The Evolving Female

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A Life-History Perspective

Mary Ellen Morbeck,
Alison Galloway, and
Adrienne L. Zihlman, EDITORS

PRINCETON UNIVERSITY PRESS
PRINCETON, N. J.

Copyright © 1997 by Princeton University Press
Published by Princeton University Press,
41 William Street, Princeton, New Jersey 08540
In the United Kingdom: Princeton University Press,
Chichester, West Sussex

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Library of Congress Cataloging-in-Publication Data

The evolving female : a life-history perspective /
edited by Mary Ellen Morbeck, Alison Galloway, and
Adrienne L. Zihlman.
p. cm.
Includes bibliographical references and index.
ISBN 0-691-02748-X (cloth : alk. paper). —
ISBN 0-691-02747-1 (pbk. : alk. paper)
1. Human evolution. 2. Women—Evolution.
3. Females—Physiology. 4. Women's studies—
Biographical methods.
I. Morbeck, Mary Ellen, 1945– . II. Galloway,
Alison, 1953– . III. Zihlman, Adrienne L.
GN281.E93 1996
573.2—dc20 96-20402

This book has been composed in Galliard

Princeton University Press books are printed
on acid-free paper and meet the guidelines for
permanence and durability of the Committee on
Production Guidelines for Book Longevity
of the Council on Library Resources

Printed in the United States of America
by Princeton Academic Press

10 9 8 7 6 5 4 3 2 1

10 9 8 7 6 5 4 3 2 1

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Acknowledgments

MANY PEOPLE contributed to this project and we are grateful to them all. We each owe an intellectual debt to Sherwood Washburn, who served as a mentor at various points in our careers. Through his comparative, functional, and evolutionary perspective that integrated the anatomical, behavioral, and social dimensions of apes, early hominids and ourselves as *Homo sapiens,* we first gained a sense of "real animals" and their lives.

We are indebted to the colleagues who contributed chapters and to their subjects, both human and nonhuman, from whom we acquired the information to formulate the discussions presented here. They allowed us to share their lives for a time, and we thank them.

Our appreciation goes to Emily Wilkinson of Princeton University Press and to her assistant, Kevin J. Downing. Both were there to answer the long stream of questions, provide practical advice on editing, and they showed confidence in the worth of this project.

We owe a huge debt to those who enabled each of us to communicate among ourselves and transmit manuscripts, revisions, and comments. Debbie Neal, Penny Stinson, Bill Hyder, and Jane Nyberg (UCSC) assisted in the translation of computer disks. Doris Sample's (UA) good humor in the face of repeated changes in word processing was also a great blessing. The late Walt Allen (UA), with infinite patience and wit, persevered in adapting computer resources to meet the needs of a changing volume. The Word Processing Center at UCSC word-scanned hard copy, under sponsorship of the Social Science Division. Jacky Leighton and the UCSC Social Science Steno Pool facilitated the printing of this manuscript. Michelle Bezanson (UA) and Kim Nichols (UCSC) toiled in checking references and quotes.

As editors, we each experienced some very personal debts. We now recognize that (1) you can't write a book without hands, and (2) you can't write a book with a two-year-old, now a three-year old. Yet despite these revelations, we managed to complete the bulk of the work during a time when one of us was disabled by repetitive strain injury and another was balancing work and child care. Although these factors substantially slowed our pace of work, they also brought new insights into "what it means to be human." For those who helped maintain our sanity and our survival during this period, we would like to express the following personal thanks.

From M. E. Morbeck: As I continue to learn how to build a new way of life, thanks to John Hoffman who kept me together and took me away at all the right times. Many other friends also continue to provide much-appreciated intellectual as well as logistical "life support" and I thank them: Virginia Morbeck and Michelle Bezanson, Alison Galloway, Virginia Landau, Ken Mowbray, Lita Osmundsen, and Jane Underwood. My Tumamoc Hill friends, especially Paul Martin, deserve special thanks for creating and maintaining an intellectually exciting and productive place to work. The natural history of "The Hill" itself has revealed its healing powers for which I am very grateful. In addition, Jane Church, Nancy and Bill Cook, and Nancy and Jim Hoffman provided much-needed retreats for quiet thinking, reading, and writing. Thanks also to a myriad of highly skilled physicians, other health-care specialists and, especially, my ever-cheery hand therapists, who nurtured my positive outlook as part of their medical practice. I am grateful to Jane Hill, John Olsen, and Holly Smith for their use of administrative powers in the best possible way—to facilitate faculty to achieve research

and teaching goals no matter how their lives are constrained.

