HISTORICAL PERSPECTIVES

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GEORGE W. BARLOW

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YEORGE BARLOW'S contributions extend G lineages of excellence including Agassiz, Carl Hubbs, and Boyd Walker in ichthyology and Konrad Lorenz in behavior. As a result, few in the world of fish behavior, and indeed in the combined circles of animal behavior and ichthyology, have escaped his influence. Undergraduates, graduates, and postdocs have known him as teacher and mentor, others discovered new ideas and approaches in his work, and still others found clarity in thinking and writing through his editing of journals and reviewing of countless dissertations, manuscripts and proposals. George's life and career reflect love of learning and family, service to his profession and its people, sensitivity to and interest in diversity of thought, and limitless curiosity about activities of all types of animals as well as their conceptual foundations in anatomy, physiology, development, and evolution.

George's history is a product of the tumultuous events of the past century intermingled with chance events and sometimes sorrowful tragedy. Facing difficult prospects after World War I, George's parents left Lancashire, England, and migrated in 1919 to the wide-open spaces of Winnipeg, Canada. One wonders what might have happened had the Barlows stayed in Winnipeg. Fortunately, the lure of a gentler climate and greater opportunities at the start of the Great Depression found the family heading south to Long Beach, California. Conceived in Winnipeg and born in a small house next to the surf in Long Beach on 15 June 1929, George would grow up in and around the ocean. That was destined to have a profound influence on many aspects of his life and career.

He came by his active mind naturally. His father, Fred, was an auto mechanic. Although schooled only to age 12, Fred's ability to learn rapidly and completely master various mechanic's manuals were a strong asset to his career. George's mother, Jessie Kenny, attended school until age 14 and then began work as a seamstress. She too was gifted with an agile intellect. She was a speed-reader and excelled at mathematics.

Tragically, talent and perseverance cannot counteract the whims of chance. Fred and Jessie's first child died as an infant in England from the Great Flu. Their third child, Jack, was injured in a swimming accident and died the following winter at age eight. Their second child, Irene, was run over by a drunk driver in 1937 at age 17. If that were not enough, in the previous year a severe auto accident had seriously injured both parents and left Fred disabled for life; eight-year-old George was asleep in the back seat at the time and escaped injury.

Blessed with a permissive climate next to the Pacific, with little money but great curiosity, George began to explore the world of animals. Both of his grandfathers had been naturalists, and his parents encouraged his interests in nature on camping trips to the desert, where he became fascinated by lizards. In the ocean in front of his home, in a baylike setting, hermit crabs by the thousands carpeted the sandy bottom like marbles under his feet. They intrigued him, and he tried in vain to keep the crabs in crude aquaria along with sea anemones from a nearby breakwater. He also spent hours angling on the local fishing pier where he marveled at the array of fishes pulled from the sea.

When about 10 years old, he set up his first aquarium—guppies in a cookie jar—but soon graduated to a donated 10-gallon tank, which he had to reglaze by himself. That started him on learning the art of fish keeping.

Then, as now, his interests in nature were broad. He caught tree frogs from local ponds and transplanted them to his garden, his pet duck followed the family to the beach, and he took up pigeon racing. He also developed an ear for and the ability to imitate birdcalls; once he performed for a service club. Several who studied with him at Berkeley remember their shock when their respected, proper professor piped up with imitations of the Western Meadowlarks and other feathered beasts during an ichthyology field trip. In elementary and junior high school, George played clarinet and bassoon, his entry into a life-long appreciation of music, especially baroque compositions. In high school, music was supplanted by outdoor sports and competitive athletics. Like any dedicated Southern California beach rat, he learned to dive and surf, and served as a city beach lifeguard. At school, he started on the varsity football team.

