Historical Perspectives

Ronald J. Schusterman

(3 September 1932-11 February 2010)

Ron Schusterman is Professor Emeritus at California State University at Hayward (CSUH), and he retired from the Research Faculty at the University of California, Santa Cruz (UCSC) in 2004. He was educated at Brooklyn College and then Florida State University, where he was mentored by Winthrop Kellogg and introduced to the study of chimpanzees and dolphins. Ron took his first research position at the original Yerkes Laboratory of Primate Behavior in Orange Park, Florida, where he investigated the cognitive and social behavior of chimpanzees, gibbons, and monkeys. In 1963, he moved to the Stanford Research Institute (SRI) in order to develop the first laboratory in North America primarily devoted to the study of the behavior and sensory physiology of pinnipeds. At SRI, Ron helped to debunk the notion that pinnipeds echolocated like dolphins and bats, and he embarked on a research program dealing with vision and hearing in pinnipeds. Ron and his sea lions relocated to the Ecological Field Station at CSUH in 1971, where Ron served as a professor in Psychology and Biology and he and his sea lions began working on an ambitious research program involving a gestural artificial sign language. In 1985, Ron made his last move, settling his program at the University of California's Long Marine Laboratory (LML), which is located on the northern coast of Monterey Bay. Today, Schusterman's original research program continues under the leadership of Dr. Colleen Reichmuth. Ron and Reichmuth continue to work together to explore the sensory systems, perception, cognition, and communication of marine mammals in a variety of lab and field studies.

Ron is a founding member of the Society for Marine Mammalogy and a Fellow of the Animal Behavior Society, the Acoustical Society of America, the American Psychological Association,

Ron Schusterman and Rocky

and the American Association for the Advancement of Science. In addition to the time he spends at LML, Ron has spent time writing and teaching at other institutions—most recently at Columbia University, the Aquarium for Wildlife Conservation in New York, and the Konrad Lorenz Institute in Altenberg, Austria.

Ron is extremely proud of the students he has been associated with over the past 40 years and still mentors a small group of graduate students at UCSC.

Pinniped Psychobiology: The Early Years

Ronald J. Schusterman

Institute of Marine Sciences, Long Marine Laboratory, University of California, Santa Cruz,
100 Shaffer Road, Santa Cruz, CA 95060, USA; www.pinnipedlab.org

"Science is you." – Anonymous

It all started in January 1956 when I returned to my parents' apartment in the Bronx. Following my honorable discharge from the military after the Korean War and armed with the GI Bill, I attended the Bernard M. Baruch College of the City University of New York (CUNY) where I took classes in psychology and statistics. One class, Experimental Psychology, would have a major impact on my life; it really opened up a whole new world for me. The instructor was Professor Mortimer Feinberg. He was an up and coming industrial psychologist at the time, who today, in his mid-80s, is extremely active, an internationally famous consultant to big business, and a regular contributor to *The Wall Street Journal.*

Feinberg was, and still is, a schmoozer, a real "bon vivant" character, who could build a buzz on just about any subject. Many times during the course of a long, somewhat tedious, information-packed lecture, he would lighten the load by kidding around and inserting Yiddish sayings, jokes, and anecdotes.

In one of his early lectures, Feinberg told us that a person's survival, just like that of any other animal, depended on knowing about its surrounding world and being able to organize that world into categories like food, friends, and foes. The ability to distinguish items between and among these categories—for example, between a clump of dried leaves or rocks and a rattlesnake—is literally a matter of life and death. Feinberg liked to point out that different types of animals, including humans, have different "windows on the world." Some animals have sensory equipment that in several ways is much inferior to humans, but in some respects may be far superior to ours. In the example where a poisonous snake needs to be distinguished from a pile of leaves, a person, or any other mammal for that matter, must see, hear, or perhaps smell the viper; recognize it; and act accordingly. If not, then the cold-blooded snake, with its specialized infrared sense organs, will produce an accurate strike on its warm-blooded prey. Mammals and birds have fallen prey to snakes for millions of years. Later in the course, Feinberg would give us several different examples of other creatures that have evolved specialized sensory abilities, much different from ours and certainly well beyond the realm of ordinary human experience. I found all of these accounts fascinating, especially since they demonstrated how remarkably idiosyncratic the sensory world is.

Some of Feinberg's early lectures dealt with the philosophical conflict between the *empiricists* and the *nativists*. The *empiricists*, led by John Locke, believed that all knowledge comes through the senses and that the mind is a *tabula rasa*, or blank slate, upon which experience leaves its marks. In contrast, the idea put forward by the *nativists*, like Immanuel Kant, asserted that many aspects of our perceptual world are innate and do not depend on learning or experience. This conflict between the empiricists and the nativists, according to Feinberg, focused attention on the role of the senses and stimulated scientific research on how the senses functioned. Feinberg believed that Experimental Psychology was born when German scientists like Gustave Fechner and E. H. Weber began investigating relationships between stimulus magnitudes, stimulus differences, and their corresponding sensory processes—an aspect of psychology and physiology that Fechner called *psychophysics*. It was Fechner who was responsible for the establishment of standardized methods whereby a clear behavioral unit of measurement, the *just noticeable difference* (JND), or *difference threshold*, was accurately calculated. For example, the "Fechnerians" of that day asked, "How much do the intensities of two sounds have to differ before one is judged louder than the other, or how many more candles have to be added to 400 candles for the total light to appear brighter?"

Furnished with these ideas about psychophysics, I and other members of the class began thinking like scientists, and rather than regurgitating facts, we did lots of experiments, which we designed ourselves. For me, Feinberg's class was a real "coming of age" experience. For the first time in my life I was learning the essential principles of inquiry—I was learning how to ask questions in an answerable way, and I was awakened to the endless possibilities of science. It gave me a rush when I thought about the prospect of collecting quantitative data.

