivity among sites when comparisons are made in the field, or to genetic variance of overall fitness among strains when comparisons are made in the laboratory. The expected costs are then expressed only at evolutionary equilibrium, when genetic variance for overall fitness has been reduced to a low level by selection. This evolutionary argument, however, implies that costs of reproduction measured as negative genetic correlations need not have any mechanistic basis in terms of functional interference. A simple illustration of this conclusion is to generate n random numbers and label them x_1, x_2 etc; then repeat the process to obtain a second set labeled y_1, y_2 etc. Plotting y_i on x_i produces a cloud of points with zero correlation. Now choose the small percentage of pairs with the highest values of $(x_i + y_i)$; plotting y_i on x_i now produces a graph with a slope of –1 (if the x_i and y_i have equal variance) and $r^2 \approx 0.5$. This striking pattern has been carved out of the original unstructured data by the act of choosing an unrepresentative set of cases, and natural selection will likewise generate negative genetic correlation among components of fitness from random life histories through the propagation of an unrepresentative set of genotypes. No causal connection between the components, for example through pleiotropic gene expression, is necessary for such correlations to arise.

Understanding the mechanistic basis for costs of reproduction is thus an important aspect of understanding life histories as a whole. Moreover, it may contribute directly to human well-being. The evolutionary reasons for senescence can be framed in terms of pleiotropy or delayed gene expression for example, whereas the physiological reasons must be framed in terms of factors such as the irreversible damage caused by reactive oxygen species, the accumulation of somatic mutations, the intrinsically limited metabolic capacity of tissues, and so forth. Much of the recent research into senescence in the *Drosophila* and *Caenorhabditis* model systems has been driven by the physiological agenda, in part because of its potential for identifying palliative therapies. The value of this research is indisputable. It would be a pity, however, if the evolutionary agenda were to be obscured or lost as a result. Part of the *raison d'être* of this volume is to emphasize that it is important to understand the physiological basis of the costs of reproduction in order to understand how life histories evolve—but conversely that it is equally important to understand how life histories evolve in order to predict how physiological processes are likely to operate. The *clk* genes of *Caenorhabditis*, which slow down vital processes and extend lifespan, are an excellent example of recent research in molecular developmental genetics at the interface between evolution and physiology (Hekimi *et al.* 2001).

A more fundamental task for the future is to build a synthetic evolutionary theory of development that would bring together all the phenomena of life cycles within the same framework. It is not even clear whether this is possible. The classical theory of life histories invokes natural selection, leading to optimal phenotypes. The most successful theories of certain aspects of the life cycle, such as gamete dimorphism and the sex ratio, invoke sexual selection, leading to evolutionary stable states. For some phenomena, such as the alternation of generations, both approaches have been tried without any decisive outcome so far; for others, such as the succession of phases, hardly any formal theory has yet been developed. But the possibility is worth contemplating, and if this volume is not the last word on the subject, it will at any rate be the next word.

Graham Bell
McGill University
23 May 2010

Preface

The major features of a life cycle are shaped by demographic traits—size at birth, growth rate, age and size at maturity, age-specific reproductive investment, number and size of offspring, age-specific survival, and lifespan—connected by constraining trade-offs. Together, these life history traits determine Darwinian fitness by affecting the two most important fitness traits, survival and reproduction. Life history theory seeks to understand the causes and consequences of genetic and environmental variation in life history traits, both within and among species. By combining quantitative genetics, artificial selection, demography, phenotypic manipulations, and optimality modeling, life history theory has had major success in explaining the diversity of life history strategies, as reviewed in three excellent books by Stephen C. Stearns and Derek A. Roff (Stearns 1992, Roff 1992, 2002).

The present book, in contrast to most previous work on life history evolution, emphasizes the mechanistic description, the "molecular natural history," of life history traits and their evolution. Traditionally, life history theory is silent on proximate mechanisms, yet recent advances in mechanistic biology have taught us a great deal about how genetics, development, and physiology affect life history. Although much of this information comes from research outside the realm of evolutionary biology, for example from fields such as the genetics of growth control or the molecular biology of aging, it is often directly relevant for our understanding of the evolution of life histories. To date, however, this mechanistic knowledge has not been adequately integrated into the life history framework. To forge such an integration, and to foster an exchange between scientists who work on organismal versus mechanistic aspects of life histories, this multi-author book brings together leading researchers who share the conviction that many fundamental problems in life history evolution can only be completely understood if we begin to incorporate information on developmental, physiological, and genetic mechanisms into the study of life histories (e.g., Barnes and Partridge 2003, Flatt *et al.* 2005, Heyland *et al.* 2005).

