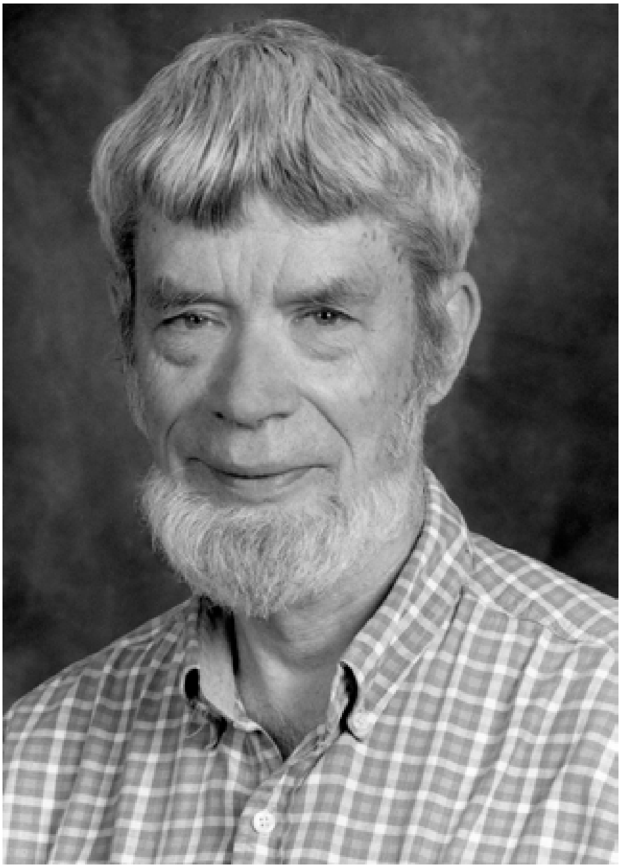
NATIONAL ACADEMY OF SCIENCES

GEORGE CHRISTOPHER WILLIAMS
1926–2010

A Biographical Memoir by
STEPHEN C. STEARNS

Biographical Memoir



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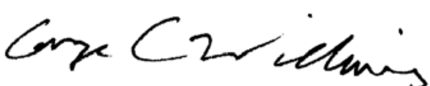

GEORGE CHRISTOPHER WILLIAMS

May 12, 1926–September 8, 2010

BY STEPHEN C. STEARNS

GEORGE WILLIAMS FUNDAMENTALLY changed how we think about natural selection and adaptation by emphasizing that selection acts much more effectively on genes and individuals than it does on groups or species. His analysis of the evolution of aging erected the structure in which evolutionary work on aging has since been conducted and yielded insights that helped him to cofound a broader field, life history evolution. And his puzzlement about the costly, complex, and nonetheless widespread presence of sexual reproduction across all major divisions of life called attention to a central problem that has occupied the attention of evolutionary biologists ever since. He accomplished this without mathematics by first thinking deeply and precisely and then writing clearly. His intellectual style, personal kindness, and self-effacing modesty resembled Charles Darwin's; his reserved demeanor, thoughtful silences, and brilliant comments resembled Bill Hamilton's.

YOUTH AND EDUCATION

George was born in Charlotte, North Carolina, where his father worked in a bank. When the bank failed in the Depression, his father lost his job, moved to New York City, and found employment as a pest exterminator. George's mother was a housewife until she separated from her husband and took the children back to Pikesville, Maryland, where her family lived. She then worked for a family doctor. George attended Fordham Preparatory School in the Bronx (a Jesuit institution offering training in Latin, Greek, English, math, and science) and Franklin High School in Reisterstown, Maryland, near Baltimore. Graduating in the middle of World War II, he entered an Army Specialized Training Reserve Program in engineering at Lehigh University, moving from there through basic training to Texas A&M, where he flunked out of the program.

After being posted to a water purification effort in Italy, he caught pneumonia; while recuperating he helped another patient fill out application forms for admission to Berkeley. "When George was asked why he didn't apply as well, he thought, Why not? So he did, and was admitted to Berkeley in August, 1946" (Erk, 2005). He graduated three years later with a degree in zoology, started graduate work at Berkeley, and transferred to the University of California, Los Angeles, to work on ichthyology for his Ph.D.