From A. Galloway: I would like to express gratitude to my family, especially my parents whose emphasis on education allowed her to pursue this career. My husband, Charlie, picked up immeasurable "slack" when my mind and efforts were devoted to the production of this volume. Without his emotional support and, as importantly, practical assistance, I would not have been able to even consider editing this book. I know he tired of my focus on this work, but he also demonstrated incredible patience and fortitude. I am deeply grateful and hope that I never have to put him through it again—although I say that as I embark on another major writing project.

My daughter, Gwyneth, may never understand how much she helped bring this book into perspective. Until now, my examination of human reproduction was theoretical. The physical demands of childbearing and rearing, combined with a professional career, drove home the delicate balance and continual negotiations women make among their various roles. Like most new parents, we never imagined how much time a child required. But, like most parents, we also never imagined how much joy a child brings. That, too, is part of the balance. In many respects, she is my best research project.

From A. L. Zihlman: I would like to acknowledge the colleagues who contributed to the genesis of this volume. The conference on which the volume is based was held at the University of California, Santa Cruz. Chancellor Robert Stevens designated the conference a cornerstone event of the campus' twenty-fifth anniversary celebration. Visits to Caroline Pond at Milton Keynes in the U.K. and to Silvana Borgognini Tarli in Pisa, Italy stimulated me to try to bring together outstanding scholars like these to exchange information and ideas about female biology and evolution. During the two years of preparation for the conference, Amy Nilson taught me logistics; Debra Bolter, Carla Daniel, Beverly McLeod, and Robin McFarland were significant in the planning and execution. Melanie Mayer, Carolyn Martin Shaw, Catherine Cooper, Sheila Hough, and Donna Haraway contributed to the conference discussions. Debbie Neal and Wanda Santos acted as hostesses. Joanne Tanner and Chuck Ernest videotaped the public lectures. Carla Daniel contributed to early stages of the editing process.

In funding the project and forming the inception of the idea, we worked closely with Marilyn Cantlay (UCSC), who assisted in seeking financial support and in grant writing. A small grant from Feminist Studies Research (UCSC) enabled the project to take its first step; the Graduate Division and Dean Geoffrey Pullum provided major funding, supplemented by the Social Science Division and Dean William Friedland (UCSC). The University of Arizona Social and Behavioral Research Institute provided funds for M. E. Morbeck's participation. Private donors covered some additional expenses. A grant from the Wenner-Gren Foundation first for Anthropological Research and the interest and support of Sydel Silverman ensured that the conference happened. Lita Osmundsen, now retired from the Wenner-Gren Foundation, first showed us the value of small conferences.

What Is Life History?

WHAT DOES it mean to be human? How did we get to be the way we are? How do we begin to define "humanness"? We can approach these questions from comparative, functional, and evolutionary perspectives, which allow us to describe and explain variation in biology, behavior, and ecology in ourselves, in our close relatives, and in our ancestors through time and across geographical and ecological space.

In this volume, a number of themes are linked. The most important one is the evolutionary heritage that each organism carries—a heritage that shapes the anatomical, physiological, and behavioral responses possible to environmental stimuli. Throughout the book, we focus, in some way, on our species, humans, the features we share with other primates, and our legacies as mammals.

Life-history theory provides a means of addressing the integration of many layers of complexity of organisms and their worlds. Although most researchers recognize the many facets of what it takes to eat, survive, and reproduce, they highlight only a few traits in their modeling of life history. We broadly define "life history" in this volume to integrate both reproductive and survival features (Morbeck chap. 1), with the goal of examining the complexity itself. Natural selection is a critical component of the optimality models often used in life-history theory, and we recognize its importance as an evolutionary mechanism. We also stress the vagaries of individual life stories and their consequences for survival and reproduction.