In 1947, he entered the University of California at Los Angeles (UCLA). At first distracted by athletics and the discovery of college coeds, he barely survived his freshman year. He got Ds in Military Science and German and loves to tell about that poor start for two reasons. First, by the time he finished his required two years of ROTC, he had advanced to the highest possible rank, company sergeant; later, he became fluent in German. Second, he wants students who have difficulties adjusting to life in large universities to take heart and forge ahead.

George was a starter on the freshman and varsity water polo teams. After graduation, he competed in AAU water polo in the national championships. Years later, firmly entrenched in the complexities of university life, he would sneak away most days for a noon swim at the university pool and, thus, maintain a trim form that many colleagues (and past students!) have lost.

His parents' educational aspirations for their son differed. His father wanted him to be a mechanical engineer while his mother wished he would teach in the local schools. As a compromise of sorts, George started in the premed program, but soon found it uninspiring.

In his second year, George took his first biology course. One of the professors in that introductory course was Boyd Walker (see Copeia 2002:1179-1182), ichthyologist, student of Hubbs, and later President of the ASIH. From Boyd, George discovered that he might apply his growing knowledge and love of fishes, and his aquatic skills, to graduate study and perhaps an eventual career as a university professor. That was an option George had never known existed. Inspired by one who knew so much and who took an interest in him, George switched to zoology, with Professor Walker as his mentor. At once, his grades shot up. As a sophomore, George accompanied Boyd and others, such as George Bartholomew and Ken Norris, on field trips to Mexico and discovered the rich combination of long field days, intellectual and physical challenge, and fun with close friends and colleagues that characterize fieldwork with fishes. Boyd was surprised to find that this young athlete was one of his best students in the classroom, a solid contributor in the field, and an

eager reader of current literature once exposed to the wonders of scientific journals.

Following his AB degree, George enlisted in officers' training with the Coast Guard as a "90day wonder" for the Korean War. He was selected as acting commandant for the graduating class and served on active duty from 1951 to 1953 as a line officer. When his basic training in New London, Connecticut, ended, he stood apart from all but one other fellow trainee; most sought posts nearest to home. George, in contrast, requested Honolulu, Guam, or Manila as his preferred home ports. We suspect he was less than completely candid about his primary motivation for requesting duty in places that coincidentally had coral reefs and abundant fishes.

Homeport for his ship was Honolulu, where he connected with Jack Randall, a classmate from UCLA then at the University of Hawaii. He also got to know Jack's major professor, Bill Gosline, who helped George continue his study of fishes. Among great adventures in the Coast Guard were periodic long visits to French Frigate Shoals in the Northwest Hawaiian Islands, still a magnificent and relatively unspoiled system; he tells great stories about beautiful reef fishes and abundant, overly friendly sharks.

After his military service, George returned to UCLA and graduate work with Boyd Walker. He joined a remarkable covey of graduate students (Fig. 1), including Dick Rosenblatt, George Williams, Bill McFarland, Fred Munz, John Stephens, and Jay Quast, names of renown in ichthyological circles. They fed off each other's energy and curiosity and pulled antics that these days would land them in jail.

A prank that lives in the memory of many was a last-day seminar meeting of a group guided by George Bartholomew and Tom Howell. It had been notable the entire term for its spirited arguments. On this occasion, the fish group set them up, and the question posed by the instructors played right into it: "If the interior plain of Australia were perfectly uniform in ecology, and a new species landed there, would it speciate?" The fish group became aggressive and almost insulting in the exchange, and tempers started to flare. In a fit of rage, Rosenblatt leaped to his feet and lunged at George with a knife (which was rubber). George jumped up, pulled out a hand gun (loaded with caps), and fired away. Tom Howell shrieked and sprang toward the combatants, who by now were rolling on the table in laughter. Class dismissed.

