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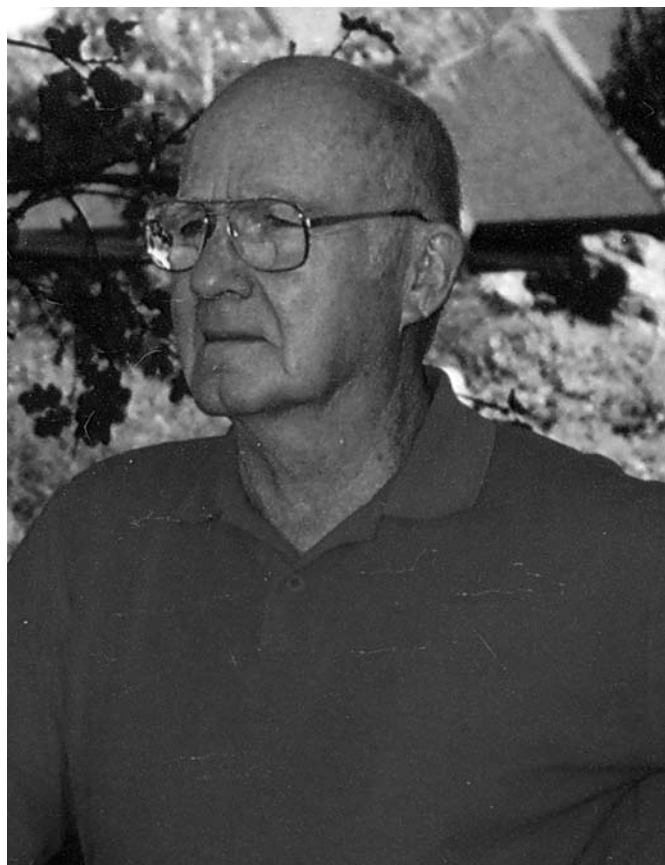
GEORGE A. BARTHOLOMEW
1919–2006

A Biographical Memoir by
WILLIAM R. DAWSON

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Biographical Memoir

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George G. Bartholomew

GEORGE A. BARTHOLOMEW

June 1, 1919–October 2, 2006

BY WILLIAM R. DAWSON

GEORGE ADELBERT BARTHOLOMEW (“Bart” to his family, students, and other friends) leaves a rich professional legacy including important observations on a proper foundation for the biological disciplines with which he was associated, an extensive body of widely cited research, and important contributions in service, teaching, and graduate mentorship. He was one of a small group of scientists primarily responsible for shaping physiological ecology, including its behavioral components, in the latter half of the twentieth century.

Bart was born to Esther Carstensen Bartholomew and George Adelbert Bartholomew Sr., in Independence, Missouri. His parents; his late brother, Richard; and Bart subsequently moved from Kansas City, Missouri, to Berkeley, California, where he attended Berkeley High School. His father was a commercial artist who created oil paintings of some of the animals studied by Bart, which were prominently displayed in the latter’s various homes. Following the family’s move to California, Esther Bartholomew worked in retailing, ultimately becoming a buyer for children’s ware.

Bart completed his A.B. (1940) and M.A. (1941) at the University of California, Berkeley. He then entered the doctoral program in biology at Harvard University. However, the entry of the United States into World War II intervened

shortly thereafter, leading to his becoming a physicist in the U.S. Navy Bureau of Ordnance in 1942. He returned to Harvard in 1945, completed his Ph.D. in 1947, and later that year joined the Department of Zoology at the University of California, Los Angeles. He retired from the UCLA faculty as an honored professor in 1987, but continued as a principal investigator in the university's Laboratory of Biomedical and Environmental Sciences until 1989.

George Bartholomew married Elizabeth ("Betty") Burnham in 1942, creating a partnership that lasted over 50 years. In addition to her domestic responsibilities, she was his traveling companion during several sabbaticals and shorter trips to such places as New Guinea, the Galápagos Islands, and Israel. She was a gracious hostess who was especially welcoming to graduate students. Following Bart's full retirement in 1989, Betty and he moved to Marin County, California, where she died in 1993. Bart married Ruth L. Myers in 1994. She shared his postretirement enthusiasm for painting and his continuing interest in travel. She died in 2006 shortly before his passing.

Bart and Betty Bartholomew's marriage produced two children, Bruce Bartholomew and Karen Bartholomew Searcy. He is also survived by four grandchildren and four great grandchildren.

BIOLOGICAL PERSPECTIVES

An important part of George A. Bartholomew's professional legacy results from his providing meaningful insights concerning the proper foundation of his field of research and other parts of biology as well. Huey and Bennett¹ identified them as "the enduring biological wisdom of George A. Bartholomew," noting their continued relevance for today's investigators. Bart's holistic view of biology still inspires in this era of disciplinary fractionation. He argued from early

in his career that this field is a continuum, but that biologists with their human limitations tend to divide themselves into categories and then pretend that these categories exist in the living systems under investigation. Consequently, he stressed that animals are indivisible functionally and that his field of physiology is not an independent organismal component because of its intimate linkage with, for example, morphology and behavior. He extended this concept of a unified biology in an essay (1986) concerning modern natural history that has important implications for an integrative biology:

Because of its focus on organisms, natural history is in a unique position to supply questions and integrating links among disciplines. Studies at lower levels will delineate the machinery of structural units, and the structure and functioning of the complex systems into which these units have been assembled through evolutionary time will be worked out by research at the intermediate and higher levels of biological integration. Biology is indivisible; biologists should be undivided.

His recognition of a hierarchy of biological explanations had also led him to a justification (1964b) of his inclusive view of biology, which emphasized that a number of levels of biological organization exist and “that each level offers unique problems and insights, and further, that each level finds its explanation of mechanism at levels below, and its significance at levels above.”