In nearly all of our experiments, we repeatedly required our human subjects to judge between two stimuli, either two sounds of identical intensity,

two lines of nearly the same length, or two weights that were almost equally as heavy. In this manner, for several different sensory modalities, we tried to establish the exact difference between stimuli that was required to produce a single JND or difference threshold of sensation.

During those heady days in Feinberg's class when I was doing psychophysics with human subjects, it never really entered my mind that a few years down the road I would be applying similar theories and methods to the study of sensory processes in aquatic mammals. By combining psychophysics with reinforcement techniques, I was able to train seals, sea lions, fur seals, river otters, and dolphins to indicate whether or not they detected a stimulus or the difference between two stimuli. Usually I trained the animals to make one response to the presence of a signal (or when two stimuli were different) and another very different response when no signal (or difference) occurred.

During one of his lectures, Feinberg referred to Dr. Winthrop N. Kellogg, who had been his mentor at the University of Indiana. He told us that Dr. Kellogg was currently at Florida State University (FSU) in Tallahassee, where he was engaged in pioneering research on echolocation in bottlenose dolphins at a place called Alligator Harbor on the Gulf Coast of Florida. Apparently, this great scientist was in the process of discovering that dolphins were able to echolocate in murky waters by emitting a train of pulsed sounds or clicks, bouncing the sounds off an object and listening to the returning echoes. Enormous scientific progress has been made since Kellogg's discoveries about dolphin sonar (Kellogg & Kohler, 1952; Kellogg et al., 1953), and we now know something about the design features of this exquisite sensory system created by natural selection.

The ideas contained in the story that Feinberg told about Kellogg's original discoveries were enough to leave me breathless—animals that could literally "see with their ears?" Bubbling with excitement, I approached Feinberg after class and asked him about the possibility of working with Kellogg. I was also curious to know whether his mentor was the same celebrated scientist who had done an extraordinary cross-fostering experiment back in the early 1930s in which he reared a young chimpanzee side-by-side with his young son for a period of nine months. I told Feinberg that I had remembered seeing a documentary film in my Introductory Psychology class at Brooklyn College. It showed the little ape, Gua, who was about seven months old, and the boy, Donald, who was about ten months old. Gua was fondled and kissed, toilet trained, and taught to eat with a spoon and drink from a glass while in a highchair, much as the parents had treated their own child. Feinberg replied affirmatively that, yes, indeed, his old professor Kellogg was the famous scientist who made the film that I saw at Brooklyn College. He went on to tell me that Kellogg and his wife wrote an account of this study entitled *The Ape and the Child* (Kellogg & Kellogg, 1933/1967). He added that in addition to the book, Kellogg had written several articles about this fascinating research concerning the question of how human a chimpanzee can become if it is raised in a human environment. After suggesting that I should look into Kellogg's writings, Feinberg told me that he would be happy to recommend me to FSU as long as I continued to do well in his class.

When I got to FSU in the fall of 1956, Dr. Kellogg was already a well-known psychologist. It would be no exaggeration to say that he was the most famous scientist on the FSU campus. The notoriety that he achieved with the book *The Ape and the Child* had grown even more with his newest and quite splendid research on the echolocation abilities of bottlenose dolphins (Kellogg, 1959, 1961) that had been kept at a laboratory site at Alligator Point about 50 miles due south of the FSU campus in Tallahassee, Florida.

My feelings toward Kellogg were almost always positive. He had a really sweet side, and we struck up a father-son mentoring relationship, which was quite comforting and reassuring. Kellogg was a terrific lecturer with an extensive knowledge about a whole array of topics, including the ones I enjoyed learning about the most: human sexuality, principles of learning, sensory psychophysics, and comparative and developmental psychology. Alfred Kinsey, the famous sexologist, had been one of his colleagues at the University of Indiana,

Figure 1. The author with Professor Mortimer Feinberg (left), my first mentor; the photo was taken at Long Marine Laboratory at the University of California, Santa Cruz in February of 2009 while Mortimer was doing a consulting job nearby at the tender age of 86.

so he frequently incorporated some of Kinsey's spicy findings into his lectures. His material was always extremely well-organized and comprehensive, almost always containing new and stimulating material. The more I got to know Kellogg, the more I tried to emulate his behavior, hoping to acquire the same self-confidence and flair that he exhibited, particularly when dealing with things of a scientific nature.

When Kellogg brought a group of his students, including me, to see the chimps at Yerkes Lab, I told him that I was delighted with the facility in Orange Park and that I planned to write a proposal to obtain funds in order to do research there; the topic would be on the reward expectancy behavior of chimpanzees and children (Schusterman, 1963). He responded by saying I could use his name as a "sponsor" for the National Institute of Mental Health Pre-Doctoral Fellowship that I would be applying for. As we drove back, Kellogg and I discussed my proposed Ph.D. thesis research. My interest in expectancy theory had been sparked by one of Kellogg's lectures. He had described some studies on learning, memory, and cognitive processing in nonhuman primates that were begun by Otto Tinklepaugh at the Anthropoid Station of Yale University in New Haven; he continued these studies when the station was moved from Yale to Orange Park, where it eventually became known as the Yerkes Laboratory of Primate Biology. This was close to the period of time that Kellogg and his wife Luella lived in Orange Park and were raising Donald and Gua as their two "children." During this time, Tinklepaugh was not only helping to get the Orange Park Primate Station operating, but he conducted several groundbreaking studies on the reward expectancy of macaque monkeys

Figure 2. The author with his second mentor, Professor Winthrop N. Kellogg (right), at Florida State University taken a few hours prior to being awarded a Doctorate in Experimental Psychology in June of 1960.

and chimpanzees (Tinklepaugh, 1932). Kellogg's description of these studies so fascinated me that I began a full library search and reading of the *expectancy literature*, including ideas about choice and decisionmaking as a function of reinforcement probabilities.