We emphasize the life story of the functionally integrated individual, as expressed within its species-defined boundaries, from conception to death, and its genetic and other contributions to its population. This approach requires empirical, multigenerational, natural history studies. Biology and behaviors of known individuals are placed in social and ecological contexts as they negotiate unique pathways through the life stages, mate and, if female, rear offspring.

Whole Bodies/Whole Lives

Our emphasis is on the role of the individual in evolution. Each human, like other organisms, brings a genetic legacy that can be passed on to the next generation. Embodied within each person is the record of our evolutionary history. We see it in what makes up our genes and how they work. The genetic and molecular mechanisms for reproduction and guiding development of species- and sex-defined attributes stretch back billions of years to the origin of life itself. Sexual reproduction allows for the recombination of genes to form unique combinations in individuals while retaining the overall pattern of the species (Jolly chap. 19).

We can see our evolutionary past in our bodies, how they function, and how we behave. Our body plan is that of a vertebrate (e.g., head, trunk, four limbs), whereas our basic way of life and how we grow to maturity and reproduce follows the pattern of other mammals. Our large complex brains, body movements, and life-cycle timing are shared with the other primates. Independent use of fore- and hindlimbs, good hand-to-eye coordination based on grasping digits (fingers), and overlapping fields of vision (in-depth vision) are tied to the primate pattern of big brains. Our reproductive pattern that emphasizes one infant and a long prereproductive period of biosocial growth and development, and long periods of gestation, infancy, childhood, adolescence, and adulthood are shared with the

Old World monkeys and apes. Our recent ancestry with these catarrhine primates is evidenced by similarities in both the form and function of our bodies, for example, full stereoscopic vision, thirty-two teeth as adults, and fine-tuned manipulative hands. From our shared history with apes, we have broad, upright trunks, and flexible forelimbs. We are unique as humans—bipedal with large brains, long childhoods, and the ability to organize and explain our worlds via language and culture (Morbeck chap. 9; Zihlman chap. 13; McLeod chap. 20).

We place the organism at the center of the evolutionary process by focusing on individuals as each maneuvers through the life stages. The importance of the individual organism has long been recognized in evolutionary theory in relation to natural selection. As Mayr stated,

> [T]he individual and not the gene must be considered the target of selection. There are many ways of documenting the primary importance of the individual. First of all, it is the individual as a whole that either does or does not have reproductive success. Second, the selective value of a particular gene may vary greatly depending on the genotypic background on which it is placed. Third, since different individuals of the same population differ at many loci, it would be exceedingly difficult to calculate the contributions of each of these loci to the fitness of a given individual. And fourth, accepting the individual as a whole makes it unnecessary to make the confusing distinction . . . between internal selection (dealing with processes going on during ontogeny) and external selection (dealing with the interactions of the adult with the environment). (1988:101–102.)

The individual also serves as the pivotal point for moving into investigations at other levels. As Bennett stated,

> Biologists are usually content to specialize their studies at one functional level of organization (e.g., molecular biology, organ morphology, population biology). They seek the bases for the phenomena they study at one level removed from their expertise and are generally satisfied with explanations at those levels. Organisms, in contrast, are integrated units that encompass all levels of biological organization. They do not make distinctions between such properties as morphology, physiology, and behavior, nor do they develop those properties in isolation from all the other traits they possess. Individual traits do not evolve independently, rather they evolve only in the context of a complete functioning organism. (1989: 191.)

We start with the whole person, you or me, for example (fig. 1.1 chap. 1). From here, for instance, we can move "up" and "out" into the empirical studies that deal with specific individuals as integral parts of populations. This is exemplified in this volume by the work of Fedigan, Morelli, Pavelka, Panter-Brick, Ono, Draper, Reiter, and Vitzthum. We can also move down, into the anatomy and physiology of the individual as seen in the chapters by Morbeck (chap. 9), Galloway (chap. 10), Pond (chap. 11), Borgognini Tarli and Repetto (chap. 14), Zihlman (chaps. 8, 13), McFarland (chap. 12), Panter-Brick (chap. 17) and Vitzthum (chap. 18).