Bart’s commitment to explore the evolutionary implications of his research findings wherever possible is one of the most important features of his research. This has led him to be regarded as a major contributor to the foundation for the emerging field of evolutionary physiology.^{1,2} Bart’s evolutionary orientation proved especially important for his field of physiological ecology. He appreciated the implications of biological variability and he reminded his readers (1987a) that

differences between individuals are the raw materials of 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.³

Huey and Bennett¹ have stressed that Bart's conceptual writings anticipated several themes prominent in today's evolutionary biology concerning the origins and nature of adaptation. These writings emphasized the important role of historical factors in shaping the functional characteristics of contemporary species. For example, in his valedictory (2005) he stated

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.”

Throughout his career Bart recognized that chance can also be a factor in evolutionary change (see, for example, 1956, 1986, 2005), but he also fully appreciated the power and limitations of natural selection. Regarding this latter process, he always emphasized (see 2005) that “it is the intact and functioning organism on which natural selection operates. Organisms are therefore a central element of concern to the biologist who aspires to a broad and integrated understanding of biology.”

He also concluded (1986) that it is important in the analysis of the adjustments of organisms to their respective environments to understand that selection results in adequacy of performance rather than perfection.

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 selection is not perfection but adequacy, not final answers but limited, short-term solutions.

In a symposium presentation (1964b) in England, Bart summarized his continuing view that elegance of design is not relevant in the adjustment of animals to their respective environments and

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 [a fact reminding his readers of historical constraints], it is to be expected that a given environmental challenge will be met in a variety of ways by different animals.

A long-term study of breeding patterns of rodents coexisting in a desert community in the Owens Valley of California provided an example of such variety (1985a). One species was found to be a predictor with a lengthy reproductive period coinciding with the historical probability for rainfall and plant productivity, which can be unpredictable in a given year. Another was a responder, breeding in direct response to pulses in food production. A third, with a dependable food supply of saltbush (*Atriplex confertifolia*) leaves, was termed an independent, for its breeding was unaffected by rainfall or pulses in food production. Two other species engaged in lengthy periods of hibernation overlapping any periods of winter rainfall and possibly extending beyond them. These were designated pulse gamblers, which in a brief period produce large litters that survive in favorable times but may succumb in unfavorable years.

A SAMPLING OF GEORGE A. BARTHOLOMEW'S ORIGINAL RESEARCH

George A. Bartholomew was a true comparative biologist, and the subjects of his studies included amphibians⁴ and even the plant *Philodendron sellowii*⁵ in addition to insects, reptiles, birds, mammals, the groups that attracted his primary efforts. He consistently operated at the interfaces of behavior, ecology, and comparative physiology. Pursuit of appropriate research animals and environmental situations led him to work in North and Central America; Australia; Europe; Africa; Antarctica; and a number of islands, including the Pribiloffs, Midway, and New Guinea. I presented a general review² of his research accomplishments in the symposium "Integrative Biology: A Symposium Honoring George A. Bartholomew" held at the 2004 annual meeting of the Society for Integrative and Comparative Biology, and the sampling here is provided primarily to illustrate the scope and orientation of his work and to indicate the extent of his research collaborations. These collaborations in which he typically served as a guiding influence in planning and implementation principally involved his graduate students, former graduate students, postdoctoral scholars, or fellow faculty members.

Bart was always careful to observe the principle first enunciated by Claude Bernard that an organism is inseparable from its environment. He emphasized that full knowledge of any species requires familiarity with not just its general surroundings but also its interaction as a self-maintaining physicochemical system with its special microenvironment. Consequently, fieldwork played a prominent role in his research. He was a patient and insightful observer whose field notes, recorded in a format learned at the University of California, Berkeley, were models of clarity.

Bart initiated field studies of the northern elephant seal (*Mirounga angustirostris*), Alaska fur seal (*Callorhinus ursinus*),

and California sea lion (*Zalophus californianus*) shortly after arrival at UCLA. These began with documentation of the resurgence of populations of the California sea lion and northern elephant seal on islands off Baja California, Mexico, and southern California and were followed by major studies of the social and reproductive behavior of all three species (1952, 1953a, 1967). In the course of these studies he was impressed by the finding that intense terrestrial activity by the seals, particularly large and well-insulated territorial males, could put them at risk of overheating, even in a cool climate. As a result of his fieldwork, Bart could explain (1966a) the seeming paradox that sea lions reproduce successfully in the equatorial Galápagos Islands, despite warm ambient temperatures and intense solar radiation. Breeding male sea lions persistently maintain terrestrial territories on islands off the west coast of California and Baja California, where thermal conditions are ameliorated by cool upwelling water and a persistent summer overcast. He found that males breeding in the Galápagos use a behavioral strategy in meeting the thermal challenges prevailing in their equatorial territories. They protect themselves from overheating during the day by holding aquatic territories in tide pools or channels, hauling out on land only at night. This seemingly simple behavioral arrangement imposes profound effects on a breeding structure that is exclusively terrestrial in other otariids (sea lions and fur seals), but it shows how behavior can contribute to the resolution of a primarily physiological problem, a recurrent theme in Bart's studies.

He participated in several studies of colonially nesting birds on tropical and subtropical islands, recognizing that such assemblages offer an excellent resource for examining the physiological and behavioral components of avian thermoregulation. In many of these colonies birds nest in exposed situations where disruption of their attentiveness could

expose eggs and young to dangerously intense insolation as well as warm ambient temperatures. One study (1954) involved three species nesting concurrently on a hot desert island in the Gulf of California, Mexico. It demonstrated how closely the attentive behavior of parents in each species was attuned to the thermoregulatory capacities of their respective hatchlings. At the extremes of the developmental spectrum evident among these species, the altricial hatchlings of the brown pelican (*Pelecanus occidentalis*) were brooded or shaded nearly continuously, whereas such attention was intermittent in the more precocial hatchlings of yellow-footed gulls (*Larus livens*) and great blue herons (*Ardea herodias*) with their more developed heat defenses.