It was at Berkeley that George was attracted to evolution.

> My interest in evolution started in the summer of 1947, when I spent six weeks in the Painted Desert with a paleontologist named Sam Welles…officially in a summer course. He was a specialist in Triassic amphibians. Evenings were spent sitting around the campfire talking about things like evolution. For the first time in my life, people—real biologists, real scholars—were willing to sit and listen to my opinions…[S]hortly after that I signed up at the University of California at Berkeley for a course in evolution with Ledyard Stebbins, who …was the world's primary expert in evolution with respect to things botanical. Stebbins' course introduced me to Theodosius Dobzhansky's *Genetics and the Origin of Species.* Stebbins was great, but Dobzhansky's book was what got me interested in natural selection as a process." (1995)

While writing his thesis at UCLA, the flow of his ideas was so rapid that George was frustrated at having to change the paper in the typewriter. His wife Doris suggested that he feed a roll of shelf paper through the cylinder so that he could type without interruption. "George produced what was probably the first thesis in modern times to be written on a scroll" (Erk, 2005).

George had met Doris Calhoun in 1950 in a Berkeley course taught at Stanford's Hopkins Marine Station in Pacific Grove, California; they married in 1951. When they moved to UCLA, Doris spent a year as a research assistant, helping to support a family that was about to grow. Son Jacques was born in Los Angeles (in 1953), daughter Sibyl in Chicago (in 1954), and daughters Judith (in 1957) and Phoebe (in 1959) in Lansing, Michigan. There are nine grandchildren.

After UCLA George got a Ford Foundation fellowship and taught at the University of Chicago in a program designed to accelerate gifted high school students toward college degrees. There he had a career-changing reaction to ideas with which he strongly disagreed (1995).

> I attended seminars by people such as Alfred Emerson, the termite specialist and recognized authority on things evolutionary. I found his ideas absolutely unacceptable. That motivated me to do something. If it was biology Emerson was discussing, I would be better off selling insurance. I remember especially his lecture on the role of death in evolution. He was all in favor of death, and said that the reason we grow old and die is to make room for successors…This seemed so totally impossible, given that evolution proceeds by natural selection…[that it] initiated my first theoretical obsession: the evolution of senescence.

In the summer of 1955 he worked on fish at the Field Museum; that fall the family moved to East Lansing, Michigan, where George had been appointed assistant professor at Michigan State. There George wrote his foundational paper on the evolution of aging and his paper with Doris on social adaptations in insects. In 1960 his friend Frank Erk, who had taught with him in Chicago, recruited him to the new Long Island campus of the State University of New York with an offer of a tenured associate professorship. After two years in Oyster Bay near a temporary campus, George and Doris moved into a house they built in Setauket, within walking distance of the permanent campus at Stony Brook, where George spent the rest of his working life, retiring as professor emeritus in 1990.

At Stony Brook, George helped to establish the Marine Science Research Center and to persuade the New York Department of Environmental Conservation to locate their headquarters on the campus. George worked in the Center until the biological sciences were divided into departments, at which point he joined the Department of Ecology and Evolution, headed by Larry Slobodkin. Other impressive talent was also appointed, and Ecology and Evolution at Stony Brook became a national and international leader, attracting outstanding graduate students, postdocs, and faculty.

It was from that environment that in the summer of 1963 the Williamses returned to Berkeley, whose mature library was then more comprehensive than the new one being assembled in Stony Brook. There, in just a few months, George wrote most of his classic *Adaptation and Natural Selection,* a book that changed how we think about evolution by explaining complex problems in simple terms.

While at Stony Brook, George spent two sabbaticals in Iceland, where he became fluent in Icelandic and traded ideas with Icelandic ichthyologists, who have direct access to dynamically evolving freshwater fish.