The many dimensions and layers of complexity of the individual and its world weave together features that have evolved to promote survival and biosocial health at each life stage with those associated directly with mating and rearing of offspring in adulthood (Zihlman et al. 1990; Morbeck 1991b). The emphasis on whole bodies and whole lives is more than a theoretical concept. It is grounded in studies detailing how the survival and reproductive "decisions" made at different biobehavioral levels of organization vary throughout life. From the point of view of the organism, such complete integration is essential.

Natural-History Studies

We view *Homo sapiens* (modern humans) as individuals operating as part of the natural world. As such, humans, too, are subject to the

same "decision-making" situations that affect all life. Decisions are often illustrated in flow diagrams as an event in the life of the "typical" organism, for example, the trade-off between growth and reproduction. We see decisions as both more complicated and more basic, such as "How do I make it through today?"—what and when to eat, when and with whom to mate, how to avoid danger, etc. It is these activities, made by many individuals, that influence the course of evolution.

We include the study of the natural history of humans within the evolutionary approach. We are interested in (1) what individuals do in particular environments in order to stay alive and healthy, to grow to biosocial maturity, to mate, and to rear offspring; (2) what survival and time-based life-history species- and sex-specific features enable or constrain organisms as they grow to maturity and reproduce; (3) what factors contribute to survival and reproduction, and in particular, from the perspective of the individual's life, what are the short- and long-term consequences of particular biobehavioral and environmental interactions for adult reproductive outcome and individual health and psychosocial well-being throughout the life stages?

Why Females?

When and how often during the life cycle can an individual female or male reproduce? How quickly can an infant achieve physical and, in addition, social independence and reproductive capability? Finally, how much time and energy does each sex devote to activities that promote successful mating and how much to protection and raising of healthy offspring to reproductive capacity?

Females and males share species characters but have different reproductive roles. Sexual reproduction is not new; it has been around for about a billion years. As Jolly (chap. 19) points out, it is the basis for information exchange from generation to generation. Sexual reproduction took an interesting turn more than 100 million years ago with the origin of mammals and a new way of raising young. This new twist, the mammals, is defined, in part, by reproductive asymmetry. The differences between the reproductive roles and "responsibilities" of females and males, especially in placental mammals like ourselves, necessitates slightly different criteria by which to measure their contribution to the vertical passage of genes.

Females have been the primary focus of life-history studies. Our choice to retain this focus in this volume reflects a multilayered set of reasons. Conventional life-history studies grounded in population biology (demography) have concentrated on the timing and extent of energy investment in reproductive events that characterize the females of a species. There are many reasons for this focus. Females are the "limiting" sex in terms of the number of offspring that can be produced. This is seen especially in primates with a single offspring per birth and extended periods of growth and development. Maternity, unlike paternity, is very rarely in question because of the nature of the mammal mother-infant relationship. Females and their offspring are observable and can be documented in field studies. Long-term, multigenerational studies of humans, nonhuman primates, and other mammals, as shown by the following chapters, record both the nature and timing of female reproductive efforts.

In addition to the influence by females on the number and identity of offspring, females are important, at the cellular and genetic level, as the source of the majority, if not all, of the nonnuclear components transferred to the next generation. Part of this component is the DNA housed in the mitochondria, the organelles that generate the cell's energy-storage mechanism. An interesting by-product of this feature is that studies of variation in mitochondrial DNA within and among modern human groups also allow analysis of maternal lineages and times of divergence of various groups in the evolutionary past.

The mother also contributes to her offspring half of the nuclear DNA, which contains the species template for the growth and develop-

ment. Along with the paternal contribution, these set the parameters by which the organism is formed and functions. Nutrients produced by the mother and carried in the ovum fuel the fertilized egg through its initial divisions until implantation in the uterus.