Given the major predictive and explanatory success traditional life history theory has had, why is it important to fill the "black box" of life history evolution with mechanism? A good example is the problem of life history trade-offs. Trade-offs, for example between survival and reproduction, are typically thought to be caused by competitive resource allocation (e.g., Stearns 1992), but whether this physiological explanation is correct is usually unknown. Without detailed knowledge of resource levels, patterns of acquisition and allocation, intermediary metabolism, and endocrine regulation we cannot properly test the assumption that trade-offs are resource based (e.g., Harshman and Zera 2007). Thus, while the existence of trade-offs can often be quite readily established, we do not understand their underlying mechanisms, and this limits our understanding of life history evolution (e.g., Stearns 2000). As several chapters in this book illustrate, the classical assumption of trade-offs being resource based might in fact not always hold.

Another example of how information on mechanisms can illuminate and expand life history theory concerns genes with major effects on life history traits and their integration (e.g., Flatt 2004, Schmidt *et al.* 2008, Paaby *et al*. 2010). Identifying the genes that affect or modulate life history traits will ultimately enable us to answer important evolutionary questions such as: Which genes or alleles affecting life history traits are evolutionarily conserved, and which genes or alleles are lineage-specific? What is the relationship between life history variation segregating within natural populations and genetic differences in life histories among species? Is there standing genetic variation for these genes within populations and are they under selection? What are the genes or alleles that make up genetic correlations and trade-offs? Can the genetic mechanisms that cause trade-offs be uncoupled and how? How do genes interact with the environment to determine life history phenotypes? Several authors in this book review impressive progress in evolutionary quantitative and molecular genetics that has lead to the identification of genes and pathways that are likely to be of major importance in life history evolution.

Although the integration of mechanistic studies into life history evolution is still in its infancy, we believe that—similar to the recent advances made by evolutionary developmental biology (evo-devo), which combines studies of evolution, development, and genetics—future work on life histories will benefit significantly from an explicit consideration of proximate mechanisms. Many examples of such an interdisciplinary approach towards understanding life history evolution can be found throughout this book.

We are targeting this book at advanced undergraduates, graduate students, postdocs, and established researchers in evolution, ecology, evo-devo, development, genetics, physiology, and aging who all aim to understand the mechanisms that shape the expression and evolution of traits that affect Darwinian fitness, including growth, development and maturation, reproduction, and lifespan. In particular, we hope that the chapters in this book will stimulate students and researchers with a strong interest both in organismal biology and molecular biology. For background reading on life histories we refer the reader to the books by Stearns (1992) and Roff (1992, 2002) who cover traditional, non-mechanistic aspects of life history evolution.

The chapters in this book have all been written by leading researchers who use studies of proximate mechanisms to solve fundamental problems in life history biology in a variety of organisms. Their chapters not only represent the current state of the art, but also offer fresh perspectives for future research. In designing the book we have attempted to present a balanced selection of authors (ranging from young to well-established), organismal taxa (e.g., algae, higher plants, nematodes, insects, echinoderms, fish, amphibians, reptiles, birds, humans), and biological disciplines and approaches relevant to life history biology (e.g., developmental biology, genetics, evo-devo, anthropology, behavior, reproductive biology, aging, phenotypic plasticity, social evolution, immunology, metabolism, and endocrinology). Although we have aimed to cover a lot of ground in this book, many interesting and important subjects had to be omitted due to space limitations. For example, while several chapters discuss the mechanisms that affect lifespan, we did not include a detailed discussion of the evolutionary biology of aging—this has been reviewed extensively elsewhere, for example by Rose (1991) and Flatt and Schmidt (2009).

Chapter authors were asked to write chapters that are equally accessible to evolutionary and mechanistic biologists, to make clear references to fundamental concepts in life history evolution, and to cross-reference other chapters in this volume. Authors obviously differ in their scientific views, the level of their exposition of material, and their writing styles, and we have therefore attempted to make chapters somewhat uniform, for example through author guidelines, editorial and external peer reviews, and several revisions. Nevertheless, differences among the chapters do remain—in fact, we feel that they are desirable since they make the perspectives offered here both more personal and pluralistic. Together with the wide range of topics, scientific approaches, and organisms covered in this volume we hope that this diversity in perspective will be stimulating for the reader.