Extensive observations of breeding seabirds on Midway Island, where intense insolation is also a problem, led to documentation of thermally important behavior by both parents and young of various ages (e.g., 1961a). A photograph of older nestling albatrosses (*Diomedea nigripes* and *D. immutabilis*) oriented with their backs to the sun, resting on their heels, and raising their shaded, heavily vascularized webbed feet off the ground into the cooling trade winds provides an especially striking image.

Behavior can have a major impact on the thermal relations of terrestrial as well as aquatic birds. The sociable weaver (*Philetairus socius*) provides an example. This weaver finch, a relative of the house sparrow (*Passer domesticus*), constructs huge, communal nests in the Kalahari Desert, which large flocks continuously occupy and maintain. Bart, F. N. White, and T. R. Howell (1975a, 1976) examined the extent of thermal protection provided by these structures in summer and winter. In the former season, outside air temperatures ranged from 16°C to 33.5°C, whereas temperatures in occupied nest chambers varied only 7°C or 8°C. Winter in the Kalahari often involves winds and temperatures that can

drop to freezing. At this season the insulation of the nest in combination with the heat production of roosting birds allowed temperatures as high as 37°C, 23° above outside temperatures. Only two sociable weavers occupied a nest chamber in the summer, whereas up to five did so in winter, convincing Bart and his colleagues that adjustment of the number of occupants is important in allowing these birds to maintain equable chamber temperatures throughout the year. This thermal stability produces energy savings of nearly 50 percent relative to estimated costs that birds roosting in the open air would incur. Reduction of thermoregulatory costs appears important for the sociable weaver both in allowing higher population densities in an area of low biological productivity and in extending breeding into the cooler parts of the year. The ability to breed under cooler conditions probably reduces the heavy reptilian predation on parents, eggs, and young that can occur in warmer weather.

Bart participated in some research projects on terrestrial mammals that helped document the contributions of behavior to their regulation of body temperature. His observations on the quokka (*Setonix brachyurus*) in Western Australia (1956) during his first sabbatical provide a pertinent example. This small macropod (the macropods include kangaroos and their relatives) proved to be highly proficient in its temperature control over an ambient range of 21°C to 44°C, helping refute a longstanding view that marsupials possess more limited homeostatic capacities than placental mammals. Drawing on its behavioral repertoire, the quokka cooled itself at high ambient temperatures by spreading saliva over its ventral surface, limbs, and tail.

Bart was the first to undertake a research program on the physiology and behavior of desert birds, and he and his collaborators produced a series of papers and reviews (e.g., 1957a, 1958b, 1959, 1962a, 1963a, 1966b). Some dealt with

the thermoregulatory responses of these animals to high ambient temperatures and the role of hyperthermia in avian heat defense. The remainder focused on their water and electrolyte metabolism. Bart ultimately developed a model explaining the ability of certain small birds to survive without drinking at cool and moderate ambient temperatures (1972). One particularly important facet of the research on water and electrolyte balance (1959) documented variation among populations of the savannah sparrow (*Passerculus sandwichensis*) in abilities to use saline solutions as a fluid source. Marked differences in electrolyte metabolism were found between the subspecies resident in salt marshes and migrant forms, with the former more proficient than the latter in obtaining physiologically useful water from NaCl or seawater solutions. A subsequent study (1962c) compared representatives of one of the salt marsh taxa (*P. s. beldingi*) and a migrant form (*P. s. brooksi*). This showed that the salt marsh residents tolerated significantly higher serum osmotic pressures and chloride concentrations and produced substantially more concentrated urine than the migrants. These studies are notable for providing early examples of variation in avian physiological performance among populations within a single species.

The capacity of certain birds and mammals to reduce environmental challenges involving heat, cold, or restriction of food or water through heterothermy⁶ always intrigued George Bartholomew. He collaborated (1957b) in the first successful laboratory study of it in the common poor-will (*Phalaenoptilus nuttallii*). This relative of the more familiar whip-poor-will (*Caprimulgus vociferus*) was known to undergo prolonged bouts of reduced body temperature in nature. Information on heterothermy was also obtained for swifts and hummingbirds. Bart also played an important role in its study in certain desert rodents (1957c, 1961b, 1969)

including Mohave ground squirrels, *Spermophilus mohavensis* (1960). Their abilities to lower body temperature and enter torpor were analyzed and the first extensive laboratory observations on the phenomenon of estivation (animals engaging in heterothermy during the warmer parts of the year) were reported.

The Bartholomew interest in mammalian and avian heterothermy was extended further through additional collaborative studies (1962b, 1970b, 1970c) involving such species as speckled mouse birds, *Colius striatus* and two small bats, the common tube-nosed fruit bat, *Nyctimene albiventer*, and the unstriped tube-nosed bat, *Paranyctimene raptor* (1970c). The results for the two bats were of interest because of their tropical distribution, fruit diet, and the lack of any previous demonstration of heterothermy within their Suborder, the Megachiroptera.⁷ Additionally, nocturnal torpor involving body temperatures as low as 26.8°C was observed by Bart, T. L. Bucher, and C. M. Vleck (1983) in two small neotropical birds, the manakins *Pipra mentalis* and *Manacus vitellinus*. These birds, like the bats, are frugivorous. Heterothermy can reduce the energy expenditures of these small animals by more than half. Fruit is not always readily available in tropical rain forests and it was hypothesized that heterothermy (and reduced energy expenditure) might well occur in other small tropical songbirds dependent upon such food.

Thermal responses of lizards received Bart's attention during a second sabbatical in Australia. Results obtained significantly expanded knowledge of the physiological capacities of these animals. For example, observations on the bearded dragon, *Amphibolurus barbatus*, (1963b) provided an early demonstration of a reptilian ability to modify the rates of change of body temperature during heating or cooling. A similar capacity was also observed in monitor lizards, *Varanus* spp., (1964a) and the large skink *Tiliqua scincoides* (1965).

In most of these lizards, though not in the monitors, heart rate at a given temperature was lower during cooling than during heating. This probably retarded heat loss during cooling and accelerated heat gain from external sources during warming.

