Mechanisms of Life History Evolution

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

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OXFORD
UNIVERSITY PRESS

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Great Clarendon Street, Oxford OX2 6DP

Oxford University Press is a department of the University of Oxford.
It furthers the University's objective of excellence in research, scholarship,
and education by publishing worldwide in

Oxford New York

Auckland Cape Town Dar es Salaam Hong Kong Karachi
Kuala Lumpur Madrid Melbourne Mexico City Nairobi
New Delhi Shanghai Taipei Toronto

With offices in

Argentina Austria Brazil Chile Czech Republic France Greece
Guatemala Hungary Italy Japan Poland Portugal Singapore
South Korea Switzerland Thailand Turkey Ukraine Vietnam

Published in the United States
by Oxford University Press Inc., New York

First published 2011

British Library Cataloguing in Publication Data
Data available

Library of Congress Cataloging in Publication Data
Library of Congress Control Number: 2011920657

Typeset by SPI Publisher Services, Pondicherry, India
Printed in Great Britain
on acid-free paper by
CPI Antony Rowe, Chippenham, Wiltshire

ISBN 978–0–19–956876–5 (Hbk.)
978–0–19–956877–2 (Pbk.)

1 3 5 7 9 10 8 6 4 2

"…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.

We are also grateful to our editors at Oxford University Press, Helen Eaton and Ian Sherman, for their timely and professional support during all stages of this project; to Laura Rosario Sanchez for major help with manuscript formatting and compiling references; and to Brenda Rascón and April Bojorquez for their work on the cover art. AHs work on this book was supported by a NSERC Discovery Grant.

Last but not least, our largest debt of gratitude is of course to the authors themselves. Despite many other academic and personal commitments, they have all written excellent chapters in a timely fashion and patiently responded to our many requests. We are especially grateful to Steve Stearns for having read and synthesized 26 chapters and for the idea of including an exchange between the three of us at the end of the book. We are also indebted to Graham Bell for contributing the foreword to this volume. All these authors, colleagues, and friends have invested major amounts of their limited time to produce the scientific content of this book: the success is entirely theirs; all failures are ours.

Thomas Flatt (Vienna) and
Andreas Heyland (Guelph)
August 2010

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CHAPTER 28

What mechanistic insights can or cannot contribute to life history evolution: An exchange between Stearns, Heyland, and Flatt

Thomas Flatt, Andreas Heyland, and Stephen C. Stearns

When discussing Steve Stearns' chapter (Chapter 27) and the rationale of this book, the three of us realized that Steve and we (the editors) differ in how we see the contribution mechanistic insights can make to life history evolution. Steve suggested that life might be more interesting for our readers if we wrote a rebuttal to some of Steve's claims and if he then wrote an answer. This postscript summarizes our discussion.

28.1 Why mechanisms are important for life history theory: A response by Flatt and Heyland

Life history theory seeks to explain, from first principles, the evolution of the main features of life cycles, in particular the design of organisms with regard to reproductive success (Stearns 1976, 1992, Roff 1992, Charlesworth 1994). The theory claims that we need to understand two things in order to understand the evolution of life histories (Stearns 2000):

- the environmental factors that affect the age- or stage-specific schedules of survival and reproduction
- the connections (trade-offs) between life history traits and the internal constraints these connections (and other factors) impose upon how life history traits can vary.

By building on these simplifying claims, life history theory has focused on general principles and deliberately ignored complicating details, such as the mechanisms of genetics, development, and physiology. For example, a keystone of life history theory is the Euler–Lotka equation, which relates demographic traits such as age at maturity, survival rates, and rates of reproduction to fitness. By using this or related mathematical frameworks, and by assuming constraining trade-offs as boundary conditions, one can derive theoretical predictions about life history evolution, most—if not all—of which have been confirmed empirically with tremendous success. This large body of work has been summarized and reviewed in several excellent books by Stearns (1992) and Roff (1992, 2002). In contrast to classical life history theory, the present book has a different aim. By focusing on explicit genetic, developmental, and physiological mechanisms, it attempts to provide a description of the "molecular natural history" of life history evolution. Given the clear-cut success of classical life history theory, what can knowledge about mechanistic details contribute to our understanding of life history evolution?