On a serious note, George learned at the feet of faculty like Walker and legendary environmental physiologists George Bartholomew, a



Fig. 1. The glorious days of a graduate student: the "UCLA 4skins" with their harvest. Standing left to right: Fred Munz, George Barlow and Dick Rosenblatt; seated: Chuck Baxter.

close friend of Boyd Walker, and the inspiring neurobiologist Ted Bullock. Consistent with Walker's training in systematic ichthyology with Hubbs, George began work on the taxonomy of gobies but then expanded into physiology under the tutelage of Bartholomew and Bullock. All the while, however, he remained interested in the behavior of wild animals, then a growing area of research in Europe where it was known as ethology (in contrast to the American school of "animal behaviorists" led mostly, though not entirely, by comparative psychologists).

George's doctoral work focused on the Longjaw Mudsucker (a goby), Gillichthys mirabilis. As a side project, he was drawn to the Desert Pupfish (Cyprinodon macularius) that occupied the Salton Sea in southeastern California; it was a brutally hot place in the summer when the pupfish were spawning. To observe and take notes, he perched on a high lab stool in the middle of shore pools, protected by a large straw sombrero. Those observations led to his earliest oral paper, awarded first prize for the best student paper at an ASIH meeting in San Francisco (1958, Ecology 39:580-587). Confidential communication from insiders indicated he would have won in a subsequent year as well, but the award committee felt the same student should

not receive the best-paper award twice. Thus, his presentation on gobies took second place. His first published paper was a tiny note in *Anatomical Record* in 1957 (128:520) on the reproductive behavior of the Desert Pupfish. His earliest article in *Copeia* was a 1958 (3:231–232) paper on the impact of high salinity on pupfishes.

When George entered graduate school in 1953, his thinking about his eventual career made a turn. He learned from Ken Norris, also interested in behavior, that Ken planned to go to Oxford to work with the ethologist Niko Tinbergen. That seemed an attractive possibility for George as well. Konrad Lorenz, the famous Austrian ethologist, came to UCLA for a series of lectures. George and his wife, Gerta, had the good fortune of having Lorenz to dinner with them in their apartment. That led to an invitation from Lorenz to work with him. George applied for and received a postdoctoral fellowship with the National Institute of Mental Health, to study with Lorenz at the Max Planck Institute in Seewiesen, Bavaria.

It was then that George began working with cichlid fishes as experimental organisms. Again, a side project led to a series of seminal papers on a small Asian fish, *Badis badis*. Included in those publications was one that erected a new and monotypic family, the Badidae (Barlow, Liem, and Wickler, 1968, *Canadian Journal of Zoology* 156:415–447). It was based initially on George's discovery that the reproductive behavior of this fish was not consistent with that seen in other members of its previous family, the Nandidae.

George's eventual attraction to cichlids grew from familiarity, for he had bred them when a boy. More important, he reasoned that biparental cichlids were an ideal model system for beginning to learn ethology because they express a range of reproductive and aggressive behavior that spans that of the other vertebrates. In addition, cichlids were among Lorenz's favorite study animals. In his two years with Lorenz (1958–1960), George broadened his horizons and solidified fish behavior as his field of study.

While working with Lorenz, one of George's close associates in the laboratory was Eberhard Curio. Curio was offered a job at the University of Illinois, but he was reluctant to leave Germany. Hence, George suggested to Curio that in his declination he mention the young American there who needed a job. The result was an invitation to apply, and he did. To his surprise, he got the appointment without being interviewed. Further, the opening was held open another year for him while he completed his fellowship in Bavaria. George spent from 1960 to 1966 in Illinois and was tenured in three years. In that brief period, he produced some good students, notably Jack Ward (parental orange chromides) and John Mertz (convict cichlids and Florida flagfish behavior).

After Paul Needham at UC Berkeley died, George applied for and won the job there in ichthyology, a position he would hold until his retirement. Initially his appointment was split between the Museum of Vertebrate Zoology, with colleagues such as Oliver Pearson, Starker Leopold, Ned Johnson, and Robert Stebbins, and the Zoology Department, with people like Paul Licht, Frank Pitelka, and Howard Bern, although the appointment soon shifted completely to zoology.