Placental mammal offspring are totally dependent on the mother for a good start in life. The mother-infant bond, so evident after birth, builds on the biological connections of the prenatal period. Internal gestation allows the mother to transfer energy directly to the offspring through the placenta. The mother is the environment, and the infant relies on her body for its survival and for its continued growth. This does not mean that the infant is without power, as fetal physiology permits capture of maternal nutrients—at times even at the expense of maternal health.

During her pregnancy, the mother must continue to promote her own survival and well-being along with that of her offspring. The requirements of the pregnant female are frequently viewed as the sum of the mother and fetus (i.e., "eating for two"). However, the physiological capabilities of the pregnant female are enhanced to capture nutrients and are combined with behavioral changes in feeding and activity levels that can substantially change the size of the nutrient supply available (Zihlman chap. 13; McFarland chap. 12). Often even an otherwise minimal diet still can sustain the pregnant female with little effect on the success of her reproductive efforts.

After birth, the biological connections are continued and, particularly in mammals such as the primates, social and ecological bonds between mother and offspring are significant. The mother feeds, protects, and socializes her one or more offspring. The primate mother in most species also transports her offspring throughout its infancy.

Among the primates, Old World monkey, ape, and human mothers continue to interact with older offspring even after giving birth to another infant. At the same time, they are still promoting both their own survival and well-being and that of the youngest offspring. In many primates, such as Japanese macaques, mother-daughter interactions apparently are crucial for maintaining group cohesion through generational time (Pavelka chap. 7). These alliances have important benefits for both mother and her offspring. In humans, the mother often also provisions and cares for the older siblings of her youngest offspring although they, in turn, may help the mother in child care.

Temporal/reproductive characters, expressed in individual life stories and aggregated in breeding groups, pattern population dynamics at the population and species level. Females are important since, as suggested above, the investment in time and energy dictates the population replacement rate. This can only be determined by when, how rapidly, and how many offspring a female can bear and rear. Yet, the female does not determine this alone, as it is also governed by the species-specific pattern of growth and development as modulated by the individual offspring itself. Social organization also influences the mating opportunities for females. Availability of males, social context, and individual life story all play a role in how each individual is involved in further reproduction.

Mechanisms that contribute to evolutionary change act on the individual, and their effects are measured in populations and higher taxonomic categories over time. Chance events as well as natural selection are known to influence survival and reproduction of the individual. Gene flow, another source of genetic change, obviously occurs between individuals and affects the extent of genetic variation. Mutation, the source of all variation at the molecular level, occurs in individuals but frequently may arise during the elaborate processes of cell division and replication that accompany sexual reproduction. These changes are measured in populations in terms of gene frequency or as expressed in morphology.

The mothers and infants, within the context of population dynamics, bring us to the level at which we can measure evolutionary change. Monkeys, apes, and humans are social as well as biological beings, and reproduction may be

said to be "costly" when measured in terms of energy investment and time. This is especially evident when, as shown by chapters in this volume, (1) reproductive success is defined in its broadest sense as the number of offspring produced during a lifetime that survive to reproductive maturity and produce their own offspring, and (2) when biological and social efforts invested in mating activities and protecting, rearing, and socializing offspring are both recognized as major contributing factors to reproductive outcome.

What Is Life History?

What is the life-history approach, and why is it important? Life-history studies grew out of the natural history tradition. These studies focused on whole organisms and whole lives by examining and documenting individuals through their life stages, survival, and reproduction. This knowledge was derived from empirical observation and some field experimentation (Fedigan chap. 2).

As the biological and social sciences developed, the amount of information that could be collected and analyzed grew dramatically. Individual scientists simultaneously came to specialize in ever narrowing fields—not only in their choice of organisms examined but also in the level at which they were observed. The "whole organism–whole life" perspective faded with the rise of theoretical population biology and quantitative population genetics. The development of mathematical modeling as part of population biology and ecology focused on understanding population dynamics in which the time and energy investments could be calculated based on populational averages or theoretical constraints.