Although not being a chapter in its own right, the book starts out with a foreword by Graham Bell, who gives a broad historical summary of research on life histories and who emphasizes the need for integrating mechanistic insights into this research area. This sets the stage for the actual book chapters which are grouped into seven parts. Each part of the book, except for the last, is preceded by a brief introduction written by the editors. Part 1 (Integrating mechanisms into life history evolution) consists of two chapters which introduce some of the basic concepts of life history theory and outline the utility of mechanistic approaches for understanding problems in life history evolution. Parts

2–6 consist of 24 chapters that make up the bulk of the book. Since many of these chapters are highly integrative and cover more than one type of organism, we have attempted to group these chapters into conceptual categories. The chapters in Parts 2–4 all address mechanisms that deal with one of the three major phases of an organisms' life cycle (Part 2: growth, development, and maturation, Part 3: reproduction, and Part 4: aging and somatic maintenance). The chapters in Parts 5–6 deal with two major concepts in life history theory, namely phenotypic plasticity and trade-offs (Part 5 life history plasticity and Part 6 life history integration and trade-offs). Despite this conceptual structure, many chapters could have easily been placed into other parts of the book. Thus, the structure of the book is not rigid, and many chapters in one part of the book directly touch on issues discussed in other parts of the book. In fact, we feel that a certain amount of overlap among book parts and chapters is desirable and helps the integration of the diverse subjects we cover. We have also aimed to achieve further integration throughout the book by writing short introductory sections that precede each book part and by asking authors to frequently cross-reference other chapters. Part 7 concludes the volume: in Chapter 27 Stephen C. Stearns summarizes and critically discusses the contributions in the book by asking whether progress on understanding mechanisms forces life history theory to change. Chapter 28 is a postscript that rounds up the book: it consists of an exchange between Stearns and the editors, discussing what mechanistic insights can or cannot contribute to our understanding of life history evolution.

The idea for this volume was conceived at a symposium on molecular mechanisms of life history evolution sponsored by the Society for the Study of Evolution (SSE), which we organized at the Evolution meetings at the University of Minnesota in Minneapolis in 2008. We are grateful to all the speakers and participants of this symposium for many stimulating discussions that have helped to shape some of the ideas in this book. Their enthusiasm convinced us to approach this book project. In particular, we thank Derek Roff for his advice and encouragement.

Each book chapter was reviewed by both editors and in most cases by two external reviewers or chapter contributors. We are extremely grateful to these experts for their help and time: without exception they have provided very thoughtful, critical, and helpful suggestions for improving the chapters. For their timely chapter reviews we are indebted to Gro Amdam, Richard Bribiescas, Goggy Davidowitz, Greg Davis, Tony De Tomaso, David Denlinger, Robert Denver, Michelle Elekonich, Peter Ellison, Caleb Finch, Klaus Fischer, Gary Freeman, Owen Gilbert, Michael Hadfield, Dan Hahn, Larry Harshman, John Hatle, Jason Hodin, Hillard Kaplan, Tad Kawecki, Ellen Ketterson, Teri Markow, Alistair McGregor, Amy Moran, Coleen Murphy, Courtney Murren, Amy Newman, Dan Noble, Mats Olsson, Bruno Pernet, Scott Pletcher, Kim Rewitz, Jens Rolff, Michael Rose, Olav Rueppell, Gerhard Schlosser, Paul Schmidt, David Schneider, Stanley Shostak, Cristian Solari, Gabriele Sorci, Stacia Sower, Michael Stern, Richard Strathmann, Stuart Wigby, Karen Williams, and John Youson, and two reviewers who wished to remain anonymous.

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Contents

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CHAPTER 1

Integrating mechanistic and evolutionary analysis of life history variation

Christian Braendle, Andreas Heyland, and Thomas Flatt

1.1 Introduction

Life histories—describing essential patterns of organismal growth, maturation, reproduction, and survival—show tremendous variation across individuals, populations, species, and environments. Understanding this variation is the goal of life history research. The analytical framework of life history theory focuses on the variation and interaction of different key maturational, reproductive, and other demographic traits, given that natural selection acts to maximize fitness of a life history as a whole (Roff 1992, Stearns 1992). Fitness integrates over the entire reproductive performance of the organism, and life history traits are the major fitness components underlying this integration. However, the investment into alternative life history traits, and thus the possible set of trait combinations, is restricted by genetic, developmental, physiological, and phylogenetic limits. Apart from explaining variation in life history strategies as a result of natural selection, identifying how such trade-offs and constraints shape life histories is the central aim of life history research.

In this chapter we introduce the basic concepts and definitions of life history theory and argue for the importance of integrating a mechanistic perspective into research on life histories. While most traditional life history research is based on mathematical, statistical, and phylogenetic approaches without explicit reference to underlying mechanisms, today's principal research challenge is to fill this gap through experimental characterization of the proximate basis of life histories. The analysis of genetic, developmental, and physiological factors that shape life history traits will ultimately allow us to determine how evolutionary changes in such mechanisms generate, facilitate, or constrain the diversification of life histories. Integrating mechanistic and evolutionary analyses of life history variation is part of a global quest in biology that seeks a shared understanding of proximate and ultimate causes of phenotypic variation.