Work on the three species of Australian lizards mentioned above also featured the first application to reptiles of a concept developed by F. E. J. Fry concerning aerobic metabolic scope⁸ (i.e., the difference between the standard and peak rates of oxygen consumption of an animal at a particular body temperature—an index of aerobic capacity for activity). In an era when investigators were primarily concerned with standard or resting metabolic rates, Bart and his collaborators extended their studies to include measurement of the highest rates of oxygen consumption resulting from spontaneous activity or stimulation of their lizards. These studies represented an important first step in the analysis of the metabolic correlates of reptilian activity and their thermal dependence, as well as fostering a substantial amount of later research on the energy cost of locomotion and the temperature dependence of metabolic scope in such animals. Bart participated in additional exploration of these topics in the Galápagos marine iguana *Amblyrhynchus cristatus* in several later studies (e.g., 1975b, 1979a, 1981a), which measured aerobic and anaerobic metabolic scope in relation to temperature, swimming performance, and energy cost of transport. This cost in marine iguanas was found to vary inversely with body mass, and foraging patterns of various size classes were size dependent. Small marine iguanas feed on algae on or near shore, whereas adults obtain this food by diving offshore.

In the early 1970s George A. Bartholomew expanded his research to include insect physiology, and this resulted in an extensive set of studies (e.g., 1971; 1973; 1975c; 1977; 1978;

1979b; 1981b; 1982b; 1984a,b; 1985b,c; 1987b; 1988a,b). He explained the basis of this expansion of interests thus in an essay on creativity (1982a):

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 of comparative vertebrate physiology and applying them to insects (see Heinrich, 1981^[9]). It is surprising that this pattern of innovation is not more deliberately employed. It is commonplace to find a biologist trained in one field and working in another. This represents a more demanding change than transferring questions and techniques between fields.

Bart's move into insect physiology is not quite as simple as this narrative suggests, for it involved some technical challenges resulting from both the miniscule size of some of the insects studied and the transient nature of several of the responses being measured. The work on insects accomplished by him and his collaborators emphasized analysis of the endothermic⁶ capacities of representatives of several orders, notably certain moths, beetles, and cicadas. More specifically, this work examined such things as thermoregulation, locomotor costs, and sometimes respiration (1971; 1973; 1977; 1978; 1982b; 1984b; 1985b,c; 1987b). In the animals studied endothermy primarily involves intense contractions of the flight muscles, with the resultant heat largely sequestered in the thoracic region during warm-up and activity (1971). It was of interest not only from a comparative standpoint but also because it allowed some species to be active with warm thoracic temperatures at surprisingly low ambient temperatures. The mass of the smallest endothermic moths of the family Sphingidae was less than 1/10th that of the smallest birds and mammals, more familiar endotherms.

In most of the endothermic insects examined the warm thoracic temperatures produced through muscular thermogenesis are required for flight. Observations on various African dung beetles (1979b) established that the functional significance of endothermy extends beyond this specific locomotor activity, for it allows these animals to compete more effectively for elephant dung. The range of capacities of endothermic insects was extended even further by K. R. Morgan and Bart's (1982b) observation of a rise in metabolic rate in the elephant beetle (*Megasoma elephas*) with a drop in ambient temperature below 20°C. The increased heat production prevented body temperature from falling below 20°C-22°C. This response seemed independent of any overt activity.

The work of George Bartholomew and collaborators on heterothermic⁶ moths allowed comparisons of the allometry of resting and active aerobic metabolic rates with that for the comparable rates in certain vertebrates. Of particular interest, the scaling of metabolic rate during flight to body mass for these insects was virtually identical with that for bats and birds (1978). The body masses of larger sphingid moths overlap those of hummingbirds (1981c), and this provided an opportunity for a direct comparison of energetics in analogous flight systems that allow nectar feeding during hovering (1987a). This comparison indicated that hovering costs in the moths and hummingbirds are very high and nearly identical, despite these animals' differences in body plans and evolutionary histories. Moreover, insect and vertebrate structural and functional patterns were found to support similar aerodynamic efficiencies at body masses of 1g-10g. Bart noted further (1987a) that the rate of oxygen consumption per g in flying hummingbirds exceeds the maximal metabolic rate of any other vertebrate and he inferred from this that moths of the family Sphingidae and hummingbirds

both are approaching the limit of aerodynamic performance for animals of their size.

Bartholomew and his collaborators also studied insects that are strictly ectothermic.⁶ Moths of the family Geometridae were of particular interest because some could fly at low body temperatures. This ability may be associated with the animals' very light wing loading and low wing beat frequency (1973). Other research on ectothermic insects in the Bartholomew laboratory examined energy metabolism and locomotor costs in several tropical or desert ants (1987b; 1988a,b). Respiration and energetics of locomotion in flightless beetles of the family Tenebrionidae from the Namib Desert (1984a, 1985c) were also studied. In a field study of the beetles (1984a), running speed of *Onymacis plana* averaged a remarkable 90 cm/s (48 body lengths/s), an apparent championship rate for any pedestrian insect. Comparable mean running speeds for *Physadesmia globosa* and *Epiphysa arenicola* were only 23 cm/s and 3 cm/s, respectively. The relative speeds of the three species were correlated with leg length and muscle mass, as well as with prothoracic temperature during activity. This temperature was elevated to 36.7°C and 30.5°C, respectively, by behavioral thermoregulation in the diurnal *O. plana* and *P. globosa*, whereas it probably approximated ambient temperature (ca. 19°C) in the nocturnal *E. arenicola*.