Although Kellogg was not a learning theorist, and certainly not a cognitivist by any stretch of the imagination, he and I agreed that Tinklepaugh's experiments left little doubt that nonhuman animals are capable of hypothesizing, predicting, or having a precognition about what the outcome of their behavior might be. They expect a certain kind of reinforcer or reward, and if that outcome is not confirmed, then the animal reacts just the way you and I would—surprised and disappointed, and sometimes resentful, as shown in their facial expression, bodily posture, vocal behavior, and reaction to the less preferred food. Indeed, it was this kind of research finding that got me so interested in the study of comparative cognition—that is, the way animals and humans use their information processing skills as they interact and adapt to their environment. After the trip to Yerkes Lab, and following my detailed discussion with Kellogg about my planned experiments for my doctoral dissertation, I became one very happy camper.

As I was finishing a post-doctoral fellowship at Yerkes, I learned that my old professor had just retired from FSU and was taking a consulting job with Stanford Research Institute (SRI) located in Menlo Park, California. Dr. Kellogg began hinting that he and his new research partner, Dr. Thomas Poulter, an SRI bigwig, might like me to head an exciting research program out there in northern California. It was to remain "hush-hush" until Kellogg's planned visit to Yerkes in March 1962; he would bring Dr. Poulter with him and then Poulter would reveal the research plan to me. It seemed to me that I had a real chance of doing innovative and groundbreaking research in California. I could hardly wait for their visit to Orange Park.

After they arrived, they questioned me about the research at Yerkes on chimps, monkeys, and gibbons. I continued droning on about several chimp studies currently going on and then began describing my own research focus at the lab, which was on food sharing with gibbons (Berkson & Schusterman, 1964) as I eagerly awaited their description of the investigation that was planned at SRI. I already knew that SRI had a close affiliation with Stanford University in Palo Alto, and the thought of being associated with this well-known, prestigious academic institution thrilled me.

We left the Yerkes grounds and met at a drug store in town that had an old-fashioned fountain service. I'm not sure if I was hungry, but I ordered

Figure 3. The author with one of his gibbons at Yerkes Lab in Orange Park, Florida (photo taken in 1961)

my usual BLT and listened carefully as Dr. Tom Poulter told me his exciting research story.

Poulter was a big, burly man. He was tall, heavy set, about 60+ years old, and bald, with a short-cropped gray fringe of hair. He had a kind face, spoke slowly in a down-to-earth Midwestern manner, and had a charming smile. He and Winthrop Kellogg were about the same age, the age of my own father, and they both reminded me very much of my loving dad's appearance and demeanor. My initial impressions of Poulter were all very positive, but later on in my life as I began meeting self-promoters and self-congratulatory individuals in the business of doing science, I became more aware and sensitive to the idea that Poulter belonged to this clan, and he was, perhaps, one of the most blatantly fraudulent and disingenuous individuals I have ever come across.

After telling me about how he was responsible for the present refinement of man-made sonar devices through his work on submarine attack and detection patterns during World War II, Poulter started talking about Dr. Donald Griffin's groundbreaking research on the sounds produced by bats, which first gave a clue to echolocation in the animal world, and then he followed up with Dr. Kellogg's studies on sonar in dolphins. He said that now that he was the Scientific Director and Manager of Physical Life Sciences of SRI, which he joined to develop an explosives lab (now named after him) in 1948, he wanted to spend the bulk

of his time developing an innovative laboratory, which would look at the sonar skills of diving mammals and birds.

Poulter began suspecting that California sea lions (*Zalophus californianus*), one of 33 species in the Suborder Pinnipedia, used an active sonar system to forage on fish in the ocean. Poulter had observed what he considered to be totally blind individuals leading perfectly normal healthy lives and remaining in good physical condition on Año Nuevo Island, about 40 miles south of San Francisco, California. He followed up on these observations by making tape recordings of sounds of captive California sea lions while they were swimming under water in their tank at the San Francisco Zoo; additional underwater recordings of *Zalophus* were made at the San Diego Zoo. Poulter said that the sounds were recorded under a wide range of lighting conditions from daylight to so dark that he and his assistants could not see pieces of fish that he had thrown into the tank, nor could they see the sea lions swimming around. The sound emissions were quite different, he said, from the raucous barks that these animals produce in air. Poulter described the sounds as a series of short pulses, analogous to the sonar pings of the porpoise as described by Dr. Kellogg and other investigators. Poulter was currently doing a detailed analysis of these signals but so far, he thought, even without completing the analysis, that these signals met the criteria for a pulse-modulated sonar system, and, in fact, he used words like "fabulous," "amazing," and "sophisticated" to describe what he was convinced were the sonar signals of the California sea lion. Of course, I, too, was tremendously excited about Poulter's descriptions and ideas, and I told him so. At that point, both Poulter and Kellogg told me they thought I should be one of the people to head up this research program at the planned Biosonar Lab for Diving Mammals at SRI. The two of them hoped to put a proposal together, with some help from me and others, and submit it to the National Science Foundation (NSF) within the next year. If all went well, I'd be hired by SRI during the summer of 1963. I replied that the timing for all of this was almost perfect because a relatively small state college in southern California, San Fernando Valley State College in Northridge, was about to offer me a tenure-track position as an Assistant Professor of Psychology beginning in the fall of 1962. This would give me the opportunity to gain one year's teaching experience before I tackled the job of supposedly demonstrating "unequivocally" that California sea lions use active sonar much like dolphins do in order to find fish prey in murky ocean waters.