1.2 The life history framework

1.2.1 What is a life history?

A life history encompasses the life of an individual from its birth to its death, describing the age- or stage-specific patterns of maturation, reproduction, survival, and death. The major objective of life history research is to understand how evolution, given selection imposed by ecological challenges, shapes organisms to achieve reproductive success. The second objective of life history research is to understand whether and how, given internal trade-offs and constraints, selection can optimize a set of life history traits to maximize reproductive success. Since organisms dispose of limited resources, which must be competitively allocated to differing functions, such as growth, reproduction, survival, and maintenance, resources invested into one function cannot be invested into another, leading to trade-offs. In addition, life history research explores taxon-specific features of life cycles and life history decisions, including patterns of sex allocation, alternative phenotypes, or larva-to-adult transitions. For in-depth treatments of the evolution of life histories and life history theory see Stearns (1992), Roff (1992, 2002), and Charlesworth (1994).

1.2.2 Life history traits and fitness

Life history traits represent quantitative, demographic properties of organisms that are directly related to the two major components of fitness, i.e., survival and reproduction. Classical life history analysis considers the following to be the principal life history traits (Stearns 1992):

- size at birth
- growth pattern
- age and size at maturity
- number, size, and sex ratio of offspring
- age-and size-specific reproductive investments
- age- and size-specific mortality schedules
- length of life.

These traits essentially represent the demographic parameters required to estimate fitness as defined by the Malthusian parameter (or similar fitness measures). The Malthusian parameter (also called the instantaneous rate of natural increase, *r*) is the solution to the Euler–Lotka equation, which describes population growth by summing reproductive events and survival probabilities over the entire lifetime of individuals (Stearns 1992). Thus, life history traits are directly linked to fitness, with fitness being defined by population growth models from demography.

In contrast to classical life history traits, morphological, physiological, or behavioral traits are considered to contribute to fitness only indirectly (e.g., Roff 2007b). However, this distinction is somewhat arbitrary. For example, certain morphological traits such as body size or gonad size may correspond to life history traits (or at least are correlates thereof). In the literature, the term "life history trait" is often used interchangeably with fitness components, so that many phenotypic characters with major effects on reproduction and survival have been called life history traits.

Because of their complexity and demographic nature, life history traits are usually treated as quantitative, polygenic traits (Falconer and MacKay 1996). The expression of life history traits is also highly contingent on the environment, so that life history research places particular emphasis onto the concept of phenotypic plasticity, i.e., the ability of a single genotype to produce different phenotypes across environments (Stearns 1992). Plasticity is described by "reaction norms", mathematical functions that relate the phenotypic values adopted by a given genotype to changes in the environment. Selection shapes life history plasticity by acting on genetic variation for plasticity, which is present when the reaction norms that represent different genotypes are non-parallel across the same range of environments (so-called genotype by environment interactions, or G × E). Reaction norms (and thus plasticity) are considered to be optimal when they maximize fitness for each of the different environments (Stearns and Koella 1986).

1.2.3 Trade-offs and constraints

A key postulate of life history theory is that the values and combinations of life history traits are limited by factors internal to the organism, namely trade-offs and constraints. These intrinsic factors ultimately limit and direct the evolutionary response to the external force of selection. A life history trade-off occurs when an increased investment in one fitness component causes a reduced investment in another fitness component, i.e., a fitness benefit in one trait exacts a fitness cost in another. Examples of classical life history trade-offs are survival versus reproduction, number versus size of offspring, or current reproduction versus future reproduction (Stearns 1992).

Trade-offs are usually described as phenotypic or genetic covariances or correlations among traits, without reference to their causal relationships. If the relationship can be shown to be genetic, negative genetic covariance among traits is expected to limit the evolution of each of these traits. Such genetic or evolutionary trade-offs are considered at the population level, i.e., as defined by genetic correlations among individuals or correlated phenotypic responses to selection. Genetic trade-offs are traditionally assumed to stem from antagonistic pleiotropy or linkage disequilibrium. These trade-offs also manifest themselves at the physiological or individual level, for example when an individual with increased reproductive effort in one year exhibits a reduction in reproductive output in the next year. Such physiological trade-offs are thought to be due energy limitations, i.e., the allocation of resources among competing functions. Importantly, trade-offs may exist at population level, but not at individual, physiological level (Stearns 1989, Houle 1991, Stearns 1992).

In contrast to trade-offs, the term "constraint" is often used to described *absolute* limits to or biases upon trait expression and combination. Constraints may describe physical factors, developmental properties, or historical contingencies that prevent an organism from expressing a certain phenotype or a population from attaining a certain fitness optimum in response to selection (Maynard Smith *et al.* 1985). The distinction between trade-offs and constraints is not strict, and trade-offs are often regarded as one type of constraint. In the life history context, constraints usually refer to phylogenetic, lineage-specific characteristics that impose *absolute* limits on trait expression in a given organismal group.