I have described in the preceding paragraphs some of the major elements of George A. Bartholomew's research on physiological ecology. He explored the implications of his results with great skill and in appropriate instances combined his conclusions with information from the literature to provide a firm evolutionary perspective for his work. Occasionally he moved beyond the usual boundaries of his empirical research to consider some general questions such as the nature of creativity (see next section of this memoir) and the ecology of protohominids (1953a). His consideration of the latter

topic featured an examination of the role of bipedalism in the ecology of the early ancestors of humans. A previous study of kangaroo rats (1951) in which he participated noted that this form of locomotion is relatively uncommon in mammals, raising the question of what advantage it might afford these rodents. They are typically associated with sparsely vegetated habitat and must forage in open areas, where they are potentially vulnerable to a variety of predators. It was concluded that the special value of bipedalism to kangaroo rats lies in the ability it imparts for changing direction rapidly in the open and thereby lowering predation risk. Bart's collaboration with the anthropologist J. B. Birdsell (1953b) concerning the early human ancestors again raised a question about the advantage of bipedalism. In this case the authors concluded that it was important to these ancestral beings because it freed the hands, thereby allowing continuous and efficient manipulation of such rudimentary tools as rocks, sticks, and bones. This concept contributed to the refinement of the definition of man from being a tool-using animal (a host of other animals have been found to employ tools) to one of being the only type of mammal that is continuously dependent upon tools for survival.

Bart's work on seals led to formulation of a model to explain the evolution of polygyny in this group, one of its most conspicuous features (1970a). This model took into account the special features of these animals, particularly terrestrial parturition and offshore marine feeding. These features were thought to have interacted with characteristics common to most mammals in a manner fostering both sexual dimorphism in size and polygynous breeding systems. Gregariousness but aggression involving exclusion of most subordinate males from contact with females in rookeries received key roles. In addition, large size and subcutaneous fat—characteristics serving to promote heat conservation

during immersion of the animals (see comments regarding risks for seals of overheating on land)—were recognized for their roles in permitting sustained fasting and prolonged territorial defense by dominant males.

TEACHING, MENTORSHIP, AND SERVICE

In a professorial career spanning 1947-1989 George Bartholomew distinguished himself in biological instruction. I was a student in two of his courses during his early years at UCLA. His lectures were models of clarity, and he showed a knack for linking individual facts and larger issues in biology.

Bart was a spectacularly successful mentor of graduate students and postdoctoral scholars, perhaps because he had a firm appreciation of the enthusiasm and creativity of such individuals and credited them with helping him maintain a youthful viewpoint. Moreover, he understood their centrality to the research enterprise, as he made clear in an interview¹⁰ by Neil A. Campbell that was published shortly after his full retirement. He responded to the question “You’ve described creativity as a form of youthful play. How can we keep playing as we get older? How can middle-aged and older professors benefit from their students?”

Associate with them. I started saying, when I was about 45, that I’m intellectually dead without my students. I know I would have bogged down into teaching the same stuff year after year and doing the same kind of research. But with students, you can’t. You know they’re all different, they all want to do different things.

Related to that, I always let the students choose their own problems. I never assign problems, which means that you have people working on all kinds of things in the lab. And that’s one way you retain your youthful point of view. I think the student is the center of the research enterprise.

Bart directed the theses of 42 doctoral candidates and hosted 15 postdoctoral scholars according to the obituary by departmental colleagues.¹¹ Bennett and Lowe¹² have created a Bartholomew academic genealogy that includes most of these individuals, postdoctoral scholars, and succeeding generations of their graduate students. In late 2010 it included an impressive 1,175 individuals with a direct intellectual linkage to George A. Bartholomew.¹³

Bart was selective concerning the graduate students he accepted to work with him. For these individuals, as well as students in general, he was a very approachable, supportive, and patient professor, stimulating them to do their best through example and personal interaction. He summarized his approach to mentoring his graduate students in comments he made during the interview by Neil Campbell cited above.¹⁰ Campbell posed the following question: “You have a remarkable history of training graduate students who go on to productive and distinguished careers. Do you have some ideas about what makes you such an effective mentor?” Bart stated,

The main thing is to get good students. I have been very, very choosy. Each of the graduate students I accepted became an important person to me and I gave them all loving attention. I worked in the lab, continuously, so I was with them every day. Anything I knew, they soon knew. When it came to writing the dissertation, they wrote the first draft and I would tear it to bits, absolutely tear it to bits, because I felt the most important thing I could do was to make sure that they were good scientific writers by the time they finished. I never published or put my name on a dissertation that was a student’s own. So I gave them the immediate rewards. The combination of hands-on attention and aggressive editing of the dissertation is the only thing I can think of, really, aside from getting good students.

With each student I’ve entered into a contract that after a year I will tell you whether I will accept you permanently. The first year is provisional. If you don’t like me, if you and I don’t strike it off, if I don’t think you have

it, or if your approach is inappropriate for my style, I will do my best to get you another advisor or another niche some place, either here at UCLA or at another school.

One other thing that was terribly important was a weekly meeting to which my graduate students came. It was a continuing seminar that ran year after year. The students participated in it from the beginning to the end of their graduate studies, so that there were always beginning graduate students and advanced graduate students and a couple of postdocs with me in the seminar and we all worked together. We would report on our research. We'd read books and articles together and discuss them. This kept me alive and up to date because I was drawing on the library resources of eight or ten people, continuously. This let me communicate to them everything I knew about science, and it let the senior grad students teach the junior ones, and let the postdocs put in different points of view that came from other institutions.

Beyond guidance in the writing of theses Bart also made a point of providing many of his graduate students with direct research experience through opportunities to participate in his own studies. This led to a mutually beneficial arrangement supplementing his efforts with additional hands while imparting to these students experience in identifying meaningful questions for investigation, implementing research, and data analysis. Students who collaborated with him in his various projects were exposed to his graceful writing style and rigorous editorial standards. Their participation in authorship of papers resulting from such research collaborations additionally schooled them in the publication process while adding to their credentials.

Bart's commitment to fieldwork and to graduate students studying in his or related fields at UCLA continues through the departmental Bartholomew Field Biology Fellowship, which he and his wife, Betty, established and which he and his second wife, Ruth, augmented. This award provides a summer fellowship and research support for the top advanced graduate student in ecology, evolutionary biology,

and/or conservation biology, whose research has a significant field component.

