INVITED PERSPECTIVES IN PHYSIOLOGICAL AND BIOCHEMICAL ZOOLOGY

Bart's Familiar Quotations: The Enduring Biological Wisdom of George A. Bartholomew

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ABSTRACT

George A. Bartholomew was one of the most influential organismal biologists of the twentieth century. His insights and research were fundamental to the establishment and growth of physiological ecology and evolutionary physiology. In the process of fostering that area of science, he created a body of literature that is striking in the clarity of its thought and presentation. Here we present some of his most insightful and important quotations, group them thematically, and comment on their original context and their continuing relevance.

Introduction

George A. Bartholomew (Fig. 1), known to family and friends as "Bart," was one of the greatest integrative biologists of the last century. If intellectual fitness is defined as the sustained impact of a scientist over time, then Bart's fitness is exceptional. His most enduring impact is in the extraordinary number and quality his academic descendants.[3] Indeed, his academic progeny dominate integrative biology and related fields, as those of G. E. Hutchison and R. Lewontin have dominated ecology and evolutionary genetics, respectively. His impact is also evident in his personal research contributions to the sciences of integrative biology and physiological ecology. He, along with C. L. Prosser, K. Schmidt-Nielsen, and P. Scholander, defined the issues, dimensions, and goals of these fields.

Also among Bart's enduring legacies—and the focus of this article—are the fundamental insights found in his writing. Bart's many papers contain pithy nuggets that synthesize the philosophical and intellectual basis of integrative science and do so in a few sentences of clear and elegant prose. At this sort of writing, Bart had no peer.

Our purpose here is to collate and highlight a few of the essential quotations of George Bartholomew. We have not tried to be exhaustive but rather have chosen quotations that have had—and continue to have—a special impact on our own thinking and research. We have organized these into major themes and have followed them with our own brief annotations. These selected quotations are necessarily abstracted from their original context, but we hope that they will encourage people to read the original articles in their entirety, to share them with students and colleagues, and to savor them again in future years.

Our article is a companion piece to William R. (Bill) Dawson's (2005) superb biographical memoir of Bart's life and contributions. Bill was Bart's first graduate student and is himself a leading integrative biologist and mentor. Bill's article was based on his presentation to a 2004 symposium of the Society of Integrative and Comparative Biology (SICB) honoring Bart and featuring the first 10 winners of the Bartholomew Award, which is given to outstanding young investigators in integrative and functional biology (Huey and Hofmann 2005). Bill's presentation led off the symposium, and Bart's own presentation was to conclude it. Sadly, Bart became ill immediately before the symposium and was unable to attend. He was able to author a paper (Bartholomew 2005) in the issue of *Integrative and Comparative Biology* containing the symposium, and this was his last published paper. It is vintage Bart and is a wonderful and fitting summary of his personal axioms for integrative biology.

Bart died at age 87 on October 2, 2006. Friends and admirers are encouraged to make a contribution in his honor to the Bartholomew Award Fund (SICB), the Bartholomew Fellowship for Field Biology at the University of California, Los Angeles, or both.

Integrative Biology and Levels of Biological Organization

> Biology is a continuum, but we biologists, because of our limitations, divide ourselves into categories, and then we pretend that those categories exist in the living systems that we study. From the functional point of view, of course, an animal is in-

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[3]The ever-ramifying genealogy of Bart's academic descendants (Bennett and Lowe 2005) is accessible at http://bartgen.bio.uci.edu/tree.

Figure 1. George A. Bartholomew in 1953 (photograph courtesy of Mullen Bartholomew, Karen Searcy, and Bruce Bartholomew).

divisible, and physiology is not in any sense an isolatable component of an organism. If physiology is defined as the study of vital functions, it becomes inseparable from morphology and behavior. (Bartholomew 1958, p. 81)

The complexity of contemporary biology has led to an extreme specialization, which has inevitably been followed by a breakdown in communication between disciplines. Partly as a result of this, the members of each specialty tend to feel that their own work is fundamental and that the work of other groups, although sometimes technically ingenious, is trivial or at best only peripheral to an understanding of truly basic problems and issues. There is a familiar resolution to this problem but it is sometimes difficulty to accept emotionally. This is the idea that there are a number of levels of biological integration and that each level offers problems and insights that are unique to it; further, that each level finds its explanations of mechanism in the levels below, and its significances in the levels above it. (Bartholomew 1966, p. 39)