1.2.4 Empirical approaches in life history research

Although classic life history analysis has been largely theory-driven, much empirical research has addressed the questions and predictions raised by life history theory, using both non-genetic and genetic approaches (Stearns 1992, Roff 1992, 2002, 2007b; also see Chapter 2). Non-genetic approaches include phenotypic correlations to examine patterns of life history trait covariation among populations and species, experimental phenotypic manipulations, and statistical tools from comparative analysis to control for phylogenetic history. Genetic approaches to the study of life history variation are predominantly based on the framework of quantitative genetics. Most of this work has concentrated on the detection and analysis of genetic trade-offs, either through the study of covariances and correlations among life history traits between relatives (e.g., pedigree analyses) or through correlated responses of life history traits to artificial selection or experimental evolution. This research framework has generated a substantial body of empirical evidence that has revealed how selection operates on life history traits, contingent on the environment and trade-offs (Stearns 1992, Roff 1992, 2002, 2007a,b). Despite these extensive efforts, very few studies have examined the mechanistic underpinnings of life history traits. For example, inferred interrelationships among life history traits rarely describe more than statistically determined associations. A major limitation common to the classical approaches in life history research is therefore the ignorance of the proximate causes that determine or modulate life histories and their evolution.

1.3 The study of causal mechanisms linking genotype to phenotype

Understanding how a genotype translates into a phenotype is one of the most fundamental problems in biology. In most cases, phenotypes cannot be simply inferred from their underlying genotypes, and vice versa, because the mapping of genotypes onto phenotypes is often a non-linear process, shaped by a multitude of complex genetic and environmental interactions. Moreover, a single genotype may generate multiple phenotypes and, conversely, multiple genotypes may generate a single phenotype. That such properties of the genotype–phenotype map are relevant for our understanding of the evolutionary process has been emphasized for a long time (e.g., Lewontin 1974, Houle 2001), but it is only relatively recently that the causal relationships between genotype and phenotype have received increased attention from evolutionary biologists (e.g., Pigliucci 2010). While research at the interface of development and evolution has begun to tackle the significance of the genotype–phenotype map in morphological evolution, the causal connection between genotypes and phenotypes for fitness components is still extremely rudimentary (e.g., Chapter 2 and Roff 2007b).

Traditionally, attempts to link the genotype with the phenotype have been regarded as the principal task of "reductionist" branches of biology, including molecular, cellular, and developmental biology. Developmental genetics in particular has emerged as the prime discipline in connecting gene function during development with phenotypic outcomes, primarily by relying on mutational analysis and forward genetics. The great power of this approach lies in the typically high degree of causal inference that can be made through carefully controlled manipulation of isolated genetic factors and their phenotypic effects. The general downside of this approach is that such studies are generally limited to the study of single, highly pleiotropic mutations with large phenotypic effects. In addition, developmental genetic analyses are generally limited to the study of a single or or a small number of laboratory populations in highly simplified artificial environments, aiming to reduce variation engendered by genetic background or environmental context as much as possible. This research approach starkly contrasts with that of evolutionary biologists, whose primary concern is the study of quantitative genotypic and phenotypic variation among populations or species. Here, in contrast to developmental genetics, the inferred genotype–phenotype relationships are generally of indirect, associative nature, rarely permitting inferences about the causal connections between genotypic and phenotypic variation.

As advocated in many chapters throughout this book, a better future understanding of many issues in life history evolution will require the integration of evolutionary and organismal biology with molecular and developmental biology (e.g., Dean and Thornton 2007). That unfortunate historical separations between biological disciplines can be overcome is well illustrated by the successful rapprochement of evolutionary and developmental biology (e.g., Raff and Kaufman 1983, Carroll *et al.* 2000, Stern 2010). Although initially mainly concerned with the description of evolutionary diversification or conservation of developmental mechanisms, the central aim of evolutionary developmental biology (evo-devo) has recently shifted to the experimental analysis of how properties of genetic and developmental architecture impact phenotypic evolution. Evo-devo therefore addresses specific issues directly relevant to the understanding of life history evolution, such as the mechanistic basis of developmental biases and constraints or phenotypic plasticity. More generally, as life history traits are high-level phenotypes that depend on the ensemble of morphological and physiological traits, the mechanistic analysis of life history evolution can consequently be regarded as an extension of the principal objective of evo-devo, namely to understand which developmental and genetic changes underlie phenotypic evolution.