George was vice president of the Society for the Study of Evolution in 1974 and became president in 1989; he was editor of *The American Naturalist* (1975-1979) and was devoted to *The Quarterly Review of Biology*, where he served as assistant editor, associate editor, editor, and editor emeritus (1964-2008). In 1989 he was named an eminent ecologist by the Ecological

Society of America and in 1992 received the Daniel Giraud Elliott Award from the National Academy of Sciences. He was elected a fellow of the American Academy of Arts and Sciences in 1990 and a member of the National Academy of Sciences in 1993. With John Maynard Smith and Ernst Mayr he was corecipient in 1999 of the prestigious Crafoord Prize, awarded by the Swedish Royal Academy.

George's major papers and books focus on issues related to adaptation and its limits—aging, altruism, reproductive investment, sex, and medicine—that illuminate two big questions. Does natural selection operate on genes and individuals or on groups, and how does selection design phenotypes for reproductive success?

INFLUENTIAL EARLY PAPERS

His first 1957 paper in the journal *Evolution*, "Natural Selection of Individually Harmful Social Adaptations among Sibs with Special Reference to Social Insects," was coauthored with Doris. It addresses Darwin's fundamental problem of the existence of reproductively sterile castes by examining the fate of a gene that causes its bearer to donate social goods to its family at a cost to itself. The argument comes very close to Hamilton's theory of kin selection, but the decision to frame it in terms of benefits to a family made it less general than Hamilton's approach.

In his second 1957 paper in *Evolution*, "Pleiotropy, Natural Selection, and the Evolution of Senescence," George posited the existence of genes with effects on fitness that are positive early in life but negative late in life (antagonistic pleiotropy). He then noted that because selection pressures decrease with age, many such genes will invade, for their positive impact on fitness early in life will outweigh their negative impact later in life. To that point he was rehearsing arguments made previously by Medawar (1952). He then went on to derive nine striking predictions that have shaped research on the evolution of aging ever since. The paper is remarkable in other respects. In dismissing Weismann's idea that aging evolved for the good of the species, George rejected group selection with arguments that he later expanded in *Adaptation and Natural Selection*. In developing the idea of antagonistic pleiotropy, he clarified the notion of tradeoffs among fitness components that lies at the core of life history evolution. Thus this paper not only established the major theory for the evolution of aging; it also stated his stance on group selection and foreshadowed the development of life history theory. The major themes of his life in science were all there in 1957, expressed when he was 31 years old.

ADAPTATION AND NATURAL SELECTION

George's masterpiece, *Adaptation and Natural Selection*, was submitted in 1963 and appeared in 1966. Long after he wrote it, George reflected that when he was in graduate school in the 1950s, textbook treatments of evolution outlined neo-Darwinian processes as a mechanism of evolutionary change, but

> thereupon any axiomatic use of the theory was abandoned, and it was merely assumed that natural selection always promoted what was in some way good…In those days few people read such mathematical discussions as Haldane's and Fisher's. We got our theory in words from Dobzhansky, Mayr, and Simpson, who were deeply concerned with natural selection, but gave little attention to its levels of operation. (1992, p. 47)

Adaptation and Natural Selection clarified the principles of selection in terms that nonmathematical biologists could understand and revolutionized the study of adaptation.

Williams described his book as "an attack on what I consider unwarranted uses of the concept of adaptation" (p. 11), which he characterized as an onerous concept that should be invoked only if other explanations were insufficient.

"Biologists have no logically sound and generally accepted set of principles and procedures for answering the question 'What is its function?'" (p. 252); nor, with exceptions such as Lack's model of optimal fecundity in birds, was there a theory of adaptation that could both summarize large masses of observations and provide logical deductions (p. 20). George suggested that the study of adaptation warrants a special branch of biology and devoted a final chapter to this theme. He often inferred function (and adaptation) by comparing character states among organisms, from a character's complexity or phylogenetic constancy, or from (admittedly fallible) evidence of "design."