Population Biology and Life-History Theory

Most current definitions of life history are part of the tradition of population-biological studies. Life-history theory can be seen to fall into two different emphases (e.g., Lessells 1991): (1) population biology at the genetic level and (2) population biology at the phenotypic level, generally with the use of optimality models. The former allows for mathematical modeling to the gene or allelic level, examining the effects of natural selection on gene frequencies. The latter concentrates on the timing of the life cycle, generating an average of the features expressed by the individuals. In essence each perspective interprets life-history theory in the manner that may be termed "life-event theory": life is marked by occurrences that are measurable and for which selection works toward the optimal pattern.

These life-history models center on the life cycle or timing of growth and maturity. They emphasize age-specific values of reproduction and death, that is, the reproductive events that pattern the life course (Partridge and Harvey 1988). Stearns (1992:9), for example, stated that "life history theory deals directly with natural selection, fitness, adaptation, and constraint," all of which involve whole bodies/whole lives. Yet, his list of principal life-history traits only includes specific measurable "events," and, in addition, "amounts" such as "size at birth; growth pattern; age at maturity; 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" (1992:10). We see problems with linking his definitions and the criteria for measured categories. For example, these events do not occur at a single point in time for the individual in the species or population, nor do they occur at the same time for all individuals. The use of fixed points hinders recognition of the wide-ranging variability of these "events" and the gradual nature of transition between life stages. Furthermore, in this reductionist version of life history, the survival features such as locomotion, feeding, predator avoidance, and social behavior so critical throughout life are assumed or, too often, never considered.

One of the central features in conventional life-history theory as part of populational studies is the concept of "trade-offs" in which the

life-history attributes are balanced against each other. These trade-offs link traits that constrain or limit their simultaneous action and evolution. Using this concept, an individual's current reproduction is suggested to imperil current survival and also have an impact on future reproduction. "Because energy used for one purpose cannot be used for another purpose, living organisms face a series of trade-offs through time. The two most fundamental trade-offs, which are at the center of all life-history theory, are those between current and future reproduction and between the number and fitness of offspring." (Hill 1993:80.) Other proposed trade-offs are made, for example, between the number, size and sex of the offspring (Bell and Koufopanov 1986; Boyce 1988; Lessells 1991; R. H. Smith 1991; Roff 1992; Stearns 1992; Charnov 1993; Zhang and Wang 1994).

Trade-offs are not generally discussed in terms of the day-to-day detail of individual's lives, yet life stories are filled with daily decisions about survival and reproduction. Each individual continually confronts and copes with situations that are unique to her/his life. Physiological trade-offs link functions that can be constrained because of reliance on the same energy resource by the individual. For instance, should a female devote energy to mating or to procuring additional food? But then what good is mating if it is unsuccessful because of poor nutrition and body health?

How is our version of life history similar to the population-biological approach? Like population biologists, we focus on females. Females, in conjunction with species-defined growth and development, determine the growth potential of the population by when, how fast, and how many offspring can be produced.

The timing of the life cycle, therefore, is important in all studies of life history. We share this emphasis with conventional life-history theorists. We also recognize the need to look at the population in order to measure aspects of genetic and phenotypic change through generational time. Mathematical models provide us with a framework for organizing information at the populational level or higher. Since we are ultimately interested in how evolution works, we focus on the individual and its links to its population. We broaden our interests beyond counting time to document how each individual's life plays out through the life stages and its survival and reproductive outcome. Our focus on the individual rather than including individuals only in central-tendency statistics sets us apart from the more conventional life-history theorists. Although the importance of the individual is mentioned in virtually all treatises on life history, this view frequently is overshadowed by the emphasis on populational calculations.