Figure 4. A 1963 photo of the entrance to the SRI Biosonar Lab in Coyote Hills, Newark, California

Figure 5. Wetlands of Coyote Hills
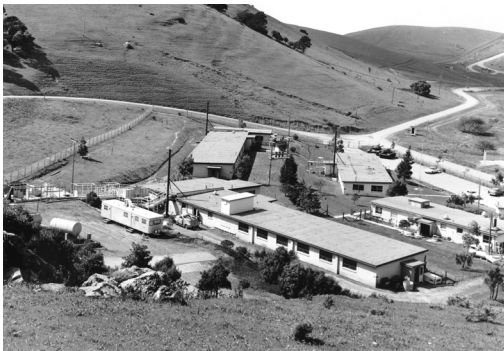
Figure 6. Aerial view of the old military buildings that we used to house different laboratories for testing echolocation in blind people as well as the buildings in which we had our offices in Coyote Hills

The laboratory that Poulter founded was made up of old military buildings that were still being used on occasional weekends by the California National Guard. The SRI Biosonar Lab was situated on nearly a thousand acres of marshland

Figure 7. Año Nuevo Island where the author first observed free-ranging Steller sea lions, northern elephant seals, and California sea lions (photo taken in 1975)

and beautiful, rolling, grassland-covered hills. In addition to our lab and the ranching and farming activities, the site also had a rock quarry and an old military Nike Missile Launch silo. Although the silo was thought to be abandoned, one day a rather ominous looking large cloud was released from the silo, which was located up on the hill above our lab. As the noxious gas descended onto the parking lot, several of us began having difficulty breathing. Phone calls to SRI in Menlo Park brought denials that anything this spooky could have really happened. We were told it was nothing, not to worry, and not to even think about it. However, a few days later, there were rumors that the cloud was made up of MACE, a temporarily disabling liquid spray that was being developed by SRI for military and police use.

When I arrived at the SRI Biosonar Lab in September 1963, I met with Poulter, Kellogg, and Charles "Chuck" Rice. Chuck had also been a Kellogg graduate student at FSU during the time I was there, and he had just collaborated with Kellogg on an experiment dealing with the visual problem-solving abilities of an eight-year-old male dolphin (*Tursiops truncatus*) named "Paddy." Indeed, the reunion with Chuck was quite special; we had not been in touch very much for the past three years, and he was just returning from the First International Symposium on Cetacean Research held in Washington, DC in August 1963. Chuck was very excited about meeting some well-known international scientists who were studying the distribution, natural history, anatomy, physiology, acoustic communication, echolocation, and cognitive and social behavior of cetaceans; these scientists included Ken Norris, John Lilly, Carl Hubbs, Bill Schevill, F. G. Wood, Melba and David Caldwell, Renee-Guy Busnel, Masahavu Nishiwaki, and many others. He was also quite elated over his own talk about Paddy's performance (more about that later).

Kellogg had spawned the two of us from neophyte graduate students at FSU to fledgling scientists now at SRI, and we both knew our appointments there were because we were his *chosen ones*. Kellogg had gotten both Chuck and me to help him and Poulter establish the SRI Biosonar Lab, and what he now required from us was to demonstrate the same rigor and controls in our own behavioral research that he demanded of himself throughout his entire career. He also expected us to be able to distinguish between scientific fact and opinion, observation and philosophy. Poulter, on the other hand, saw Chuck and me as his "hand maidens." We were to follow his mottos of never looking back or correcting any errors or mistakes that he, Poulter, may have made, nor letting Poulter's visions on biosonar or animal echolocation be bounded or limited by present or new knowledge. In fact, what Pouter wanted from us was the opposite of good science; he fervently believed that we should start with conclusions that are deemed to be true and work backward from them. In this way, we would be constructing a monument to his pioneering ingenuity regarding animal sonar systems.

At this first meeting, several things became apparent: First, that the large research grant from the NSF to study *Zalophus* biosonar and the one from the National Institute of Neurological Diseases and Blindness to study sonar use in blind humans were obtained primarily because of Winthrop Kellogg's pioneering echolocation studies with *Tursiops* (Kellogg et al., 1953; Kellogg, 1959, 1961) and his most recent work on human
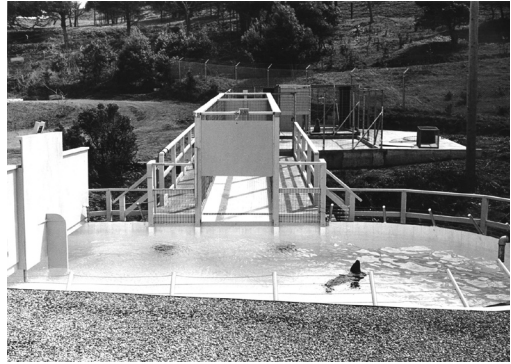
Figure 9. Sea lion stationing in the testing tank