In his chapter, Stearns argues that, while mechanistic studies have resulted in several striking conceptual advances, none of these insights is forcing the theory to change, at least not yet. Currently, most mechanistic descriptions of life history traits and their evolution neither directly test theoretical predictions, nor require the existing theory to be revised. While the predictive theory is deliberately void of explicit mechanism (as is common in evolutionary biology), the study of mechanisms is motivated by a reductionist description and analysis of function (as is typical in molecular biology). As Stearns points out, there is still a long way to go before mechanistic insights and the theory can cross-fertilize each other. While we agree with Stearns that, despite impressive progress, the study of molecular mechanisms that mediate life history evolution is still in its infancy and has not yet made sufficient contact with the theory, there are in our opinion several important issues in life history evolution that can be illuminated by taking a mechanistic approach. Here we discuss four of them:

- trade-offs
- antagonistic pleiotropy and the evolution of aging
- hormones as a feature of the genotype-phenotype map
- the evolution of life history transitions.

Some but not all of these issues contact the classical theory; for others, mechanistic insights are likely to improve our general understanding of life history evolution and might lead to extensions of the classical theory in the future.

The first issue is that of trade-offs. The existence and importance of trade-offs in life history evolution is undisputed (Roff 1992, Stearns 1992), but as has been pointed out by Stearns (e.g., Stearns 2000, 2005, Stearns and Magwene 2003) and many others, we lack fundamental knowledge about their genetic, developmental, and physiological causes. In most cases, trade-offs are simply assumed to exist, for example as constraining boundary conditions in models of life history evolution, and even when they are measured (through genetic correlations or correlated responses to selection), their underlying mechanisms remain typically unknown (Stearns 1989, 2000, Stearns and Magwene 2003). This lack of mechanistic insight into the nature and structure of trade-offs is problematic for at least three reasons.

First, while the theory is in most cases silent on the causes of trade-offs (S. C. Stearns, personal communication; Stearns 1992), many life history models assume that trade-offs are caused by competitive resource allocation (Kirkwood 1977, van Noordwijk and de Jong 1986, Houle 1991, de Jong and van Noordwijk 1992, Shanley and Kirkwood 2000, Worley *et al.* 2003). However, as work in this volume illustrates, this might not always necessarily be the case. Trade-offs can occur for structural reasons or be caused by signaling processes independent of resource allocation (Tatar and Carey 1995; also see Chapters 11 and 13). Moreover, when reading the recent experimental life history literature it becomes obvious that most empirical studies of trade-offs uncritically assume that such trade-offs *must be* caused by competitive resource allocation (Barnes and Partridge 2003, Harshman and Zera 2007, Flatt and Schmidt 2009; also see Chapter 24). However, only very few studies have actually attempted to demonstrate the resource basis of trade-offs by quantifying acquisition or allocation of resources, i.e., energetic investment (Stearns 1992; see also Chapter 24). Thus, uncovering the causes of trade-offs might lead to us reconsider, at least in some instances, one of our most commonly made assumptions about the nature of trade-offs, an issue that directly touches upon aspects of the theory. While many life history models and predictions will be unaffected by this knowledge, others that rely on the assumption of resource allocation might need to be revisited. In any case, as good scientists, we should probe and question our assumptions and find out when they hold or not. Moreover, where resource allocation trade-offs do exist, different species might vary in the way resources are acquired and allocated to survival and reproduction, suggesting that unknown internal (developmental and physiological) mechanisms interact in unknown ways with extrinsic factors that affect survival and reproduction: without mechanistic insight we cannot develop a theory to explain such variation (Stearns 2000).

Second, life history theory distinguishes between physiological and microevolutionary trade-offs (Stearns 1989, 1992). A physiological trade-off is caused by competition among two or more processes for limited resources (or by mutually exclusive signaling processes independent of allocation) within a single individual, whereas a microevolutionary trade-off is defined at the population level as a change in a trait that increases fitness and which is linked to a change in another trait that decreases fitness—thus, there must be a negative genetic correlation in the population between the two fitness components in question. What is the relationship between physiological and microevolutionary trade-offs? For example, a physiological (intra-individual) trade-off can be genetically fixed in the population, and all individuals will physiologically respond in the same way, without the physiological trade-off contributing to the microevolutionary trade-off. Alternatively, physiological trade-offs might be genetically variable and contribute to, or modulate, evolutionary trade-offs among individuals in the population and can thus contribute to the response to selection (Stearns 1989, 1992). Without detailed knowledge about the physiological nature of trade-offs, it will be difficult to understand or predict when and how physiological trade-offs contribute to, or modulate, evolutionary trade-offs or not (for an empirical example see Flatt and Kawecki 2007).