George recognized that selection can be seen as operating at several levels, and he argued that parsimony requires us to attribute an adaptation to no higher a level than the evidence demands. He made the critical point that selection can be effective only if the selected entity has, relative to the selection coefficients, "a high degree of permanence and a low rate of endogenous change" (p. 23) (i.e., for DNA a low mutation rate) without which the entities cannot increase in number. By this argument the genotypes of individual organisms in sexually reproducing populations cannot be units of selection, for they are dissolved and mixed in meiosis, nor are local populations. Only genes (operationally defined as "that which segregates and recombines with appreciable frequency") are units of selection. He later suggested that individual selection might best be considered the mechanism of gene-level selection (1992, p. 18).

Together with Bill Hamilton's closely related concept of the inclusive fitness of an allele, George's invocation of gene-level selection to explain the adaptations of organisms evoked both immense enthusiasm (see, for example, Dawkins [1989, p. 11] and the criticism that it minimizes genetic and organismal integration (Sober and Lewontin, 1982; Sober, 1984). Despite the criticism (which prompted George to write "A Defense of Reductionism in Evolutionary Biology" in 1985), genic selection, memorably captured by Dawkins's label "the selfish gene," has continued to be useful in analyzing puzzling phenomena, especially those arising from genetic conflict (Haig, 2002). As for minimizing organismal integration, that criticism is misplaced, for in no part of biology is organismal integration more central than life history evolution, a field that George cofounded by emphasizing how tradeoffs connect traits across the entire life cycle.

Other than theoretical population geneticists, no one before George had so remorselessly applied to biological problems the principle that evolutionary change requires that alleles invade populations by increasing in frequency from nearly zero. Utterly lacking any romanticized view of Nature, George argued that "there is nothing in the basic theory of natural selection that would suggest the idea of any kind of evolutionary progress" (p. 34); nor is there any clear criterion for judging "progress," or even betterment of a species. Natural selection of genes need not increase genetic "information" (e.g., gene number), or the numerical abundance of a species, or its rate of increase, or its prospect of long-term survival. And selection at the gene or individual level resists the evolution of features that benefit groups but reduce the fitness of individuals—the defining characteristic of features that could evolve only by group-level selection.

In the first part of *Adaptation and Natural Selection* George mounted a powerful critique of group selection and group-level adaptation with lasting impact on evolutionary biology. Group selection will almost always be weaker than selection within populations because the characteristics of populations are less stable than those of genes, and because populations are much less numerous than genes and have a much lower turnover rate. Because there are fewer groups than there are individuals, chance will be more important than selection in determining group survival, just as genetic drift overwhelms individual selection within small populations. Crucially, variation among populations in the frequency of group advantageous but individually disadvantageous alleles requires that such alleles increase in frequency within some populations. This could occur only by genetic drift, but that would require a "rather improbable concatenation of population parameters" (p. 112).

Looking back in 1995, George recalled the kind of thinking he had encountered and objected to in the 1950s.

> Mostly, the group-selection idea was necessary to the way people were thinking about adaptation, although—and I find this extremely strange—they didn't realize it. They kept talking about things being for the good of the species. If it's for the good of something, and it's to arise by natural selection, it has to be produced by the natural selection of those somethings. In other words, one species survives as another one goes extinct...you can't have things that work for the good of the group unless you have selection at the level of groups. (1995)

In the second part of the book George analyzed supposed group-level adaptations of the genetic system (e.g., mutation), reproductive physiology and behavior (e.g., reproductive rate), social systems (especially cooperation), and others such as senescence, multicellularity, the self-regulation of population size, and the supposed integration of communities or ecosystems. While crediting others for explanations based on gene and individual selection, he presented many novel interpretations. For example, there can be no prescient selection for evolutionary adaptability, and the optimal mutation rate should be zero, for a gene that mutates has failed to reproduce itself. Species do not have high fecundity to compensate for high mortality, as had often been supposed; rather, high mortality is the consequence of high fecundity in ecologically limited populations. Delayed reproduction may be individually advantageous or not, depending on the balance between risk of mortality and growth that could increase fecundity later in life. The formation of fish schools and bird flocks is explained by the advantage gained by an individual that places itself inside a group and puts others between itself and sources of danger, such as predators (p. 213), an idea that Hamilton (1971) later developed formally. All the processes observed in ecosystems are the aggregate consequences of features, such as photosynthesis and predation, that are advantageous to individual organisms.