Awareness of the individual with its unique life story becomes crucial when we look beyond natural selection to the effect of "luck" or chance events in individual lives. Variability among individuals becomes apparent as researchers have begun to test mathematical models with organisms in the real world. Phenotypic plasticity, the range of variation within a species boundaries, must be viewed as essential, rather than deviations from an "optimal" pattern. As R. H. Smith stated, "Individuals that are "lucky" for some non-genetic reason will tend to perform better in several components of fitness than others that by chance are less fortunate. It is the confounding of effects of luck with those of constraints within individuals that make the simple **E** matrix hard to interpret." (1991:92–93.) Factors that appear critical at one period of the life cycle may be less important later. This can most readily be seen in tracking individuals within populations. As the chapters in this volume show, we can understand the importance of the individual life story and the contributions to population dynamics only with an empirical natural history approach combined with a broad view of life-history variables.

Therefore, we wish to return the primary focus to the whole organisms–whole lives as the appropriate starting point for understanding life history. This viewpoint aligns with a trend toward the reemergence of the impor-

tance of the individual in biology and ecology (Mayr 1982, 1988; Bock 1989; Kohn 1989; Wake 1990).

In this context, the emphasis on statistical central tendencies, so prevalent in current life-history models, ignores the complexity of reproductive and survival tactics. By stressing "optimality" and emphasizing life events, the variation in biological and behavioral responses to environmental stimuli is underestimated. Rather than proposing that selection works toward a single optimal strategy, we propose that natural selection may actively favor two or more parallel or complementary effective strategies for survival and reproduction. Each will allow the transmission of genetic material into the next generation but retain flexibility within the species to cope with the environmental fluctuations that may periodically favor one or the other for short periods of time. We see flexibility itself as an evolutionary adaptation.

A New Focus to Life-History Theory

As becomes evident in this volume, we are not fully comfortable with the translation of life-history theory, as it presently stands, into analyses of the long-lived and socially complex mammals such as the primates, including humans. Traditional life-history theory is difficult to apply to organisms with life cycles in which the stages and events are not punctuated by abrupt transitions. Primates are particularly prone to "blurring" of the boundaries between life stages, resulting in great variability in the timing of major life events such as the age at first birth. Much of this variation is due to flexibility in the response to pressures from the physical environment, but the social environment also can impede or accelerate the rate of passage through the life course. Drastic simplification of complex organisms such as primates is required before they can fit a model in which life-cycle timing and energy/time trade-offs can be readily calculated (e.g., Charnov and Berrigan 1993).

How, then, does our approach differ from the traditional approach to life-history theory? First, in the perspective of this volume, which emphasizes individual life stories, the data on each individual are then aggregated to produce a portrait of the population without losing the focus on the individual. In part, our work reflects a more positive approach to life history since our emphasis is on what the animal *does* in order to live and reproduce rather than relying largely on the single features, for example, age at death.

Second, we do not see trade-offs as the best way to understand life-history features. This concept has been traced to the laws of thermodynamics, which provide the principles by which energy is exchanged in *closed* systems (e.g., Hill 1993). The idea that energy cannot be used for two life processes at the same time—a useful world view if one wants to follow mathematical models—does not reflect the situation encountered in real animals living real lives.

As seen in this volume (Pavelka chap. 7; Panter-Brick chap. 17; Vitzthum chap. 18) the life of highly social animals such as primates consists of doing many things simultaneously. Rarely do we see the "choice" as simply one of eating or reproducing. Time and energy, in most cases, do "double duty" or even "triple duty" in that time the mother spends feeding, for instance, also is time spent showing her offspring what to eat, how to find it, and how to claim it.

The use of trade-offs in life-history theory has often been equated with a consistent level of energy and time available to the organism. In real life, the amount of available energy is a constantly shifting quantity. In part, this is due to changes in the availability of resources as a result of seasonal shifts, climatic fluctuations, habitat changes, and so on. The animal, however, also plays a major role in determining the level of energy. This can be done by choosing or getting preferential access to higher-quality foods, or focusing attention on certain food sources. Digestive tracts are not consistent: there is individual variation and, throughout the lifetime, the size and function of the digestive system will vary to accommodate different

levels of demand for nutrients. Behaviorally, animals may forgo nonessential occupations such as grooming or resting in favor of meeting the demands of feeding and reproduction. Although the concept of trade-offs may be appropriate in some tightly controlled situations, in the real world the complexity of the choices confounds attempts to force them into a simple dichotomy.