echolocation abilities (Kellogg, 1962). Second, that it was the influence Tom Poulter had with SRI management in persuading them to help develop and build the Biosonar Lab at Coyote Hills that enabled both research programs to get off the ground so quickly. Third, that it would be Chuck Rice's role to take charge of the human echolocation studies and that my assignment was to investigate biosonar abilities of pinnipeds, or more precisely, one species of pinniped—*Zalophus*. It was my belief from what was said that morning that the primary and continuing focus of Poulter would be the pinniped echolocation research. He was so extremely invested in these investigations. On the basis of his own studies and beliefs, he thought that *Zalophus* used a sophisticated sonar system not only to locate fish, but also to differentiate a piece of desirable fish from a piece of undesirable horse meat of the same size, and also to avoid adroitly any obstacles in his pathway. In Poulter's mind, it was already firmly established that *Zalophus*'s biosonar compared favorably to that of *Tursiops* because, even though these two species belong to different orders or suborders, their echolocation signals were so much alike. This idea became a continuing theme at our lab, particularly with Poulter as the major spokesman. For me, it remained largely a hypothesis that I needed to test as thoroughly and as carefully as possible. Both Chuck and I could tell as time went by that this ass-backwards approach taken by Poulter to the *Zalophus* echolocation question was becoming a very strong source of irritation to Kellogg. During our daily morning routine of devouring donuts and gulping coffee, Kellogg would have little fits of frustration describing Poulter to Chuck and me as "that old faker" or as "Horsemeat Poulter." Kellogg went on to say that, in his opinion, Poulter secretly understood himself to be unfit to conduct biobehavioral research but that he "wanted to be boss" and so might resent the three of us for knowing more than he.

Figure 8. A California sea lion, "Cathy," exiting the holding area and about to dive into the test tank

As Chuck started developing his research program with five young blind people (Rice et al., 1965), I began mine with three female, one-year-old *Zalophus* (Schusterman et al., 1965). Chuck outfitted one room in our building as a laboratory by providing it with a low ambient auditory environment, and he developed an apparatus and procedure to determine echolocation thresholds as a function of target size at each of several distances and took this as a measure of "echo acuity" for each of his blind subjects. I, in turn, got an oval, redwood tank constructed, and I also constructed a holding area to house and feed the sea lions as well as to move them either individually or collectively to the pool where they would be tested.

Once these facilities were in place, I began training the sea lions who arrived at our laboratory on 26 February 1964, each weighing about 25 kg

Figure 10. The author feeding sea lions in an enclosure at the Coyote Hills facility

Figure 11. The author running a test trial

and ranging in age from about 17 to 20 months. The female *Zalophus* I worked with the most during these early training phases were called "Bibi" and "Cathy." The temperaments of these two animals were diametrically opposed. Whereas Bibi was feisty, aggressive, high strung, and very vocal, and would snap with her teeth if anyone tried to touch her, Cathy was calm, submissive, not at all vocal, and could readily be touched and even petted by the experimenters. I used a variety of Skinnerian operant conditioning techniques and ideas, including the concept of *response differentiation* or *shaping*. This approach consists of the trainer or teacher modifying the behavior of an individual by reinforcing successive approximations of the ultimately desired behavior and has frequently been applied to the training of simple as well as complex motor skills, including the vocal responses of animals. First, Bibi and Cathy were shaped to station on a handheld target and, then, by a similar shaping procedure, they were trained in a large, oval, redwood tank—painted white and filled with fresh water—to push with their noses and press against a single square target.

Poulter, in the meantime, continually published (Poulter, 1963, 1966) and spoke at venues all over the country and in Europe as well, stating that he had definitive proof of *Zalophus*'s echolocation ability. Finally, in 1969, he stated in the *Proceedings of the California Academy of Sciences* that his studies, with an assistant by the name of Jennings, had demonstrated that the sonar discrimination ability of the California sea lion is nothing short of phenomenal (Poulter & Jennings, 1969)! As I conducted my experiments in those days, I can remember feeling such self-doubt, and I often wondered what I was doing in trying to understand the nature and determinants of *Zalophus*'s sound production under water. Why was I designing experiments to test for their echolocation and other sensory abilities? It seemed to make no difference in Poulter's thinking. He knew with certitude that

Figure 12. Kellogg observing a harbor seal at Coyote Hills

if his underwater microphones, or hydrophones, and his sound picture analysis (usually sonograms plotting frequency against time) showed evidence of click trains and there were sea lions or seals in the vicinity, then, by God, these pinnipeds were surely using their fabulous sonar systems. Perhaps one could characterize these ghostly sounds emanating from pinnipeds and being reflected back again as indeed "*echoes of Poltergeist*"!

As I reflect back on Tom Poulter and sea lion echolocation, I realize that, at the time, there were so many people out there who looked at him as some sort of god. Here was the man who invented the Snow Cruiser, rescued Admiral Byrd, and invented all kinds of techniques for using shock waves to find reservoirs of oil, and he conducted himself with such a sense of confidence about his thoughts and his work. Could anyone really challenge his assertions without seeming to be almost sacrilegious? I was the new kid on the block on his first research job, and I was already thinking about disputing Poulter's observations and theories regarding pinniped echolocation. However, there were a few marine mammal scientists at the time who certainly had their doubts about Poulter's ideas and data regarding the echo-ranging ability of California sea lions; these included Bill Evans, Bill Schevill, and Carleton Ray.