THE COSTS OF REPRODUCTION

In a 1966 letter in *The American Naturalist* George published a distillation and refinement of Chapter 6 of *Adaptation and Natural Selection.* By distinguishing between current and residual reproductive value, he set up the analytic framework within which life history theory was subsequently developed by focusing on the marginal impact of a change in allocation to alternative functions at evolutionary equilibrium. From these three pages of translucent thought stems the entire program of applying optimality theory to the design of phenotypes for reproductive success under the constraints of tradeoffs. In the first paragraph Williams encapsulates in one clause the evolutionary forces that make the soma disposable. "[T]he use of resources for somatic processes is favored to the extent that somatic survival, and perhaps growth, are important for future reproduction." This idea, derived from his 1957 paper on aging, later sparked Kirkwood's many contributions on this subject (e.g., Drenos and Kirkwood, 2005).

SEX AND EVOLUTION

By 1975 unease with the available explanations for the evolution of sex had been gathering for some time. The ideas of Weismann, Muller, and Crow and Kimura all relied on benefits to the population, not to the individual, making it no accident that it was the major critics of group selection who tried to explain the paradox of sex. In *Sex and Evolution* George (1975) made it clear that the widespread existence of sexual reproduction signaled a crisis in evolutionary theory that required new ways of thinking about the problem. His approach used the comparative analysis of whole-organism adaptations. The central chapters of the book, entitled "The Aphid-Rotifer Model," "The Strawberry-Coral Model," and "The Elm-Oyster Model," signal that the costs and benefits of sex are to be assessed in an ecological context tied to the natural history of life cycles. The book immediately attracted attention to the issue, stimulating an outpouring of papers and books that lasted at least two decades, most of them focused more on the genetic than on the ecological causes and consequences of sex. His book reminds us that whatever the genetic implications of sex, they must make a difference to the reproductive success of whole organisms if sex is to outcompete asex.

NATURAL SELECTION: DOMAINS, LEVELS, AND CHALLENGES

George's hope for a science of adaptation was met by a surge in theoretical and empirical studies of behavior, life histories, and reproductive biology, but this development was disparaged by Gould and Lewontin (1979) as adaptive storytelling. The irony is that George had insisted from 1966 onward that we should not invoke adaptation unless other explanations fail. In 1992 he continued this theme in *Natural Selection: Domains, Levels, and Challenges*, a collection of essays in which he reacted to the huge literature that had appeared since his earlier books and advanced some new ways of thinking about enduring issues. The "domains" of selection in the title, for example, are the codical (consisting of genetic information) and the material (consisting of physical objects such as DNA sequences and organisms). He developed the idea that codical units of selection persist longer than their material carriers and must be able to persist and proliferate faster than they change. If this is the case, their proliferation can be represented by a genealogy or dendrogram, and George claimed that "a good test of the susceptibility of an entity to natural selection is whether its history can be modeled successfully by a dendrogram." This is the case for genes but not for genotypes or individuals in sexual populations.

George used much of *Natural Selection* to discuss macroevolutionary issues, often agreeing with Stephen Jay Gould. For example, he agreed that selection among species and more inclusive clades has greatly affected the history and pattern of diversity, although it cannot generate organismal adaptations. He did not think such selection requires "emergent" group properties, few of which can be identified. Evolutionary history cannot be ignored: every organism is a historical document, a consequence of countless historical contingencies, many of which have resulted in nonadaptive configurations, features that no intelligent engineer would design. The imprint of history often decays very slowly: long-term rates of evolution are orders of magnitudes lower than evolutionary change in contemporary populations, and the phylogenetic conservatism of some features is a mystery that calls for explanation. Announcing the breadth of his approach in the book's first sentence, he wrote, "Successful biological research in this century has had three doctrinal bases: mechanism (as opposed to vitalism), natural selection (trial and error, as opposed to rational plan), and historicity," the role of historical contingency (p. 3). All three explain the features of organisms, not natural selection alone.