Third, we raise the question of concept of time. Most organisms, including long-lived ones, do not appear to use long-term planning in making decisions. The decisions are based on the opportunities available now, the hazards apparent, the hormonal milieu of the organism, and its energetic resources. Basically, it is asking, "Will I feed or mate?" not "Will I reproduce now or postpone it until a later date when the environment may be better?"

Even for humans who have a concept of past, present, and future, we often live for the present and make decisions about survival and reproduction that are immediate. Hill (1993) pointed out our unwillingness to forgo the pleasures of a high-fat diet or of smoking at the risk of disease later in life. We understand that we have life after the present but infrequently negotiate our pathway with these ultimate goals in mind. For example, few people will admit to being fully aware of how the act of reproduction would alter their lives.

Fourth, to follow the natural history approach we advocate expansion of the current concept that highlights the timing of growth and development markers and reproductive events so that they intertwine with survival features with their biological foundations in functional anatomy, biomechanics, feeding ecology, and so on. Additional features, at an individual level, would encompass well-being—including the influences of disease, trauma, and psychosocial health—and, as aggregated groups, would reflect population demography. This broadly defined life-history approach allows for greater recognition of the multiplicity of factors that constitute the individual's environment. We see natural selection as enhancing the flexibility within species-defined systems. The range of flexibility is seen in hard times; therefore, cross-sectional studies, lacking generational time, often fail to explore this essential aspect of life history.

Fifth, the approach, therefore, should be both multilevel and multigenerational. Within the organism, the shifting roles of biological factors (anatomical and physiological) must be acknowledged. Compilation of data on specific individuals tracked over time will permit an understanding of the mechanisms of populational change. In order to test hypotheses, information on parent-offspring relationships are necessary. Although females will remain the primary focus, the availability of DNA paternity testing in mammals, including nonhuman primates, is providing a window on the reproductive outcome of males.

Finally, returning to our beginning, the need for grounding of life-history studies in natural historical, empirical work is essential. As Southwood concluded: "More holistic studies are needed on communities and organisms along one or other of these axes to test the systems and the predictions that have been made. Combinations of field observations with information from the literature may be a powerful comparative approach" (1988:14.) The use of this approach also permits integration of humans with the natural world.

The population-biological concept of life-history theory has recently emerged in cultural and ecological anthropology (Hill 1993; Worthman 1993; Chisholm 1993; also see Low [1993] on ecological demography). Although the term "life history" has been used by cultural and social anthropologists to refer to recorded biographies, this new usage follows the current but narrow version of life-history theory.

Studies of growth and development have a long history in human biology (Tanner 1978) and has contributed to our understanding of nonhuman primates (Schultz 1956; E. Watts 1985b, 1990; Brizzee and Dunlap 1986). "The problems of human ontogeny and phylogeny will never be solved by the study of man alone, but are largely dependent upon new and

more adequate data on the growth and evolution of all the Primates. Since any phylogenetic change has to affect primarily the processes of growth, additional information on the developmental changes in monkeys and apes is one of the first requirements for a thorough appreciation of the peculiarities of human growth, which have separated man and the anthropoids." (Schultz 1933:61.) There has been a recent resurgence of interest in shifting between levels in order to understand the processes of growth and development and apply this to the fossil record (Bromage 1992; B. H. Smith 1992, 1994). Growth and development are now being integrated into biological anthropology with an important evolutionary twist. Data generated from this new research are exciting because combining them with an emphasis on life-history studies on human and nonhuman primates (Hiraiwa-Hasegawa chap. 6; Morelli chap. 15; Pereira and Fairbanks 1993) allows us to begin to synthesize lifeways and life-history features as integrated in individuals throughout their lives. The combination of these studies with life-history theory is a powerful approach to understanding our evolution.

We recognize the phylogenetic as well as the present-day connections among our own species, other primates, and mammals. Via cross-cultural studies, we are able to see and describe the complexities of our lives in the natural, economic, political, and cultural world. We must be evaluating real animals, living real lives, in real time and real environments.