George entered the Berkeley scene just as Peter Marler was leaving. Although unfortunate for George, who would have delighted in having him as a colleague, Marler's departure led to George's leadership of the behavior program and offerings of courses such as Animal Behavior and Sociobiology.

After joining the faculty at Berkeley, he had two yearlong experiences that greatly influenced his scientific perspective. The first was a sabbatical leave in 1974–1975 with Niko Tinbergen at Oxford University (George joined the joyous celebration there of Tinbergen winning the Nobel Prize). Tinbergen was the ethologist who pioneered asking the question, how is this behavior adaptive? His group laid the foundation for behavioral ecology.

The second experience, in 1977–1978, was participating in a yearlong workshop on behavioral development at Bielefeld University, in Germany. Working closely with Klaus Immelmann, they organized the project and produced a large volume containing the fruits of the labors of the many participants (1981, *Behavioral Development*, Cambridge University Press).

At Berkeley, George continued to teach ichthyology, a course that reflected his broad and integrative knowledge of fishes, and one that consolidated his approach in the supervision of graduate students and launched the careers of a number of active ichthyologists. Some of these students, usually undergraduates, first came to appreciate systematics, nomenclature, and structural diversity when they served as curators of the Berkeley fish collection, a relatively small teaching collection (approximately 600 lots in the late 1960s) under George's direction.

For many, however, field trips served up a totally new taste of academics and field studies. On his first ichthyology field trip at Berkeley, after a long day of driving and collecting, and en route to the evening's camp, George announced to the students packed in the vehicle that they would stop in the next small town for candy to serve as late-night snacks. Curiously, it was the only candy shop around. Oddly, they were out of candy but they still had beer on hand. The subsequent evening's casual and open discussions about fishes, science, academics, the university, and personal histories became the norm for ichthyology field experiences. So, too, did the one or two students who played guitar, and that became the cement for many lasting friendships.

On another trip, several years later, George and a visiting student from that first class decided to show the budding ichthyologists how to set a beach seine from a rowboat. As they turned for shore, an unusually large wave arrived to speed them on their way, turn, roll and swamp the boat, and dump professor and dignitary unceremoniously into the water. The students, now well educated by their leader's fine example, made several subsequent sets without mishap.

Such memories loom large, for they teach about learning in nature and forging of bonds between students and mentors. Never easy to organize and ever more expensive, invaluable field experiences often fall tragic prey to budget shortfall or emphasis on other disciplines.

Such experiences, combined with his courses, frank and supportive mentoring, and frequent acceptance of students as both colleague and friend, influenced many throughout George's career at Berkeley. George guided students whose names are familiar to many. These include undergraduates Gene Helfman, Bob Warner, Linn Montgomery, David Soltz, Sandra Vehrencamp, Jeffrey Shima, Suzanne Alonzo, and Amelia Martins and doctoral students David Noakes, Jeffrey Baylis, Judy Stamps, Kenneth McKaye, Paul Loiselle, Eric Fischer, Axel Meyer, and Frank von Hippel. Postdocs included Richard Francis, Ron Coleman, and Abby Schwartz.

In addition to his contributions to and through students, George published over 160 papers and reviews and three books. Many of these works focus on cichlids, but they also include important studies of pupfishes, gobies, the Asian teleost *Badis badis*, surgeonfishes, filefishes, leaf fishes, and sticklebacks. Major themes that run through his writings include parental care, reproductive behavior, aggression, structure of stereotyped displays, speciation, life-history strategies, and polychromatism. Fortunately, he continues to write.

In retrospect, George views this body of work and his talents lying especially in detecting patterns in nature. He was nurtured by the founders of ethology, great integrators of ideas. Lorenz was anchored in neurobiology and often focused on structurally inflexible aspects of behavior such as motor patterns, as did Tinbergen. George, however, came to regard behavior as more plastic than did his mentors. Perhaps this was a natural consequence of his doctoral research. He was enmeshed in the problem of sorting out differences in populations of gobies: to what extent were they genetic, and to what extent were they environmental? That resulted in one of his most cited and influential papers, on sources of morphological variation (1961, Systematic Zoology 10:105–117).