EVOLUTIONARY MEDICINE

George may have "retired" in 1990, but in 1991 he coauthored with Randy Nesse a paper in *The Quarterly Review of Biology* titled "The Dawn of Darwinian Medicine" and in 1994 a book titled *Why We Get Sick: The New Science of Darwinian Medicine.* That paper and book helped to launch evolutionary approaches to medical issues. Randy and George asked, Why is such an exquisitely designed body so vulnerable to disease? Their answers include tradeoffs and evolutionary legacies. They explained evolution to the medical community with clear, striking examples, many of which reveal the power of evolutionary thinking to suggest novel alternatives to received wisdom. While the field has since developed rapidly, with major contributions from evolutionary genetics and genomics, phylogenetics, and evolutionary immunobiology, those developments have not obscured their founding role and essential insight: evolutionary ideas have practical consequences that can reduce suffering and save lives. Developing that insight is a profoundly important strategic move both for the health and comfort of the human population and for the acceptance of evolutionary thinking by the general public.

HIS CHARACTER

An articulate, daring writer, George was soft-spoken, unassuming, and taciturn. Although he said little, his colleagues and students learned to listen carefully when he did speak, for he often posed a provocative question, provided a novel point of view, or cleared away confusion with a simple, enlightening analysis. He was consistently friendly and eager to discuss science and human affairs with peers or students. As Paul Ewald put it (e-mail message, April 10, 2011),

> George wasn't one to pour on enthusiastic approval or angry criticism. Nor was he one to ally himself in divisive confrontations…much of his commu-

nication was by facial expression. When he was deliberating he would push out his lower lip. If he found a flaw he would furrow his brow and shake his head. When he agreed, it was often with a nod of the head, a smile, or twinkle in the eye.

Greg Wray (conversation, May 3, 2011) remembers that shortly after he started work as an assistant professor at Stony Brook, George dropped by his office to say hello. Only later did Greg realize how unusual that was, for he rarely interacted with George in his six years at Stony Brook. George had come with some advice: be creatively incompetent. Accept departmental chores, and do them, but do them less well than you might. You will find that eventually you are not asked to do them anymore, and people will still like you. I suspect that George was simply communicating a strategy that he had long practiced.

When I started graduate school in 1970, my mentor at Wisconsin, Stan Dodson, recommended that I read *Adaptation and Natural Selection*. I did so on a trip home that Christmas. It strongly influenced my work on life history evolution, which began in September 1974, when I submitted a long manuscript to *The Quarterly Review of Biology*. By then I was in the third year of my Ph.D. program at the University of British Columbia, and this would be my first substantial scientific publication. I sent it off with high hopes and considerable trepidation, fearing rejection, but by return post I received a three-page, single-spaced review from George, suggesting changes and signaling acceptance. I was astonished that such a famous scientist would react so quickly and work so hard to improve something I had written. The paper (Stearns, 1976) established my reputation and launched my career.

Paul Ewald had a similar experience when he met George in a seminar at the University of Michigan in 1980.

> George was talking with a student about whether some phenotype was adaptive…He said in a forceful, measured way…, "Maybe it's a manipulation." He immediately shot me a glance with a serious look that transitioned into a knowing smile. He was telling me that he had read a paper of mine that had just come out in the *Journal of Theoretical Biology*. It was my first paper dealing with evolution and medicine. (e-mail message, April 10, 2011)

George's self-deprecating modesty was striking. John Brockman, a literary agent, recalls meeting with George and Randy when they were looking for a publisher for their book on evolutionary medicine.