In addition to his direct interactions with students George A. Bartholomew contributed to the educational process by producing some useful instructional materials. These include chapters in two textbooks, one for introductory students in biology and the other, a physiology text, for seniors and even graduate students, which enjoyed several editions.¹⁴ His chapters in the latter book, which are especially relevant to the interests of physiological ecologists, deal with the general features of energy metabolism and with body temperature and energy metabolism, respectively, and are notable among textbook chapters in the wealth of useful reference information for researchers as well as students. Thirty-two educational films provide another important part of the Bartholomew educational legacy. These analyze significant behaviors and processes of animals and illustrate a number of biological principles. The film series on the Galápagos Islands as an evolutionary laboratory is especially noteworthy.

Bart's fairness and calm good judgment also allowed him to contribute important service to UCLA. He was chair of the Department of Zoology at UCLA (1958-1961) and is credited by colleagues with shifting it to a more participatory form of governance.¹¹ He was concurrently tasked with heading the Department of Botany and in the course of this assignment helped facilitate the ultimate merger of the two units into a Department of Biology. His colleagues also note¹¹ that he was influential in the founding of UCLA's Molecular Biology Institute and in the recruitment of molecularly oriented faculty.

Bart participated in several boards and committees at the national level. These included advisory panels for the National Science Foundation and service on the Board of Trustees of the California Academy of Sciences and the Council of

the Smithsonian Institution. He also served as a scientific adviser to the U.S. Marine Mammal Commission. As chief scientist of R/V *Alpha Helix* expeditions to New Guinea and the Galápagos Islands he facilitated the activities of groups of colleagues and graduate students while conducting his own research. His service to scientific societies included terms as vice president of the American Ornithologists' Union and president of the predecessor of the Society of Integrative and Comparative Biology, the American Society of Zoologists.

AWARDS, FELLOWSHIPS, AND OTHER HONORS

Professor George A. Bartholomew's major role in shaping ecophysiological studies of animals for more than four decades and his accomplishments as a teacher and graduate mentor led to several forms of recognition. He was the recipient of the Brewster Medal of the American Ornithologists Union (1968); Fellow's Medal of the California Academy of Sciences (1978); Grinnell Medal of the Museum of Vertebrate Zoology, University of California, Berkeley (1983, first recipient); and the Miller Award of the Cooper Ornithological Society (1993, first recipient). He received Fulbright (1953-1954) and Guggenheim fellowships (1961-1962), which supported sabbatical years in Australia. His contributions to UCLA were recognized with a Distinguished Teaching Award (1966) and inclusion at the recent Millennium in a listing of the 20 top professors in the history of the institution. Bart became a fellow of the American Academy of Arts and Sciences in 1981 and was elected to membership in the National Academy of Sciences in 1985. He also received an honorary doctorate of science from the University of Chicago in 1987. Further recognition occurred through appointments to honorary memberships in the Cooper Ornithological Society and the American Society of Zoologists (1989 and 1990, respectively).

The Society of Integrative and Comparative Biology's George A. Bartholomew Award, which has been conferred annually since 1993, provides a tangible reminder of the esteem in which he is held by colleagues. In keeping with Bart's appreciation of the creativity and enthusiasm of young scientists, this award recognizes distinguished young investigators in comparative physiology, comparative biochemistry, or related fields of functional biology. Bart (2005) noted that of his various professional awards none yielded more satisfaction to him than this one bearing his name.

CONCLUDING STATEMENT

An effective teacher, inspiring graduate mentor, and productive researcher, George A. Bartholomew maintained a vision of what can be accomplished by realizing that biology is a continuum and working at interfaces between disciplines. His holistic view of biology and his recognition of the ultimate connection of organismal studies with enquiries conducted at other levels of biological integration made him a voice of reason in elucidating the drawbacks for creative scholarship of excessive disciplinary fractionation. His commitment through both field and laboratory observations to understanding how animals function in their natural environments, his interest in how diverse species respond to particular environmental challenges, and his appreciation of the importance of intraspecific variation imparted a special flavor to his research. As Huey and Bennett¹ note, he consistently showed a willingness to adjust his methods to fit each of the diverse organisms he studied, an approach that often required innovation. Perhaps we can give George A. Bartholomew no higher accolade than by remembering him as a truly broad scholar who had a major impact on his

many students and postdoctoral scholars as well as on their students, on physiological ecology, and on comparative and integrative biology generally.

NOTES

1. R. B. Huey and A. F. Bennett. Bart's familiar quotations: The enduring biological wisdom of George A. Bartholomew. *Physiol. Biochem. Zool.* 81(2008):519-525.
2. W. R. Dawson. George A. Bartholomew's contributions to integrative and comparative biology. *Integr. Comp. Biol.* 45(2005):219-230.
3. T. L. Bucher and G. A. Bartholomew. Analysis of variation in gas exchange, growth patterns, and energy utilization in a parrot and other avian embryos. In *Respiration and Metabolism of Embryonic Vertebrates*, vol. 3, ed. R. S. Seymour. *Perspectives in Vertebrate Science*, pp. 359-372. Dordrecht: Dr. W. Junk, 1984
4. M. J. Ryan, G. A. Bartholomew, and A. S. Rand. Energetics of reproduction in a neotropical frog *Physalaemus pustulosus*. *Ecology* 64(1983):1456-1462.
5. R. S. Seymour, G. A. Bartholomew, and M. C. Barnhart. Respiration and heat production by the inflorescence of *Philodendron selloum* Koch. *Planta* 157(1983):336-343.
6. Animals are divided into two groups based on the principal source of heat affecting their body temperature. A minority of species (mammals and birds, a few large reptiles, some fast swimming marine fish, and certain insects) either persistently or intermittently display high rates of endogenous heat production and effective heat conservation that allow attainment of body temperatures significantly above ambient levels. These animals are referred to as "endotherms." On the other hand, the vast majority of animals have relatively low rates of heat production and limited abilities to conserve heat. Consequently, their body temperatures are primarily determined by thermal conditions in their environment and they are identified as "ectotherms." Endothermy is continuous in most adult mammals and birds. However, some species in these classes are facultative endotherms that may reduce rates of heat production for hours or much longer periods and cool to body temperatures that can approach ambient levels. These animals are referred to as "heterotherms." George A. Bartholomew also applied this term to those insects that are ectothermic when inactive but establish relatively high body temperatures through endothermy as a prelude to activity.
7. G. A. Bartholomew, P. Leitner, and J. E. Nelson. Body temperature, oxygen consumption, and heart rate in three species of Australian flying foxes. *Physiol. Zool.* 37(1964):179-198.