After physiology has taken Humpty Dumpty apart, it is difficult (perhaps even unfashionable) to put him back together again. (Bartholomew 1986, p. 327)

It is the intact and functioning organism on which natural selection operates. Organisms are therefore the central element of concern to the biologist who aspires to a broad and integrated understanding of biology. (Bartholomew 1987, p. 15)

Biology as a discipline would benefit enormously if we could bring together the scientists working at the opposite ends of the biological spectrum. Students of organisms who know natural history have abundant questions to offer the students of molecules and cells. And molecular and cellular biologists with their armory of techniques and special insights have much to offer students of organisms and ecology. (Bartholomew 1986, pp. 328–329)

Over the years it has become clear that adjustments to the physical environment are behavioral as well as physiological and are inextricably intertwined with ecology and evolution. Consequently, a student of the physiology of adaptation should not only be a technically competent physiologist, but also be familiar with the evolutionary and ecological setting of the phenomenon that he or she is studying. (Bartholomew 1987, p. 17)

Commentary

During the 1950s and 1960s, the increasing complexity and growth of biology was beginning to force its subdivision. Departments of biology, zoology, and botany began to split into departments of cell biology, molecular biology, physiology, and ecology and evolution. Disciplines such as physiology began to fracture into subfields, such as endocrinology, neurobiology, respiratory physiology, physiological ecology, and functional morphology. This division and fragmentation made sense in terms of the amount of information that any one individual can absorb, retain, and process. However, this specialization came with a cost.

Bart clearly observed that this trend toward the atomization of the organism and the fragmentation of biology would inevitably lead to a Tower of Biological Babel. His response was characteristically constructive: he argued that animals themselves were not divisible and were not designed to conform to the artificial boundaries being erected by biologists. Bart's philosophy of the positive interplay among levels of organization is given most clearly in his famous quote ("each level finds its explanations of mechanism in the levels below, and its significance in the levels above"). More than any statement of which we are aware, that single quote laid an eloquent philosophical foundation for what later became integrative biology. This philosophy also clarified the nature of explanation in biology, distinguishing the complementary roles of reductionism and synthesis. He argued that the reductionism and synthesis should be partners, not opponents in battle, and that the organism, not the isolated parts thereof, is the unit on which selection acts.

The Themes and Topics of Physiological Ecology

Since an organism is inseparable from its environment, any person who attempts to understand an organism's distribution must keep constantly in mind that the item being studied is neither a stuffed skin, a pickled specimen, nor a dot on a map. It is not even the live organism held in the hand, caged in a laboratory, or seen in the field. It is a complex interaction between a self-sustaining physicochemical system and the environment. An obvious corollary is that to know the organism it is necessary to know its environment. (Bartholomew 1958, p. 83)

Life is inseparable from water. For all terrestrial animals, including birds, the inescapable need for maintaining an adequate state of hydration in a hostile, desiccating environment is a central persistent constraint which exerts a sustained selective pressure on every aspect of the life cycle. It has been said, with some justification, that the struggle for existence is a struggle for free energy for doing physiological work. It can be said with equal justification for terrestrial organisms that the struggle for existence is a struggle to maintain an aqueous internal environment in which energy transformations for doing work can take place. (Bartholomew 1972, pp. 237–238)

For terrestrial vertebrates, the climate in the usual meteorological sense of the term would appear to be a reasonable approximation of the conditions of temperature, humidity, radiation, and air movement in which terrestrial vertebrates live. But, in fact, it would be difficult to find any other lay assumption about ecology and natural history which has less general validity. … Most vertebrates are much smaller than man and his domestic animals, and the universe of these small creatures is one of cracks and crevices, holes in logs, dense underbrush, tunnels, and nests—a world where distances are measured in yards rather than miles and where the difference between sunshine and shadow may be the difference between life and death. Actually, climate in the usual sense of the term is little more than a crude index to the physical conditions in which most terrestrial animals live. (Bartholomew 1966, p. 40)

Behavioral avoidance, not physiological adaptations, is an organism's primary response to an environmental challenge. … This point is elementary, but it is by no means trivial. (Bartholomew 1987, p. 18)