Dr. Edmond Hobson, an ichthyologist and naturalist from the University of California, Los Angeles (UCLA), was another scientist who

was not too impressed with Poulter's theory about sea lions and seals having a built-in sonar system and bouncing their vocalizations against prey objects and locating them by picking up the
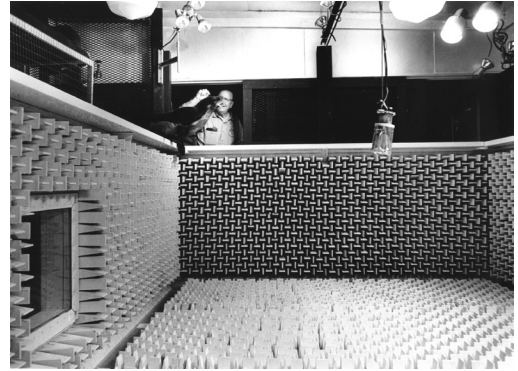
Figure 14. Dr. Tom Poulter feeding a sea lion before testing its echolocation ability in his anechoic tank at Coyote Hills

Figure 15. Tom Poulter with an elephant seal pup at Coyote Hills

Figure 13. The author with Steller sea lion "Runner" at Coyote Hills
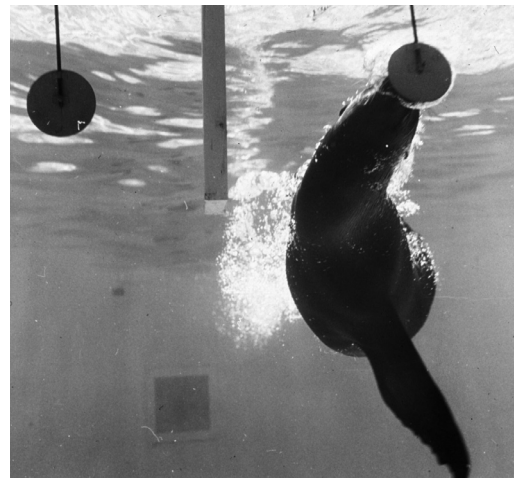
Figure 16. Sea lion "Sam" pressing a target in a size discrimination task

returning echoes. He offered another view about how some pinnipeds catch large numbers of fish prey, particularly at night, to nourish their great bulk. I knew of Hobson's views and observations through my communications with Bill Evans as well as through having direct communication with Hobson about a year or so before he published in *Nature*, in April 1966, an article entitled "Visual Orientation and Feeding in Seals and Sea Lions." According to Hobson, the ability of *Zalophus* to locate bait under the conditions of darkness, as originally described by Poulter, "*seems of questionable significance in an argument for an echo ranging ability in this animal*" (p. 326). There was already a great deal of anatomical and physiological evidence summarized in Gordon Walls' (1942) classic treatise on the "vertebrate eye," indicating that sea lions possess nocturnal adaptations of the pupil and retina as well as an extensive *tapetum lucidum*. The tapetum is a specialized layer of cells behind the retina that reflects light much like a mirror and thus aids the eye in gathering light in dimly lit environments. It is the tapetum that causes the eyes of cats and dogs to glow in the dark, as would sea lion or seal eyes if one were to shine a flashlight at them during the night. Thus, sea lions presumably have eyes that are far more sensitive to low-light intensities than human eyes. Therefore, in Poulter's observations, while it was too dark for a human looking down into the tank to distinguish the bait and often the animals, the sea lion was below the surface of the water looking up at the bait. Hobson maintained that, aside from a sea lion's nocturnal vision being superior to human nocturnal vision, even human vision is good enough to locate fish in a night-black ocean if the person is swimming at a depth greater than that at which the fish are swimming.

Hobson had spent ten years and many thousands of hours under water both during the day and at night observing the behavior of fishes. He claimed that in clear water at night he had been able to see objects above him using the surface as a contrasting background when the only light source was starlight. He believed that this visual capability must be much more striking in an animal possessing the nocturnal visual capacity of a sea lion or seal. Hobson's underwater observations were extended when he swam with trained sea lions and seals at the U.S. Naval Missile Center in Point Mugu, California, and saw them invariably approach targets and baits from below, sometimes swimming on their backs; even when targets were lowered to a depth of more than 100 m, a trained *Zalophus* descended to an even greater depth and was seen shooting up after swimming in under the target from below. Interestingly, there is additional evidence about the visual hunting strategy that

Zalophus use in the dark. More than ten years earlier, Paul Bonnot (1951), a fisheries and wildlife biologist, reported that *Zalophus* may indeed use a foraging strategy that takes advantage of the relatively light surface in locating prey at night. He saw them feeding at night on flying fishes that were milling about under a night light next to his boat. One sea lion consistently approached the area while swimming on its back at a depth of about 10 m, and once the sea lion reached a point right below the milling fish, it shot right up and succeeded in capturing the fish. Bonnot observed these capture patterns about six times, suggesting, along with Hobson's observations and assertions, that such a hunting pattern is regularly performed by *Zalophus*.

Anatomical surveys by Gordon Walls (1942) indicated that most pinniped eyes are adapted for good vision under water even at night; experiments by Evans and Haugen (1963) suggested that *Zalophus* may not echolocate; and the observations by Bonnot (1951) and Hobson (1966) clearly showed that some pinnipeds eat well, not necessarily due to superior echolocation ability but because their vision is very sharp under darkened conditions in water. All of these objective findings supported my hunch that Poulter was probably wrong about pinnipeds echolocating. It made me realize that the first set of experiments we were required to conduct should be on the visual performance of pinnipeds.

In November 1963, we brought on Steve Feinstein, who worked with Kellogg as an undergraduate student at FSU on Kellogg's echolocation studies with humans. For a short time afterwards at the Yerkes Lab, while I was there in 1962, Steve had also assisted Bill Mason in studies on the social development of chimpanzees. Although he mainly worked with Chuck on the blind echolocation project, Steve loved to work with the pinnipeds and proved to be an invaluable assistant in that program as well. Thus, the four of us did the first laboratory experiments dealing with the visual performance of pinnipeds, finding that they could readily discriminate between targets of different sizes.