Uncovering the mechanistic basis of life history variation is a non-trivial challenge. Life history traits were defined by evolutionary ecologists with the intent of reducing phenotypic complexity by focusing on a small number of traits that summarize the essential fitness components and by ignoring the underlying genetic, developmental, and physiological mechanisms that govern the expression of these traits. A given life history trait can thus be thought of as a functionally complex phenotype resulting from the integration of a suite of morphological, physiological, or behavioral phenotypes. At the level of the individual, their characteristics have therefore to be understood in terms of both the construction of multiple individual traits as well as their spatial and temporal integration into a higher-level phenotype. As such, life history traits are *a priori* composite, quantitative, polygenic traits whose expression is often highly contingent upon plasticity, pleiotropy, and epistasis. All these properties render the mechanistic analysis of life history traits extremely difficult in practice.

1.4 How can mechanistic insights contribute to understanding life history evolution?

Despite the inherent difficulties in studying the proximate basis of life histories, considerable progress has been made in our mechanistic understanding of life history evolution, with major contributions stemming from molecular genetic studies on experimental model organisms. Here we briefly discuss the importance of integrating such mechanistic information into organismal life history research; many more detailed examples can be found throughout the chapters in this book. For further reading on integrative approaches in life history biology we recommend the reviews by Houle (2001), Leroi (2001), Barnes and Partridge (2003), Harshman and Zera (2007), Chapter 5 in Van Straalen and Roelofs (2006), Roff (2007b), and Flatt and Schmidt (2009).

1.4.1 Why understanding mechanisms is important for answering evolutionary questions

While it is clear that knowledge of the proximate basis of life histories does not provide information about the ecological or evolutionary relevance of such mechanisms, it enables evolutionary biologists to address several fundamental questions about life history evolution, including, for example:

- What is the function of genes that are genetically variable in natural populations and that contribute to ecological adaptation?
- Are major candidate genes, as identified by molecular genetics, variable in natural populations?
- If so, do polymorphisms at these loci actually contribute to the evolution of life history traits in the wild?
- Are the genes that impact life history evolutionarily conserved or lineage-specific?
- What genetic and physiological mechanisms determine or modulate the expression of ecologically and evolutionarily important trade-offs?
- Are such trade-offs, as commonly assumed, resource based, or are they due to mechanisms independent of energy allocation?
- What are the mechanisms that mediate life history plasticity?

1.4.2 The molecular identity and function of genes that affect life history

Studies in molecular and developmental genetics inform us about the molecular identity and function of genes, including those that affect life history traits and other fitness components. The functionally best-understood genes that affect life history traits have been analyzed in model organisms such as *Arabidopsis*, *Drosophila*, or *C. elegans*. Information about the function of such genes is useful, for example, when evolutionary biologists want to investigate the consequences of allelic variation at such loci in natural populations. Although natural alleles might have much more subtle phenotypes than laboratory induced mutant alleles, detailed knowledge about gene function might help organismal biologists to understand whether and how particular genes contribute to ecologically relevant phenotypes and thus why selection acts on such loci. This does not mean that every gene with a major phenotypic effect on a fitness-related trait, as identified by molecular genetics, is in fact ecologically or evolutionarily relevant in natural populations; many such genes might not harbor standing genetic variation affecting life history phenotypes and might therefore not contribute to evolutionary change in the wild. Yet, it is also clear that loci that do contribute to phenotypic variation in fitness-related traits and thus to ecological adaptation in natural populations are a subset of all genes, including those that have been functionally studied by molecular geneticists (e.g., Stern 2000, Flatt 2004, Flatt and Schmidt 2009).

While developmental and molecular genetic approaches do inform us about the ecological or evolutionary significance of specific genes, they have proved powerful in identifying the molecular mechanisms that affect life history traits, for instance their endocrine regulation (Tatar *et al.* 2003, Fielenbach and Antebi 2008). Perhaps the best examples are genes known to affect adult survival and longevity in the nematode, fruit fly, and mouse; these have received particular attention, not only from biomedical researchers because of their potential implications for human gerontology (see Chapter 16), but also from evolutionary biologists because of their potential relevance for understanding the evolution of aging. During the past 20 years, numerous mutations that extend lifespan have been identified in diverse model organisms (e.g., Kenyon 2010; also see Chapter 14). Many of these mutations were found to affect a key metabolic pathway—the insulin/insulin-like growth factor signaling pathway—indicating that decreased effectiveness of insulin/IGF-like signaling causes lifespan extension, linked to correlated responses in reproduction, growth, and metabolism. These pivotal discoveries, many of which are discussed in this book, not only demonstrate the feasibility of molecular genetic analyses of complex life history traits such as lifespan, but also suggest that certain evolutionarily conserved signaling pathways are potential key regulators of major life history traits (also see Chapters 27 and 28). Many of these findings have also contributed to our understanding of life history trade-offs (see below and Chapters 11 and 13). The molecular genetic analysis of lifespan has thus rapidly become of great interest to many researchers studying life histories, and this interest is now paving the way for an integration of mechanistic and evolutionary approaches towards the understanding of life history variation (e.g., Partridge and Gems 2006, Flatt and Schmidt 2009).