> Randy Nesse…did *all* the talking…about their planned book on Darwinian Medicine. Finally, I interrupted Nesse and asked the taciturn Dr. Williams, "Professor, what can I tell publishers about you?" "Well," he replied, "I once wrote a little book for a university press, but it was thirty years ago. It probably won't be of interest to them. (www.edge.org/documents/williams_index.html)

That book was *Adaptation and Natural Selection.*

In his testimonial to Bill Hamilton, George wrote (2000), "My wife and I had published a clumsy treatment of a related topic, natural selection among nuclear families. It was a relief to have our ideas replaced by Bill's simple proposal of selection among individuals for the adaptive use of cues indicative of kinship with any conspecific." Actually, George and Doris had made a flawless argument up to the decision to concentrate on sibships rather than individuals, coming very close to developing kin-selection theory seven years before Hamilton did.

When Maynard Smith's *Evolution of Sex* appeared three years after George's *Sex and Evolution,* George wrote that Maynard Smith's book had made his own obsolete. And when George, the cofounder of the field, was invited to speak on Darwinian medicine at a symposium on applied evolution, he replied that the organizers should get someone who knew something about the topic (Bull et al., 2011).

Niles Eldredge recalled, "John Maynard Smith remarking to me that he was astonished to find out that George Williams wasn't [yet] in our National Academy…George really is the most important thinker in evolutionary biology in the United States since the 1959 Darwin centennial…He's a shy guy, but a very nice guy, and a very deep and a very careful thinker" (*www.edge.org/documents/williams_index.html*).

EVOLUTION AND THE HUMAN CONDITION

George was a progressive liberal concerned about socially significant misunderstanding or abuse of evolutionary theory, especially the "naturalistic fallacy," whereby people try to justify behavior by claiming that "natural" is "good." In an essay that accompanied a reprinting of T. H. Huxley's 1893 essay on evolutionary morality, George (1989) characterized natural selection as "a process for maximizing short-sighted selfishness" and found much of nature, including our own selfish genes, a "morally unacceptable, powerful and persistent" enemy, concluding that "we need all the help we can get in trying to overcome billions of years of selection for selfishness." In 1993 he repeated that message in a chapter strikingly titled "Mother Nature Is a Wicked Old Witch:"

> A century of progress in biology confirms Huxley's thesis: the universe is hostile to life in general and human life in particular; the evolutionary process and its products are contrary to human ethical standards; human ethical advance can be achieved only in opposition to the cosmic process.

When interviewed about his views on evolutionary morality in 1998 (Roes, 1998), George reemphasized the brutal nature of natural selection.

> Natural selection maximizes short-sighted selfishness, no matter how much pain or loss it produces. There are far more losers than winners, and great losses often arise from trivial gains. The killing of monkey infants for minor male reproductive gain is the example that most persuasively led me to use words like evil…As to its stupidity, natural selection produces what seem

to be ingenious devices, like eyes and hands and the human capacity for language, but a close examination shows these devices to be just the sorts of things that can arise from trial and error…As a result, all organisms are burdened with maladaptive historical legacies.

George felt that only by being aware of the morally unacceptable elements in human nature could we hope to find our better angels.

ILLNESS AND DEATH

I first realized that George's cognitive function was starting to decline when I asked him to write a background chapter for a symposium on evolutionary medicine that I organized in Sion, Switzerland. The document he submitted was so far below his previous standards that I thought it would damage his reputation to publish it, and I asked him to withdraw it. He did so, but I knew he was bothered.

In 2002 when I visited Stony Brook to give a seminar, George and Doris had my wife and me to their house for lunch. There, appearing to accept his fate cheerfully, George told us that he had Alzheimer's. Children and grandchildren lived nearby, and Doris cared for him lovingly, but the last years were hard for all. When I returned to give the Darwin Day talk at Stony Brook in 2009, George was not able to attend, and his colleagues told me that they had not seen him for some time. It is ironic that it was a person who understood aging so well who suffered from an illness that so dramatically demonstrates how vulnerable our aging bodies are. He died on September 8, 2010, surrounded by his loving family.

THIS MEMOIR IS BASED in part on the memorial that Doug Futuyma and I wrote for *Evolution* (Futuyma and Stearns, 2010) and on the papers written for a symposium held in George's honor at the State University of Stony Brook on April 24, 2004, and published in *The Quarterly Review of Biology* in March 2005.

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