We were cognizant of Kellogg and Rice's (1966) findings with the *Tursiops*, Paddy, in which they discovered that a big difference existed when they presented visual patterns to Paddy in air to be viewed from beneath the water, and when they presented the same patterns to Paddy from below the water surface. Out of 25 pairs of stimuli that were presented under water, the dolphin successfully discriminated 21 pairs, or 84%, whereas none could be discriminated from water to air unless Paddy had already differentiated the patterns under water. Kellogg discovered this glitch

in their experimental design when he made some dives to see what the apparatus looked like from the dolphin's point of view. I remember him fussing and fuming and berating himself for not doing this when he and Chuck started the experiment with Paddy. He said he was shocked to see that when there is the smallest ripple in the water, the angle of entry of the refracted light rays is so garbled as to prevent a clear image of the patterns in the air. In contrast, the stimulus patterns when submerged are perfectly clear. Kellogg said he was ashamed to admit they had been so dumb when presenting the stimuli in air as the dolphin approached the stimulus pairs from under water. In our experiments with the sea lions Bibi and Cathy, we made sure to present a pair of visual forms under water as the submerged animals approached. However, what I now understood is that Kellogg, unlike Poulter, readily admitted his scientific mistakes and corrected them by often acquiring, in a firsthand-way, an understanding of why an animal behaved as it did. This lesson of trying to perceive the world from the animal's viewpoint was never lost on me.

When we started measuring visual performance in pinnipeds, they were required, as was the case with my human subjects back in Mort Feinburg's class, to judge the size difference between two stimuli in the context of the *psychophysical method of constant stimuli.* This method got its name from the fact that the same stimuli are used repeatedly in order to derive a JND or difference threshold; we generally used nine to 11 black circular discs of various sizes. The animal's task was to station at a head stand about 6 m in front of the testing platform, which was built over the other end of the tank. The different targets were attached to two rods, and deflection of either rod when pushed by the animal activated a microswitch that produced a light signal behind what we called *the stimulus panel*. Throughout these experiments, there was always a perpendicular divider projecting outward from an opaque screen, preventing the animals from moving laterally between targets and forcing them to decide which target to push at a distance of at least 300 cm before a response was recorded. It is ironic that these early visual size discrimination problems were derived from some earlier ideas I had about testing *Zalophus* on echolocation problems. Thus, the targets were cut from 20-gage sheet metal with the thought that the differently sized targets would reflect echoes of different strength to a clicking California sea lion. However, as I began hypothesizing that vision might be a more dominant sensory modality than echolocation in *Zalophus,* I began conducting experiments measuring visual performance as a function of size cues.

Our findings from this series of psychophysical experiments testing the underwater visual discrimination abilities of *Zalophus,* Steller sea lions (*Eumetopias jubatus*), and harbor seals (*Phoca vitulina*) showed that, in all three pinniped species, as the magnitude of the size difference ratios decreased, there was a corresponding decrease in correct responses. The smallest difference threshold ratios ranged from about 1.05:1 to 1.09:1, with *Zalophus* (Schusterman et al., 1965) and *P. vitulina* being somewhat superior to *Eumetopius*. Thus, these pinnipeds could make fine visual size discriminations under water that were comparable to the Java monkey, a highly visual primate species performing a similar task in air. Incidentally, we found that *Zalophus*'s aerial performance on the same task equaled its underwater capability (Schusterman, 1968).

Following the completion of our studies on pinnipeds, a similar psychophysical experiment on underwater size discrimination was conducted on a sea otter by Roger Gentry in collaboration with his professor Dr. Richard Peterson from the University of California, Santa Cruz (UCSC) (Gentry & Peterson, 1967). Two Asian river otters were also tested in a similar psychophysical experiment. This research was done by Paul Nachtigall as part as his Master's program at San Jose State University (Nachtigall, 1969). Gentry had worked for Poulter for a short time in 1964 before getting fired and then went on to do a seminal study on *Zalophus*'s sound localization ability under water for his Master's thesis from San Francisco State University (Gentry, 1967). Concurrently, he began working with me on some of my underwater sound production studies at Coyote Hills (more about that later). These two studies on otter underwater vision showed that although their visual performances were quite good, they were significantly poorer than the performance of the pinnipeds—especially that of the California sea lions and harbor seals. The smallest difference threshold ratio obtained for the sea otter in water was about 1.25:1 (Gentry & Peterson, 1967), and for the river otters, it was about 1.20:1 (Nachtigall, 1969). In summary, all the pinnipeds except one male Steller were capable of differentiating area differences as small as 6% under water, but a sea otter and two river otters were only capable of differentiating an area difference of about 20% under comparable conditions. Although I took these combined results to suggest that pinnipeds in general used vision to forage for food and navigate under water, I decided that these studies were somewhat flawed and probably didn't provide an uncontaminated measure of visual acuity *per se*, but, rather, these early measurements probably involved aspects of the sensitivity of the eye to light. In other words,

all the studies of pinniped visual performance that I helped to design in 1964 and 1965 (Schusterman et al., 1965) confounded measures of the resolving power of the eye with measures of the sensitivity of the eye to light. In addition, the follow-up studies on otters by Gentry, Peterson, and Nachtigall inherited the same confound in terms of determining how the eyes of otters worked.

Although our experiments with three pinniped species on visual size discrimination suggested that the accommodating mechanisms of their eye (i.e., the cornea, pupil, and lens) combine to provide decent vision under water, the debate raging within me about whether these amphibious marine mammals, especially *Zalophus*, depended primarily on echolocation or vision for foraging on fish and squid could only be settled, in my opinion, if it was found that pinnipeds had the same capacity to discriminate the fine detail of objects in their marine environment as did some terrestrial carnivores. In that case, vision would be considered the dominant sense for foraging for pinnipeds, and Poulter's ideas about pinnipeds having a fabulous echolocation system that they used for foraging would be a much less viable hypothesis. Good visual acuity, measured properly, means that an animal like a cat can discriminate the fine detail of an object in view; whereas poor visual acuity, like that of some rodents, implies that only gross features of the object can be seen.