Taking his cue from Lorenz's concept of fixed action patterns (FAP), among his earliest and most influential essays was a critique of that approach. Rethinking the FAP, he presented a more dynamic interpretation, termed the modal action pattern. That essay was included in a collection of papers regarded as the most influential in animal behavior in the latter half of the 20th century (L. D. Houck and L. C. Drickamer, *Foundations of Animal Behavior*, University of Chicago Press, Chicago, 1996).

Always interested in sharing his knowledge beyond the bounds of the academy, his recent

book, Cichlid Fishes: Nature's Grand Experiment in Evolution (Perseus Publishing, Cambridge, MA, 2000), produced 10 years into his purported retirement, reflects a desire and ability to speak about his beloved cichlids to audiences from hobbyist to professional. In a characteristically lucid and integrative tour de force, George treats topics ranging from systematics and morphology through physiology, behavior, and ecology, all woven into a seamless view of evolution in this remarkable family. Chapter titles tell much about George's wit and imagination (e.g., Jaws Two, Plastic Sex, Beauty Is Only Fin Deep . . .). No one could ask for better recognition of one's writing than Les Kaufman's review of the book in Natural History (May 2001), which states, "Barlow's fertile synthesis belongs in the pantheon of natural history classics ... " beside works by G. E. Hutchinson, Konrad Lorenz, Niko Tinbergen, and Howard Ensign Evans.

Although many of his studies of cichlids were conducted in packed aquarium rooms at Berkeley, George developed an early appreciation of the underwater world. He started as a boy diving for golf balls in a golf-course water hazard. The facemask at that time was made of hard black rubber that he sandpapered to fit his face. No snorkel. He started abalone diving at the end of his high school years.

In 1949, Boyd Walker introduced his group to a French visitor who told them how his new invention, called the Aqualung, could make life underwater possible. The visitor was, of course, Jacque Cousteau. Most of the graduate students soon became scuba divers, though the equipment was primitive. More important, no dive suits were yet available, and the ocean in California is cold! George Williams (who also wrote the Forward to Cichlid Fishes) was snorkeling in a "wet" suit sewed together by his wife from a shower curtain; it filled with water at once, and George looked like a plastic pear when he came out of the water. A few years later, the graduate students got neoprene, glue, and a pattern for cutting out and pasting up an innovation called a wet suit. Time in the water increased greatly.

Since the late 1960s, George Barlow has dived in many parts of the world including Nicaragua, Puerto Rico, Enewetok Atoll, and other places in the tropical Pacific Ocean. His long-standing love of Pacific reefs led him to initiate negotiations with a donor to establish a biological station on the French Polynesian Island of Moorea. The donor was the department store magnate Richard Gump, who provided property as well as funds to create the Richard B. Gump South Pacific Research Station. George was its first director. Berkeley now offers a semester-



Fig. 2. Derrick Isles, Meg Stewart, and George Barlow at the ASIH picnic, Pennsylvania State University, 8 July 2001. Photo by Jerry Smith.

long field course there, as does UCLA. The station also hosts visiting researchers.

Always true to and involved in his profession, George first joined the ASIH in 1949 (Fig. 2). He has served on the Board of Governors, the Editorial Board of Copeia, and other committees. Annual meetings were particularly important early in his career, but as interest in fish behavior failed to grow among members he directed his activities to the Animal Behavior Society. He continues to find special pleasure in the meetings of the EEEF (Ecological and Evolutionary Ethology of Fishes) and other societies where he can communicate with other students of fish behavior, as well as in behavior symposia at ASIH meetings. ASIH meetings are coming to hold more attraction for him these days because of the renewed activity in fish behavior and ecology there. His interests have also returned to taxonomic issues, speciation in cichlids in particular, which has been an area of intense integrative activity at recent meetings.