In addition to functional studies of individual mutations, genome-wide gene expression analyses have also been widely used by both molecular and evolutionary biologists to investigate the proximate basis of life history variation (as is discussed in detail in Chapter 2). For example, genome-wide transcriptional profiling has been used to identify candidate genes involved in lifespan regulation (e.g. Murphy *et al.* 2003), or to describe gene expression patterns associated with particular life history stages, for example dauer larva formation in *C. elegans* (Wang and Kim 2003). Many of these studies illustrate the complex and manifold changes in gene expression associated with life history variation and further indicate that life history trade-offs might emerge through "conflicts over gene expression", i.e., antagonistic pleiotropic effects of genes involved in multiple functions (Stearns and Magwene 2003, Bochdanovits and de Jong 2004). However, the functional interpretation of such data remains challenging because the precise causal connections between transcriptional changes and the resulting phenotypes are rarely known. Thus, while it is clear from these few examples that we have learned a great deal about the molecular genetic basis of life history traits, a current key challenge is to integrate such mechanistic insights into the evolutionary framework (also see Chapters 27 and 28). One obvious question for the evolutionary biologist is, for example, whether the candidate genes identified by molecular geneticists actually matter in natural populations.

1.4.3 Are candidate life history genes ecologically and evolutionarily relevant?

Mutational, transgenic, and genomic analyses in model organisms have been successful in identifying at least some of the key mechanisms that affect life history traits. However, while many of these mechanisms show a surprisingly high degree of conservation across widely divergent taxa, their relevance in shaping evolutionary life history variation in natural populations is not yet sufficiently clear. Determining whether and how such mechanisms evolve to generate natural life history variation represents a promising starting point for the integration of functional and evolutionary analysis of life histories. In most cases, however, such studies are limited to model organisms. Such an analysis requires testing of whether the genes involved in these candidate mechanisms show actual variation in natural populations and, as a more challenging step, to functionally demonstrate that this allelic variation impacts the life history trait in question.

Several studies suggest that genes identified through molecular and developmental genetic analyses indeed harbor natural allelic variation that contributes to population variation in life history traits, for example in *Drosophila* (e.g., Schmidt *et al.* 2000, Paaby and Schmidt 2008, Paaby *et al.* 2010; also see Chapter 18), or in *Arabidopsis* (e.g., Todesco *et al.* 2010; also see Chapter 9). Although the screening of natural polymorphisms in candidate life history genes only provides a first glimpse of the molecular basis of life history variation, such initial findings are encouraging since they indicate that developmental and molecular genetic studies indeed generate valuable candidate genes of interest for evolutionary biologists.

In contrast to the analysis of natural allelic variants at major candidate loci identified by molecular and developmental genetics, quantitative trait locus (QTL) mapping provides a less biased, yet technically challenging, approach to the characterization of the genetic basis of polygenic quantitative traits, including life history traits (Falconer and Mackay 1996). While classical QTL mapping approaches have been useful in determining the basic genetic architecture of life history traits (e.g., the number and effect size of the involved loci), they rarely achieve sufficient resolution to pinpoint individual candidate genes (see discussion in Roff 2007b and Mackay *et al.* 2009). However, recent technological advances, such as rapid and cost-effective genotyping methods and refined statistical and mapping methods, have increased the feasibility of high-resolution mapping, now allowing the identification of candidate genes within QTL regions for organisms with well-annotated genomes, in some cases down to the level of single nucleotide polymorphisms (e.g., Mackay *et al.* 2009). High-resolution mapping through recombinant inbred lines and genome-wide association studies have already been successful in characterizing natural polymorphisms underlying genetic variation in complex developmental or life history traits in *C. elegans* (e.g., Kammenga *et al.* 2007, Palopoli *et al.* 2008), *Drosophila* (e.g., De Luca *et al.* 2003, Schmidt *et al.* 2008, also see Flatt and Schmidt 2009 for a recent review), and in *Arabidopsis* (e.g., Atwell *et al.* 2010, also see Chapter 9). Moreover, recent progress in genomic methods now allows the researcher to treat genome-wide expression patterns as complex quantitative traits (e.g., Rockman 2008).