Plants, generally speaking, meet the impact of the terrestrial environment head on, although of course they in turn modify the physical environment by adventitious group activity. The individual plant cannot select its habitat; its location is largely determined by the vagaries of the dispersal of seeds or spores and is thus profoundly affected by chance. Because of their mobility and their capacity for acceptance or rejection terrestrial animals, in contrast, can and do actively seek out and utilize the facets of the environment that allow their physiological capacities to function adequately. This means that an animal by its behavior can fit the environment to its physiology by selecting situations in which its physiological capacities can cope with physical conditions. If one accepts this idea, it follows that there is no such thing as The Environment, for there exist as many different terrestrial environments as there are species of animals. (Bartholomew 1958, p. 84)

It usually develops that after much laborious and frustrating effort the investigator of environmental physiology succeeds in proving that the animal in question can actually exist where it lives. It is always somewhat discouraging for an investigator to realize that his efforts can be made to appear so trite, but this statement does not belittle the ecological physiologist. If his data assist the understanding of the ways in which an animal manages to live where it does, he makes an important contribution to the study of distribution, for the present is necessarily a key to the past." (Bartholomew 1958, p. 84)

Commentary

The quotations in this section deal with the holistic nature of biological entities and of the study of biology itself. Bart continually stressed the interaction and, to an extent, the unity of the organism and its environment. The key insight of physiological ecology was that design and function cannot truly be understood if the organism itself is abstracted from its natural environment. Bart's thinking in this regard was very much influenced by his choice of terrestrial vertebrates as objects of study. The harsh nature of life in terrestrial environments, with its many challenges in regard to temperature, energy, and water, emphasized the dependence of the organism on its environment and its need to select an appropriate environment that permits survival.

Bart recognized that natural environments are heterogeneous and specifically that the microenvironments experienced by animals often differ radically from those physiologists themselves experience or from those that weather stations record. Accordingly, he challenged physiologists to develop experiments that were sensitive to the actual conditions experienced by the organism.

One of the Bart's most consistent themes in this regard was the fundamental importance of behavior in coping with and adapting to the environment. He perceived that behavior is the first line of defense when an organism is confronted with environmental change or challenge. He recognized that behavior should not be separated from physiological ecology; rather, it has to be incorporated into it as a basic part of its warp and woof. Once again the unity of the organism and environment is evident in his writings.

Bart also recognized that plants and animals deal with environments in different ways. He noted (Bartholomew 1958) that plants—unlike mobile animals—cannot use behavior to evade environmental stresses and thus must "meet the impact of the terrestrial environment head on." Bart's comment anticipated the major paper by A. D. Bradshaw on differences in how plants and animals deal with stress (Bradshaw 1972; Huey et al. 2002).

Not surprisingly, Bart wrote extensively on behavioral topics, including landmark papers on the evolution of polygyny in pinnipeds (Bartholomew 1970) and on the ecology of early humans (Bartholomew 1953). His thinking about the importance of evolutionary history and phylogeny in shaping form and function in current organisms (see below) was greatly influenced by the phylogenetic insights of comparative ethologists (see the extensive quotation from Hinde and Tinbergen [1958] in Bart's pinniped paper [Bartholomew 1970, p. 546]).

Adaptation and Evolutionary Physiology

Despite the high long-term probability of extinction, every organism alive today, including every person reading this paper, is a link in an unbroken chain of parent-offspring relationships that extends back unbroken to the beginning of life on earth.

Every living organism is a part of an enormously long success story—each of its direct ancestors has been sufficiently well adapted to its physical and biological environments to allow it to mature and reproduce successfully. Viewed thus, adaptation is not a trivial facet of natural history, but a biological attribute so central as to be inseparable from life itself. (Bartholomew 2005, p. 330)

Since natural selection demands only adequacy, elegance of design is not relevant; any combination of behavioural adjustment, physiological regulation, or anatomical accommodation that allows survival and reproduction may be favoured by selection. Since all animals are caught in a phylogenetic trap by the nature of past evolutionary adjustments, it is to be expected that a given environmental challenge will be met in a variety of ways by different animals. The delineation of the patterns of the accommodations of diverse types of organisms to the environment contributes much of the fascination of ecologically relevant physiology. (Bartholomew 1964, p. 11)

Natural selection produces systems that function no better than necessary. It results in ad hoc adaptive solutions to immediate problems. Whatever enhances fitness is selected. The product of natural selection is not perfection but adequacy, not final answers but limited, short-term solutions. (Bartholomew 1986, p. 325)