8. F. E. J. Fry. *Effects of Environment on Animal Activity*. Publications of the Ontario Fisheries Research Laboratory No. 68, 1947.
9. B. Heinrich, ed. *Insect Thermoregulation*. New York: John Wiley, 1981.
10. N. A. Campbell. A conversation with George Bartholomew. *Am. Biol. Teacher* 52(1990):136-141.
11. M. S. Gordon, H. Hespendeide, and K. A. Nagy. George A. Bartholomew (June 1, 1919-October 2, 2006) Professor Emeritus, Department of Biology, UCLA. Department of Ecology and Evolutionary Biology newsletter, 2007. www.eeb.ucla.edu/bartholomew.php?p=obit.
12. A. F. Bennett and C. Lowe. The academic genealogy of George A. Bartholomew. *Integr. Comp. Biol.* 45(2005):231-233.
13. C. Lowe. Pers. comm.
14. M. S. Gordon, G. A. Bartholomew, A. D. Grinnell, C. B. Jørgensen, and F. N. White. *Animal Physiology*, 4th ed. New York: MacMillan, 1982.

SELECTED BIBLIOGRAPHY

1951

With H. H. Caswell Jr. Locomotion in kangaroo rats and its adaptive significance. *J. Mammal.* 32:155-169.

1952

Reproductive and social behavior of the northern elephant seal. *U. Calif. Publ. Zool.* 47:369-472.

1953

- (a) With P. G. Hoel. Reproductive behavior of the Alaska fur seal, *Callorhinus ursinus*. *J. Mammal.* 34:417-436.
- (b) With J. B. Birdsell. Ecology and the protohominids. *Am. Anthropol.* 55:481-498.

1954

With W. R. Dawson. Temperature regulation in young pelicans, herons, and gulls. *Ecology* 35:466-472.

1956

Temperature regulation in the macropod marsupial *Setonix brachyurus*. *Physiol. Zool.* 29:26-40.

1957

- (a) With T. J. Cade. The body temperature of the American kestrel, *Falco sparverius*. *Wilson Bull.* 69:149-154.
- (b) With T. R. Howell and T. J. Cade. Torpidity in the white-throated swift, Anna hummingbird, and poor-will. *Condor* 59:145-155.
- (c) With T. J. Cade. Temperature regulation, hibernation, and aestivation in the little pocket mouse, *Perognathus longimembris*. *J. Mammal.* 38:60-71.

1958

- (a) The role of physiology in the distribution of terrestrial vertebrates. In *Zoogeography*, ed. C. L. Hubbs, Pub. No. 51, pp. 81-95. Washington, D.C.: American Association for the Advancement of Science.
- (b) With W. R. Dawson. Body temperatures in California and Gambel's quail. *Auk* 75:150-156.

1959

With T. J. Cade. Sea-water and salt utilization by savannah sparrows. *Physiol. Zool.* 32:230-238.

1960

With J. W. Hudson. Aestivation in the Mohave ground squirrel *Citellus mohavensis*. In *Mammalian Hibernation*, eds. C. P. Lyman and A. R. Dawe. *Bull. Mus. Comp. Zool.* 124:193-208.

1961

- (a) With T. R. Howell. Temperature regulation in Laysan and black-footed albatrosses. *Condor* 63:185-197.
- (b) With R. E. MacMillen. Oxygen consumption, estivation, and hibernation in the kangaroo mouse, *Microdipodops pallidus*. *Physiol. Zool.* 34:177-183.

1962

- (a) With J. W. Hudson and T. R. Howell. Body temperature, oxygen consumption, evaporative water loss, and heart rate in the poor-will. *Condor* 64:117-125.
- (b) With J. W. Hudson. Hibernation, estivation, temperature regulation, evaporative water loss, and heart rate of the pygmy possum, *Cercaetus nanus*. *Physiol. Zool.* 35:94-107.
- (c) With T. L. Poulson. Salt balance in the savannah sparrow. *Physiol. Zool.* 35:109-119.

1963

- (a) With T. J. Cade. The water economy of land birds. *Auk* 80:504-539.
- (b) With V. A. Tucker. Control of changes in body temperature, metabolism, and circulation by the agamid lizard, *Amphibolurus barbatus*. *Physiol. Zool.* 36:199-218.

1964

- (a) With V. A. Tucker. Size, body temperature, thermal conductance, oxygen consumption, and heart rate in Australian varanid lizards. *Physiol. Zool.* 37:341-354.
- (b) The roles of physiology and behaviour in the maintenance of homeostasis in the desert environment. In *Homeostasis and Feedback Mechanisms*, ed. G. M. Hughes, *Symp. Soc. Exp. Biol.* 18:7-29.
- (c) With J. W. Hudson. Desert ground squirrels. *Sci. Am.* 205:107-116.

1965

With, V. A. Tucker, and A. K. Lee. Oxygen consumption, thermal conductance, and heart rate in the Australian skink *Tiliqua scincoides*. *Copeia* 1965:169-173.

1966

- (a) Interaction of physiology and behavior under natural conditions. In *The Galápagos*, ed. R. I. Bowman, pp. 39-45. Berkeley: University of California Press.
- (b) With M. Smyth. The water economy of the black-throated sparrow and the rock wren. *Condor* 68:447-458.