Third, development and physiology (for example, hormonal signaling, as amply demonstrated in this volume) can modulate the expression of genetic (microevolutionary) trade-offs in a way that depends on the environment (Stearns 1989, 1992). This is illustrated by the fact that the sign of a genetic correlation can change across different environments. For example, a genetic correlation might be negative in one environment but positive in another. Similarly, a trade-off might be present in one environment but absent in an alternative environment, suggesting that trade-offs can be "broken" or "uncoupled." In addition to this environmental dependency, trade-offs might or might not change under selection. In none of these cases do we really understand the causes that underlie this dynamic and flexible behavior of trade-offs (Stearns 1989). As several chapters in this volume suggest, mechanistic insights might help us to understand this issue better. Even though recent insights into the mechanistic nature of trade-offs might not yet directly change the way we construct life history models, we agree with Stearns (2000) that "the explanation of variation in life histories will not be complete until those mechanisms are understood."

The second issue relates to the importance of trade-offs in the evolutionary theory of aging, which can be considered a part of life history theory (Stearns 1992, Charlesworth 1994). While the evolutionary theory of aging has not been given much attention in this volume (for overviews see Rose 1991, Stearns 1992, Stearns and Partridge 2001, Flatt and Schmidt 2009), work on aging serves as a good example for how mechanistic insights can touch upon the theory. In short, two major models have been proposed to explain the evolution of aging (Medawar 1952, Williams 1957). One of them posits that early fitness components are negatively connected to fitness components late in life by alleles with antagonistic pleiotropic effects; under this model, the evolution of aging can be seen as a byproduct of selection for increased fitness early in life, with weak selection at advanced ages being unable to oppose the pleiotropic and negative effects late in life (Williams 1957). Thus, Williams' postulate predicts that early and late fitness components are coupled by trade-offs that are due to the existence of alleles with antagonistic pleiotropic effects. This is clearly a mechanistic prediction of an evolutionary model that is part of life history theory broadly construed (Stearns 1992, Charlesworth 1994).

While selection experiments and phenotypic manipulations have lent much support to Williams' hypothesis (Stearns and Partridge 2001, Flatt and Promislow 2007, Flatt and Schmidt 2009), formally testing the "antagonistic pleiotropy" model requires us to identify genes and to functionally characterize them. Without this knowledge we cannot know whether the observed trade-off pattern is caused by antagonistic pleiotropy, linkage disequilibrium, or a correlation with a third unobserved trait (Clark 1987, Charlesworth 1990, Houle 1991). This is an important mechanistic issue regarding trade-offs: it not only concerns trade-offs between early and late fitness traits that are relevant in the evolution of aging, but in fact relates to trade-offs between fitness components in general. While knowledge about the genetic nature of trade-offs might not affect most classical life history models, where trade-offs are simply assumed as boundary conditions, it is relevant for our understanding of the evolution of aging. So what have genetic insights contributed to this problem?

Recent research in molecular genetics of aging now tells us that Williams probably got it right and that many mutations (at least in the laboratory) exhibit the kind of life history pleiotropy he envisaged. With the advent of improved methods for genetic mapping, evolutionary geneticists have also recently begun to successfully identify single loci and quantitative trait nucleotides with major pleiotropic effects on life history traits in natural populations, including polymorphisms in insulin/IGF-1 signaling and other pathways (Carbone *et al.* 2006, Schmidt *et al.* 2008, Paaby *et al.* 2010; also see Chapter 18). We consider this an example where genetic insights have confirmed a postulate that can be considered part of life history theory broadly construed (Flatt and Promislow 2007, Flatt and Schmidt 2009). Moreover, as discussed by Stearns and other authors in this book, this work has led to the realization that the insulin/IGF-1 signaling pathway might play a major evolutionarily conserved role in pleiotropically affecting lifespan and other life history traits connected with it. This finding has come as somewhat of a surprise to evolutionary biologists working on aging who, starting with Williams (1957), had intuitively assumed that it would be hard to identify major homologous genetic effects upon lifespan (Flatt and Schmidt 2009).