The contributions of physiological knowledge to an understanding of distribution are necessarily inferential. Distribution is a historical phenomenon, and the data ordinarily obtained by students of physiology are essentially instantaneous. However, every organism has a line of ancestors which extends back to the beginning of life on earth and which, during this immensity of time, has invariably been able to avoid, to adapt to, or to compensate for environmental changes. (Bartholomew 1958, p. 84)

It is tautological to say that an organism is adapted to its environment. It is even tautological to say that an organism is physiologically adapted to its environment. However, just as in the case of many morphological characters, it is unwarranted to conclude that all aspects of the physiology of an organism have evolved in reference to a specific milieu. It is equally gratuitous to assume that an organism will inevitably show physiological specializations in its adaptation to a particular set of conditions. All that can be concluded is that the functional capacities of an organism are sufficient to have allowed persistence within its environment. On one hand, the history of an evolutionary line may place serious constraints upon the types of further physiological changes that are readily feasible. Some changes might require excessive restructuring of the genome or might involve maladaptive changes in related functions. On the other hand, a taxon which is successful in occupying a variety of environments may be less impressive in individual physiological capacities than one with a far more limited distribution. (Dawson et al. 1977, p. 891)

Differences between individuals are the raw materials for evolutionary change and for the evolution of adaptations, yet of course most physiologists treat these differences as noise that is to be filtered out. From the standpoint of physiological ecology, the traditional emphasis of physiologists on central tendencies rather than on variance has some unhappy consequences. Variation is not just noise; it is also the stuff of evolution and a central attribute of living systems. … The physiological differences between individuals in the same species or population, and also the patterns of variation in different groups, must not be ignored. (Bartholomew 1987, pp. 32–33)

One may summarize by saying that by a combination of behavior and physiology mammals can successfully occupy all but the most extreme environments on earth without anything more than quantitative shifts in the basic physiological pattern common to all. (Bartholomew 1958, p. 87)

Commentary

In the decades before 1980, most physiological ecologists—indeed most biologists—treated natural selection as an all-powerful adaptation machine, relentlessly churning out perfection and optimality. They ignored phylogenetic and genetic constraints. They ignored the impact of chance events and history. That Panglossian mind-set would eventually be challenged by publications such as those of Gould and Lewontin (1979), Lande (1979), Arnold (1983), and Felsenstein (1985)—papers that helped define latter-day themes in evolutionary physiology.

But while reviewing Bart's early conceptual writings, we were struck by the degree to which Bart anticipated and prefigured many of these challenges. From the very beginning, Bart emphasized historical constraint, which he termed the "phylogenetic trap," as a limitation on possible pathways of evolutionary change. He repeatedly wrote about natural selection and its operation on the whole organism, rather than on its individual characters. He cautioned that selection and evolution do not produce perfection and optimality but only an expedient adequacy. These views are strikingly modern and have a great resonance because they were so clearly articulated so early. These and many other evolutionary concepts, including the significance of chance events, the importance of trade-offs, and the limits of adaptive interpretations, were part of Bart's deep and prescient understanding of evolution.

Evolutionary biologists such as Williams, Gould, Lande, and Felsenstein undeniably had a revolutionary impact on the thinking of contemporary comparative biology, and they certainly did on us personally. But our own receptivity to their radical ideas—and our incorporation of them into our own research—was undeniably fostered by our having been primed by Bart's writings. He sensitized us to a nuanced view of how evolution works rather than to an idealized vision of universal adaptive perfection.

Strategies for Making Scientific Progress

One precept for the scientist-to-be is already obvious. Do not place yourself in an environment where your advisor is already suffering from scientific obsolescence. If one is so unfortunate as to receive his training under a person who is either technically or intellectually obsolescent, one finds himself to be a loser before he starts. It is difficult to move into a position of leadership if one's launching platform is a scientific generation whose time is already past. (Bartholomew 1982, p. 229)

Although I must say that research problems I worked on were frequently the result of serendipity and often grew out of my interest in some species or some environment which I found to be particularly appealing—marine birds and tropical islands for example. (Bartholomew, April 1993, unpublished remarks when receiving the Miller Award from the Cooper Ornithological Society)

The chances for favorable serendipity are increased if one studies an animal that is not one of the common laboratory species. Atypical animals, or preparations, force one to use non-standard approaches and non-standard techniques, and even to think non-standard ideas. My own preference is to seek out species which show some extreme of adaptation. Such organisms often force one to abandon standard methods and standard points of view. Almost inevitably they lead one to ask new questions, and most importantly in trying to comprehend their special and often unusual adaptations one often serendipitously stumbles upon new insights. (Bartholomew 1982, p. 234)