George's service to other organizations includes President of the Animal Behavior Society. He was also one of the first Americans on the International Ethological Committee. He became editor of *Ethology* and has been appointed to numerous editorial boards, most notably today *Behavioral Ecology and Sociobiology* and *Environmental Biology of Fishes*. He has also drawn fish hobbyists into the arena of fish behavior through the American Cichlid Association. He believes much is to be gained in professional biology by interacting with amateurs in any field.

Consistent with his professional contributions, George has received many honors. He is a fellow of the American Association for the Advancement of Science, the California Academy of Science, and the Animal Behavior Society, and he has been an invited keynote speaker for



Fig. 3. George and Gerta Barlow at wedding of their daughter Bicka in May 2003.

many symposia and meetings. He was awarded a Miller Professorship at Berkeley in 1972.

Given such a productive career, can George Barlow be anything but a myopic workaholic? Time spent with the Barlow family beyond the university makes it clear that, despite the demands of his profession, George never lost sight of the priority of his wife and family. Gerta Offczarczyk's (Fig. 3) first designs on George developed when she saw him working in the laboratory at UCLA. Gerta's friend, Al Ebeling (later the ichthyologist at the University of California, Santa Barbara) arranged a date, and the two married in 1955.

Gerta's life had seen much strife. She was born in Germany in 1928. Half Jewish by birth but raised as a Catholic, she spent time in a labor camp during World War II but survived the Holocaust, unlike so many others. Emigrating alone, she entered the United States through New Orleans in 1949 and traveled on to Los Angeles. Supporting herself, she enrolled at UCLA and majored in parasitology and bacteriology. After graduation, she did research on toxoplasmosis at the UCLA medical center but quit when the work became too dangerous because of her anticipated pregnancy. A strong, thoughtful, and articulate woman, Gerta served with George as the foundation for their family and a constant source of support throughout his career. In recent years, Gerta pursued a career as a realtor.

Gerta and George's three daughters serve as examples of the value of strong family and as rightful sources of pride to their parents (Fig. 4). Linda was born in Germany in 1960. She did a postdoctoral fellowship with Glenn Northcutt at Scripps and now works in developmental neurobiology in her capacity as a faculty member at the University of Colorado School of Medicine.

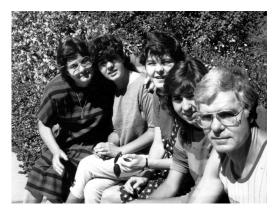


Fig. 4. The Barlow family before the daughters fledged. Left to right: Gerta, Nora, Bicka, Linda, and George.

In 2000, Linda won a Presidential Young Investigator's Award for development of chemosensory systems in axolotls. Linda has a daughter, Cordelia. Bicka and Nora were both born in Champagne, Illinois. Bicka (b. 1962) worked on plant molecular genetics at Cornell where she almost completed a doctorate but then switched to law. She now litigates capital cases dealing with forensic law in California; her expertise in molecular biology has proved especially useful. Nora (b. 1964) was a biology major but then became a lawyer. She is a Deputy District Attorney in Anchorage, Alaska, and is married with two children, Aidan and Maeve.

So what flavors George's life beyond the lab? His hobbies are current affairs and gardening, his latest passion being dahlias and orchids. And he continues to work out in the swimming pool. He loves corny jokes and shaggy dog stories, the more twisted the pun the better. He reads widely in many fields, supporting a breadth of interest that is obvious in conversations with him. He communicates easily, both orally and in writing. One feels the presence of a strong ego and a confident but considerate personality. He is now an Emeritus Professor at the University of California at Berkeley, where he continues to mentor undergraduate students, dote on grandkids, and look back on a distinguished career and a job well done.

Postscript.—George Barlow was interviewed by Meg Stewart and Ronald Coleman on 9 July 2001 at the meetings of ASIH at Pennsylvania State University.

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