1967

With R. S. Peterson. *The Natural History of the California Sea Lion*. Spec. Pub. No. 1. Stillwater, Okla.: American Society of Mammalogists.

1969

With J. H. Brown. Periodicity and energetics of torpor in the kangaroo mouse, *Microdipodops pallidus*. *Ecology* 50:705-709.

1970

- (a) A model for the evolution of pinniped polygyny. *Evolution* 24:546-559.
- (b) With C. H. Trost. Temperature regulation in the speckled mousebird, *Colius striatus*. *Condor* 72:141-146.
- (c) With W. R. Dawson and R. C. Lasiewski. Thermoregulation and heterothermy in some of the smaller flying foxes (Megachiroptera) of New Guinea. *Z. vergl. Physiol.* 70:196-209.

1971

With B. Heinrich. An analysis of pre-flight warm up in the sphinx moth *Manduca sexta*. *J. Exp. Biol.* 55:223-239.

1972

The water economy of seed-eating birds that survive without drinking. In *Proceedings of the XVth International Ornithological Congress*, pp. 237-254. Leiden: E. J. Brill.

1973

With B. Heinrich. A field study of flight temperatures in moths in relation to body weight and wing loading. *J. Exp. Biol.* 58:123-135.

1975

- (a) With F. N. White and T. R. Howell. The thermal significance of the nest of the sociable weaver *Philetairus socius*: Winter observations. *Ibis* 117:171-179.
- (b) With A. F. Bennett and W. R. Dawson. Effects of activity and temperature on aerobic and anaerobic metabolism of the Galapagos marine iguana. *J. Comp. Physiol.* 100:317-329.
- (c) With R. J. Epting. Allometry of post-flight cooling rates in moths: A comparison with vertebrate homeotherms. *J. Exp. Biol.* 63:603-613.

1976

With F. N. White and T. R. Howell. 1976. The thermal significance of the nest of the sociable weaver *Philetairus socius*: Summer observations. *Ibis* 118:402-410.

1977

With T. M. Casey. Body temperature and oxygen consumption during rest and activity in relation to body size in some tropical beetles. *J. Therm. Biol.* 2:173-176.

1978

With T. M. Casey. Oxygen consumption of moths during rest, pre-flight warm-up, and flight in relation to body size and wing morphology. *J. Exp. Biol.* 76:11-25.

1979

- (a) With D. Vleck. The relation of oxygen consumption to body size and to heating and cooling in the Galapagos marine iguana, *Amblyrhynchus cristatus*. *J. Comp. Physiol.* 132:285-288.
- (b) With B. Heinrich. Roles of endothermy and size in inter- and intraspecific competition for elephant dung in an African dung beetle, *Scarabaeus laevistriatus*. *Physiol. Zool.* 52:484-496.

1981

- (a) With D. Vleck and T. T. Gleeson. Oxygen consumption during swimming in Galapagos marine iguanas and its ecological correlates. *J. Comp. Physiol.* 141:531-536.
- (b) With D. Vleck and C. M. Vleck. Instantaneous measurements of oxygen consumption during pre-flight warm-up and post-flight cooling in sphingid and saturniid moths. *J. Exp. Biol.* 90:17-32.
- (c) A matter of size: An examination of endothermy in insects and terrestrial vertebrates. In *Insect Thermoregulation*, ed. B. Heinrich, pp. 45-78. New York: John Wiley.

1982

- (a) Scientific innovation and creativity: A zoologist's point of view. *Am. Zool.* 22:227-235.
- (b) With K. R. Morgan. Homeothermic response to reduced ambient temperature in a scarab beetle. *Science* 216:1409-1410.

1983

With C. M. Vleck and T. L. Bucher. Energy metabolism and nocturnal hypothermia in two tropical passerine frugivores, *Manacus vitellinus* and *Pipra mentalis*. *Physiol. Zool.* 56:370-379.

1984

- (a) With S. W. Nicolson and M. K. Seely. Ecological correlates of locomotion speed, morphometrics, and body temperature in three Namib Desert tenebrionid beetles. *S. Afr. J. Zool.* 19:131-134.
- (b) With M. C. Barnhart. Tracheal gases, respiratory gas exchange, body temperature and flight in some tropical cicadas. *J. Exp. Biol.* 111:131-144.

1985

- (a) With G. J. Kenagy. Seasonal reproductive patterns in five coexisting California desert rodent species. *Ecol. Monogr.* 55:371-397.
- (b) With J. R. B. Lighton. Ventilation and oxygen consumption during rest and locomotion in a tropical cockroach, *Blaberus giganteus*. *J. Exp. Biol.* 118:449-454.
- (c) With J. R. B. Lighton, and G. N. Louw. Energetics of locomotion and patterns of respiration in tenebrionid beetles from the Namib Desert. *J. Comp. Physiol. B* 155:155-162.

1986

The role of natural history in contemporary biology. *Bioscience* 36:324-329.

1987

- (a) Interspecific comparison as a tool for ecological physiologists. In *New Directions in Ecological Physiology*, eds. M. E. Feder, A. F. Bennett, W. W. Burggren, and R. B. Huey, pp. 11-37. Cambridge, UK: Cambridge University Press.
- (b) With J. R. B. Lighton and D. H. Feener Jr. Energetics of locomotion and load carriage and a model of the energy cost of foraging in the leaf-cutting ant *Atta colombica* Guer. *Physiol. Zool.* 60:524-537.

1988

- (a) With J. R. B. Lighton. Standard energy metabolism of a desert harvester ant *Pogonomyrmex rugosus*: Effects of temperature, body mass, group size, and humidity. *Proc. Natl. Acad. Sci. U. S. A.* 85:4765-4769.
- (b) With J. R. B. Lighton and D. H. Feener Jr. Energetics of trail running, load carriage, and emigration in the column-raiding army ant *Eciton hamatum*. *Physiol. Zool.* 61:57-68.

2005

Integrative biology: An organismic biologist's point of view. *Integr. Comp. Biol.* 45:330-332.