All scientists must focus closely on limited targets. Whether or not one's findings on a limited subject will have wide applicability depends to some extent on chance, but biologists of superior ability repeatedly focus on questions the answers to which either have wide ramifications or lead to new areas of investigation. One procedure that can be effective is to attempt both reduction and synthesis; that is, direct a question at a phenomenon on one integrative level, identify its mechanism at a simpler level, then extrapolate its consequences to a more complex level of integration. (Bartholomew 1982, pp. 230–231)

Heavy dependence on direct observation is essential to biology not only because of the complexity of biological phenomena, but because of the intervention of natural selection with its criterion of adequacy rather than perfection. In a system shaped by natural selection it is inevitable that logic will lose its way. (Bartholomew 1982, p. 229)

Biological disciplines tend to guide research into certain channels. … One consequence is that disciplines are apt to become parochial, or at least to develop blind spots, for example, to treat some questions as "interesting" and to dismiss others as "uninteresting." As a consequence, readily accessible but unworked areas of genuine biological interest often lie in plain sight but untouched within one discipline while being heavily worked in another. For example, historically insect physiologists have paid relatively little attention to the behavioral and physiological control of body temperature and its energetic and ecological consequences, whereas many students of the comparative physiology of terrestrial vertebrates have been virtually fixated on that topic. For the past 10 years, several of my students and I have exploited this situation by taking the standard questions and techniques from comparative vertebrate physiology and applying them to insects. … It is surprising that this pattern of innovation is not more deliberately employed. (Bartholomew 1982, p. 233)

To ask what qualities distinguish good from routine scientific research is to address a question that should be of central concern to every scientist. We can make the question more tractable by rephrasing it, "What attributes are shared by the scientific works which have contributed importantly to our understanding of the physical world—in this case the world of living things?" Two of the most widely accepted characteristics of good scientific work are generality of application and originality of conception. … These qualities are easy to point out in the works of others and, of course extremely difficult to achieve in one's own research. At first hearing novelty and generality appear to be mutually exclusive, but they really are not. They just have different frames of reference. Novelty has a human frame of reference; generality has a biological frame of reference. Consider, for example, Darwinian Natural Selection. It offers a mechanism so widely applicable as to be almost coexistent with reproduction, so universal as to be almost axiomatic, and so innovative that it shook, and continues to shake, man's perception of causality. (Bartholomew 1982, p. 230)

In the context of biological research one can reasonably identify creativity with the capacity (1) to ask new and incisive questions, (2) to form new hypotheses, (3) to examine old questions in new ways or with new techniques, and (4) to perceive previously unnoticed relationships. (Bartholomew 1982, p. 231)

Each species has evolved a special set of solutions to the general problems that all organisms must face. By the fact of its existence, a species demonstrates that its members are able to carry out adequately a series of general functions. … These general functions offer a framework within which one can integrate one's view of biology and focus one's research. Such a view helps one to avoid becoming lost in a morass of unstructured detail—even though the ways in which different species perform these functions may differ widely. A few obvious examples will suffice. Organisms must remain functionally integrated. They must obtain materials from their environments, and process and release energy from these materials. … They must differentiate and grow, and they must reproduce. By focusing one's questions on one or another of these obligatory and universal capacities, one can ensure that one's research will not be trivial and that it will have some chance of achieving broad general applicability. (Bartholomew 2005, p. 331)

Until its results have gone through the painful process of publication, preferably in a refereed journal of high standards, scientific research is just play. Publication is an indispensable part of science. "Publish or perish" is not an indictment of the system of academia; it is a partial prescription for creativity and innovation. Sustained and substantial publication favors creativity. Novelty of conception has a large component of unpredictability. … One is often a poor judge of the relative value of his own creative efforts. An artist's ranking of his own works is rarely the same as that of critics or of history. Most scientists have had similar experiences. One's supply of reprints for a pot-boiler is rapidly exhausted, while a major monograph that is one's pride and joy goes unnoticed. The strategy of choice is to increase the odds favoring creativity by being productive. (Bartholomew 1982, pp. 233–234)