The recent advent of refined QTL and genetical genomics approaches is emblematic for an integrative and novel research program, namely the use of natural genetic variation as a tool to understand the causal connection between genotype and phenotype. By explicitly taking evolutionary variation into account, this approach holds great promise for facilitating the detection of mechanistic features that are involved in phenotype construction. However, the identification of individual genes or nucleotide polymorphisms that contribute to quantitative trait variation remains a major challenge because of subtle phenotypic effects, complex genetic interactions, pleiotropy, and genotype-by-environment interactions (e.g., Weigel and Nordborg 2005, Mackay *et al.* 2009).

1.4.4 How do trade-offs work?

One central and recurring theme in this book is the mechanisms that underlie life history trade-offs (see the chapters in Part 6). Given the central importance of such trade-offs in life history evolution, uncovering their mechanistic basis is one of the most fundamental but unresolved problems in life history research (e.g., Stearns 2000, also see Chapters 27 and 28). Despite numerous and seemingly obvious trade-offs between life history traits in a wide range of taxa, most reported trade-off relationships basically describe no more than a statistically inferred negative correlation. The description of trade-offs by means of trait correlations or covariances is, however, insufficient for evaluating how genetic architecture influences evolutionary trajectories (e.g., see Chapter 2 and Roff 2007b). Specifically, it remains to be determined to what extent presumptive trade-offs are conclusively due to actual competition for limited resources or caused by alternative mechanisms, such as hormonal signaling independent of resource allocation (see Chapters 11, 13, 27, and 28). The very limited knowledge on the mechanistic underpinnings of trade-offs therefore represents a current key problem in our understanding of life history evolution (e.g., Stearns 2000, Flatt *et al.* 2005, Roff 2007b, Flatt and Schmidt 2009).

Recent progress in this area comes again from the molecular genetic analysis of lifespan. Several studies on the relationship between lifespan and reproduction in worms and flies have challenged the fundamental notion that reproduction exacts an energetic cost in terms of reduced survival (e.g., see Chapter 11, Leroi 2001, Barnes and Partridge 2003). Of particular relevance was the observation of a *C. elegans* insulin receptor mutant with extended lifespan (Kenyon *et al.* 1993). Although this mutant exhibited decreased fecundity—consistent with a resource-allocation trade-off where investment in longevity extension lowers investment in reproduction—detailed experimental analysis of this relationship indicates that decreased reproduction is not the causal agent in extending longevity (e.g., Kenyon *et al.* 1993, Leroi 2001). Therefore, reproductive versus somatic investment may not necessarily be coupled through resource competition but rather via independent underlying signaling processes (see Chapters 11, 13, and 24, and Hsin and Kenyon 1999, Flatt *et al.* 2008b). While these findings do not prove the absence of a cost of reproduction (Barnes and Partridge 2003, Flatt and Schmidt 2009), they underscore the difficulty of inferring resource-allocation trade-offs without a precise understanding of the proximate mechanisms involved. For example, a major technical challenge in demonstrating the resource basis of trade-offs is to experimentally track resource allocation to different organismal functions by detailed measurement of relevant parameters, such as nutrient ingestion and assimilation (see Chapter 24 and O'Brien *et al.* 2008).

Other valuable information on the mechanistic basis of life history trade-offs comes from research exploring the fitness consequences of organismal defensive mechanisms against pathogens, parasites, stresses, or toxins. For example, studies in both vertebrates and invertebrates indicate that elevated immune and other defense functions incur fitness costs in terms of reproduction and survival (see, for example, Chapters 2 and 23, Flatt *et al.* 2005, Harshman and Zera 2007). Similarly, the evolution of pesticide tolerance in insects often results in a fitness cost, which is generally supposed to stem from increased energy allocation to corresponding detoxification mechanisms. Remarkably, however, it turns out that such fitness costs can result from collateral metabolic costs rather than energetic costs due to the detoxification mechanism (Van Straalen and Hoffmann 2000).

Thus, while many observations support the existence and evolutionary relevance of life history trade-offs, their underlying causal mechanisms still remain rather poorly understood. Importantly, one of the central postulates of life history theory, namely that trade-offs are caused by competitive resource allocation, might not necessarily always hold. As discussed in many chapters throughout this book (e.g., Chapters 11, 13, 27, and 28), major efforts are currently under way to dissect the mechanistic basis of life history trade-offs.

1.5 Conclusions

Combining mechanistic and evolutionary analyses of life history variation is a fundamental yet ambitious aim in current biology. On the one hand, there are inherent biological and technical problems with studying complex quantitative phenotypes such as life history traits. On the other hand, there are cultural divides that necessitate a combination of diverse research approaches and concepts from both molecular and organismal biology. Despite these challenges, the chapters in this book illustrate that the successful integration of mechanisms into life history research is fully under way.

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