The third issue concerns hormones as intermediate components of the genotype–phenotype map. Since hormones are critical physiological regulators of decisions about growth, storage, maturation, and reproduction, life history theorists postulated that they might play a major role in life history evolution, for example in terms of acting as mediators of trade-offs (Stearns 1989, Finch and Rose 1995). Indeed, over the last 15 years or so we have accumulated a wealth of data that seem to confirm this intuition. As many chapters in this book showcase, we have now many excellent examples that suggest that hormones are key players in physiologically mediating life history transitions, trade-offs, and phenotypic plasticity (see many chapters in this book and reviews by Zera and Harshman 2001, Flatt *et al.* 2005, Heyland *et al.* 2005, Toivonen and Partridge 2009). Again, one might say that insights into hormonal mechanisms do not force the theory to change, but it is also amply clear now that changes in endocrine function are central to the coordination, integration, and modulation of life history traits in response to changes in the environment. One (perhaps naive) prediction would then be that genes involved in endocrine signaling might be "hot spots" for the evolution of life histories. If so, we would have learned something important about the functional architecture of life history traits.

A fourth issue is the evolution of life history transitions, such as metamorphosis and transitions between alternative life history strategies. Although the classical theory does not make specific predictions about these phenomena (Stearns 1992, 2000; also see foreword to this volume), an improved knowledge about the biology of life history transitions is clearly important for our understanding of life history evolution. We believe that mechanistic insights will be particularly helpful for extending the classical theory into this uncharted area. Indeed, many chapters in this book provide good examples of how mechanistic studies are beginning to uncover important commonalities and differences in developmental aspects of life history transitions (see Chapters 3, 5, 6, 7, and 8.).

More generally, this body of work holds great promise for expanding the scope of classical work on life histories by conceptually integrating it with recent advances in evolutionary developmental biology (evo-devo). One major current and successful avenue is to integrate evo-devo with molecular population genetics and phylogenomics (Carroll 2005, Barrett *et al.* 2008, Rebeiz *et al.*, 2009, Stern 2010). We predict that in the future life history evolution will significantly benefit from cross-talk with these disciplines; such advances will allow us, for example, to test for signatures of selection at the DNA level and, in a comparative and phylogenetic context, to determine whether particular molecular changes that affect life histories are homologous or caused by convergence.

There is no doubt that classical life history models have derived their impressive predictive power from the fact that they are phenotypic models that are silent on mechanism. Yet we are convinced that in order for us to arrive at a more complete understanding of life history evolution we need to learn more about the mechanisms that affect life history traits and their evolution. Regarding the classical tension between organismal and molecular biologists Stearns (2000) notes: "We will see more cooperation between these fields, for it is in the interest of both to use each other's methods and to ask each other's questions, and there are solid grounds for mutual respect. People with one foot solidly in each camp will do exciting research." One of the principal motivations for editing this volume was to bring these two camps together more closely. If this book has helped this integration a bit, then it has fulfilled its purpose.

28.2 Reply by Stearns: Mechanisms do not yet force the theory to change

Thomas and Andreas have done a good job of defending their project, and I find it hard to disagree with a statement that cites my work 28 times in 7 pages. We do not have any fundamental differences. Here I only want to state explicitly where we agree and reiterate some distinctions that I tried to draw in my chapter.

We agree that studies of mechanism have illuminated the nature of trade-offs. Uncovering those mechanisms has revealed that energy allocation is not all there is to trade-offs, and some of the mechanisms mediating aging appear to be ancient and widely shared. These are significant advances, but because life history theory was silent about the mechanisms that produce trade-offs, uncovering those mechanisms was not going to change that *kind* of theory.

Some of our disagreement arises from what we consider to be life history theory. I consider it to be the part of the study of life history evolution that can be expressed in mathematical models. They consider it to include, in addition to that, assumptions about the mechanisms that cause trade-offs. Where those mechanisms make a difference to the predictions of theory, they should be included in the theory. My point is, that has not yet been done, and doing so does not appear to have been on the agenda of most of those who authored chapters in this book. That is not a criticism, it is simply a comment about what future research might address. I do not expect it to be a top priority for those working on mechanisms, to whose strengths it does not play, but it might attract those with a gift for theory.

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