> Obviously we biologists should fit our methods to our materials. An interesting response to this challenge has been employed particularly by persons who have entered biology from the physical sciences or who are distressed by the variability in biology; they focus their research on inbred strains of genetically homogeneous laboratory animals from which, to the maximum extent possible, variability has been eliminated. … These biologists have changed the nature of the biological system to fit their methods. Such a bold and forthright solution is admirable, but it is not for me. Before I became a professional biologist, I was a boy naturalist, and I prefer a contrasting approach; to change the method to fit the system. This approach requires that one employ procedures which allow direct scientific utilization of the successful long-term evolutionary experiments which are documented by the fascinating diversity and variability of the species of animals which occupy the earth. This is easy to say and hard to do. (Bartholomew 1982, p. 232)

> This brings me to the final point of my remarks, the relation between creativity and aging, a topic with which I have had substantial experience. Scientific research, until it has gone through the grueling and sometimes painful process of publication, is just play, and play is characteristic of young vertebrates, particularly young mammals. In some ways, scientific creativity is related to the exuberant behavior of young mammals. Indeed, creativity seems to be a natural characteristic of young humans. If one is fortunate enough to be associated with a university, even as one ages, teaching allows one to contribute to, and vicariously share, in the creativity of youth." (Bartholomew 2005, p. 331)

Commentary

It should come as no surprise that Bart—one of the most successful mentors ever (Bennett and Lowe 2005; Dawson 2005)—would have thought long and hard about strategies for making progress in science and for encouraging young scientists. Many of his insights are distilled in his past-presidential address to the American Society of Zoologists (Bartholomew 1982), and this paper should be required reading by all graduate students and their advisors.

Bart's fundamental strategy for generating novel biological insight involves intentionally putting oneself in a foreign environment in which serendipity is fostered and in which one is forced to challenge preconceived ideas and dogma. For Bart himself, this often meant either studying animals in extreme environments or crossing boundaries of independent fields (e.g., moving from vertebrates to insects). The key is to put oneself in a position of uncertainty or unpredictability, thereby intentionally challenging oneself to be innovative both in methodology and in understanding.

Bart's commitment to the importance of studying the organism in its natural environment is also clear. One should change one's methods to fit the organism, not change the organism to fit one's methods. Variation and diversity are fundamental to biology and should also be fundamental to biologists.

Bart on Bart

> Fortunately, a scientist's worth is judged on the basis of his accomplishments, not the tidiness of his work habits. (Bartholomew 1982, p. 231)

> A week or so after I learned that I was to receive the Miller Award, our president, Marty Morton, phoned and asked me if I would utter a few words of scientific wisdom as a part of the ceremony. Unfortunately for me, and perhaps for you, I agreed to do so. In retrospect I fear that my response was a serious error, because I do not feel wise. I do not know whether to attribute my response to foolhardiness, to conceit, to an inordinate susceptibility to flattery, to stupidity, or to some combination of these unfortunate attributes all of which I have been told are recognizable in my personality. Personally, I tend to favor stupidity, because that is a condition over which I have little control. (Bartholomew, April 1993, unpublished remarks when receiving the Miller Award from the Cooper Ornithological Society)

> As one of the elder members of the community of integrative biologists, I am overwhelmingly aware that during this continuing intellectual revolution, seniority is more likely to be correlated with obsolescence than with wisdom. (Bartholomew 2005, p. 330)

> Ironically one's scientific obsolescence is a direct result of the creativity of his peers. (Bartholomew 1982, p. 229)

> Consider the plight of a scientist of my age. I graduated from the University of California at Berkeley in 1940. In the 41 years since then the amount of biological information has increased 16 fold; during these 4 decades my capacity to absorb new information has declined at an accelerating rate and now is at least 50% less than when I was a graduate student. If one defines ignorance as the ratio of what is available to be known to what is known, there seems no alternative to the conclusion that my ignorance is at least 25 times as extensive as it was when I got my bachelor's degree. Although I am sure that my unfortunate condition comes as no surprise to my students and younger colleagues, I personally find it somewhat depressing. My depression is tempered, however, by the fact that all biologists, young or old, developing or senescing, face the same melancholy situation because of an interlocking set of circumstances. (Bartholomew 1982, p. 228)

> I will end on a highly personal note. The wisest decision I ever made with regard to science, I made as a child. In the summer of 1932, shortly after my thirteenth birthday, I decided to become a zoologist, because I thought it would be fascinating to visit distant parts of the world and study exotic animals. I was right. It has been. (Bartholomew 2005, p. 332)

Commentary

Any further comments here would be superfluous.

George A. Bartholomew: A Prospectus, Not a Retrospectus

Reading the classical papers of a field enables one to appreciate not only how the field came to be where it is today but also who led the way. Many times over the years, we ourselves have read and thought about Bart's papers. But while rereading those papers as we prepared this article, we were both struck by the impact his papers have had in guiding and challenging our own views and careers. We were both struck by two important aspects of his contributions and writing style.

First, looking back at Bart's papers between 1958 and 1966 in particular, we come to a somewhat startling conclusion: in the space of those few years, Bart laid out the intellectual framework for integrative biology and for evolutionary physiology, and he did so decades before these fields were officially born (Garland and Carter 1994). Bart saw that the whole organism in its environment provided not only a unifying focus for biological research but also a conceptual way to unify the complementary contributions of reductionist and synthetic approaches.

Second, Bart's written prose is remarkably verbal and conversational. Reading Bart's words, we hear his voice. It is a calm, confident, and rational voice—his words flow effortlessly and with the conviction of an internally coherent understanding of the complexities of the biological world and of the proper methods for its study.

Bart died in 2006, but his legacy is timeless. His words are lasting because of what they say and how they say it. If anything, his words are more relevant now than when penned and will continue to be relevant to future generations of biologists.

Literature Cited

Arnold S.J. 1983. Morphology, performance and fitness. Am Zool 23:347–361.

Bartholomew G.A. 1953. Ecology and the protohominids. Am Anthropol 55:481–498.

———. 1958. The role of physiology in the distribution of terrestrial vertebrates. Pp. 81–95 in C.L. Hubbs, ed. Zoogeography. Publ. 51. American Association for the Advancement of Science, Washington, DC.

———. 1964. The roles of physiology and behaviour in the maintenance of homeostasis in the desert environment. Symp Soc Exp Biol 18:7–29.

———. 1966. Interaction of physiology and behavior under natural conditions. Pp. 39–45 in R.I. Bowman, ed. The Galapagos. University of California Press, Berkeley.

———. 1970. A model for the evolution of pinniped polygyny. Evolution 24:546–559.

———. 1972. The water economy of seed-eating birds that survive without drinking. Proc Int Ornithol Congr 15:237–254.

———. 1982. Scientific innovation and creativity: a zoologist's point of view. Am Zool 22:227–235.

———. 1986. The role of natural history in contemporary biology. BioScience 36:324–392.

———. 1987. Interspecific comparison as a tool for ecological physiologists. Pp. 11–35 in M.E. Feder, A.F. Bennett, W.W. Burggren, and R.B. Huey, eds. New Directions in Ecological Physiology. Cambridge University Press, Cambridge.

———. 2005. Integrative biology: an organismic biologist's point of view. Integr Comp Biol 45:330–332.

Bennett A.F. and C. Lowe. 2005. The academic genealogy of George A. Bartholomew. Integr Comp Biol 45:231–233.

Bradshaw A.D. 1972. Some of the evolutionary consequences of being a plant. Evol Biol 5:25–47.

Dawson W.R. 2005. George A. Bartholomew's contributions to integrative and comparative biology. Integr Comp Biol 45: 219–230.

Dawson W.R., G.A. Bartholomew, and A.F. Bennett. 1977. A reappraisal of the aquatic specializations of the Galapagos marine iguana (*Amblyrhynchus cristatus*). Evolution 31:891–897.

Felsenstein J. 1985. Phylogenies and the comparative method. Am Nat 125:1–15.

Garland T., Jr., and P.A. Carter. 1994. Evolutionary physiology. Annu Rev Ecol Syst 56:579–621.

Gould S.J. and R.C. Lewontin. 1979. The spandrels of San Marcos and the Panglossian paradigm: a critique of the adaptationist program. Proc R Soc B 205:581–598.

Hinde R.A. and N. Tinbergen. 1958. The comparative study of species-specific behavior. Pp. 251–268 in A. Roe and G.G. Simpson, eds. Behavior and Evolution. Yale University Press, New Haven, CT.

Huey R.B., M. Carlson, L. Crozier, M. Frazier, H. Hamilton, H. Harley, A. Hoang, and J.G. Kingsolver. 2002. Plants versus animals: do they deal with stress in different ways? Integr Comp Biol 42:415–423.

Huey R.B. and G. Hofmann. 2005. Introduction: a symposium honoring George A. Bartholomew. Integr Comp Biol 45:217–218.

Lande R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain : body size allometry. Evolution 33:402–416.