In order to arrive at a reasonable empirical solution to this problem, I had to study and think about what went on inside the structure of the mammalian eye. Mechanically, the eye is an instrument that collects light rays and focuses them into an image registered on its rear photosensitive surface, which is called the *retina.* Light enters the front of the eye through the *cornea*, which has a rounded shape and acts like a convex lens of a camera bending light rays together. Along with the cornea, the focusing process of the eye depends on the *pupil* and the *lens,* which are the accommodating or *dioptric* mechanisms of the eye. After light has been focused precisely on the photosensitive cells of the retina, these cells convert the light energy into neuronal signals that are carried to the brain by the optic nerve. In Gordon Walls' (1942) book, *The Vertebrate Eye and Its Adaptive Radiation*, he suggests that the dioptric mechanisms and the retinal structures of the eyes of both pinnipeds and otters have specialized adaptations for seeing both in air and under water.

Since the speed of light is faster in air and slower in water, focusing light rays on the photosensitive retina in back of the eye is quite different under water than in air. In terms of the physics of light, we say the index of refraction, or light bending, is greater in water than in air. Therefore, light will bend when it travels from air into water or any medium that is optically as dense as water such as the surface and interior of the eye. This means that in water the cornea can no longer focus light on the retina as it does in air.

Human divers and swimmers encounter this problem of blurry vision because, like other terrestrial mammals, the ability to focus in water is eliminated, and their eye becomes farsighted. Humans correct this problem by using a face mask or goggles, which provide an aerial medium that allows the eye to focus as on land. Pinnipeds and otters have each evolved an independent adaptation for visual accommodation under water. Pinnipeds have developed an extremely spherical, fish-like lens which focuses light appropriately for underwater vision. However, this rounded lens makes it more difficult for pinnipeds to see clearly in air because this lens combined with some irregularities in the shape of the cornea results in light rays being refracted at the wrong angle in air, leading to nearsightedness, or *myopia,* as well as an *astigmatism* (i.e., warping the retinal image vertically and obliquely).

In order to more precisely measure visual acuity in pinnipeds, both in water and in air and under a wide variety of lighting conditions, I contacted Dr. Tom Cornsweet, a visual scientist on the staff of SRI. I had become familiar with his work in visual psychophysics. He had developed a variation on the psychophysical *method of limits*, which is frequently used in measurements in absolute thresholds by presenting a stimulus either well above or well below threshold. On each successive stimulus presentation, the threshold is approached through changing the stimulus intensity by a small amount until the boundary of sensation is reached. Cornsweet's variation, which my students and I were to use quite frequently later on in research on pinniped hearing, became known as the *up-and-down* or *staircase method.* In animal psychophysics, the experimenter presents a sequence of stimuli, which usually progressively decrease in value. When the animal fails to respond, the stimulus sequence is reversed from descending to ascending until the animal again responds. Cornsweet, who is currently Chief Scientific Officer and Director of Visual Pathways Inc., a company that he cofounded several years ago, recommended back in 1965 that I use a visual acuity task in which the animals were kept at a relatively fixed or minimum distance from the stimuli so that accurate visual angles could be calculated. Most importantly, he suggested using stimulus configurations in which visual resolving power could be measured (in standard units of visual angle), uncontaminated by intensity discriminations. These acuity targets were produced from photos of *Ronchi Rulings*,

composed of black and white stripes of precisely equal widths, that were specifically designed to measure visual acuity with the rulings varied from coarse to fine.

A familiar visual acuity test is the Snellen Eye Chart. The eye doctor's test has its rows of smaller and smaller letters that the patient, at a given distance from the chart, is asked to read. One of the most common units of measurement in acuity is angular. A person is considered to have normal acuity if he or she can resolve the detail of an object that creates a visual angle of at least one minute (1'). An angle of 1' of arc is the angle made, for example, by a one-inch target viewed at 100 yards. If the target has to be increased by

Figure 17. Use of the conditioned vocalization technique to measure aerial visual acuity in California sea lion Sam

Figure 18. A schematic of the experimental setup for measuring visual acuity in sea lion "Spike"; the apparatus was designed to measure acuity under different lighting conditions.

two inches for the subject to see its details, or if the subject has to come within 50 yards to make out the details of a one-inch target, then the visual angle will increase accordingly to 2' of visual arc, etc. Thus, the larger the visual angle, the poorer the subject's visual acuity.

In my experiments on marine mammal visual acuity, I used three pinniped species, including *Zalophus*, *Eumetopias*, and *P. vitulina* (Schusterman & Balliet, 1970a, 1970b), and I also used Paul Nachtigall's Asian river otters (Nachtigall, 1969) for comparative purposes. For all animals, I always presented the Ronchi Ruling targets with the stripes in a horizontal orientation. As Cornsweet had recommended, although targets varied by line width, each target had equal areas of black and white in order to eliminate any brightness differences. As well as controlling for brightness cues, these black and white, equally spaced gratings lend themselves to a quantitative measure of visual acuity in the form of the minimum angle of resolution or MAR. The MAR is determined by measuring the size of the line gratings at the animal's threshold and the distance that the animal's eye is from the target. This calculation becomes the threshold angle. In other words, the visual acuity or spatial resolving capacity of the visual system is specified in terms of the angular width of the stripes of the finest grating that could be resolved. Most primates that are active during daylight hours have incredible aerial visual acuity, and their threshold MARs are about 30" to 1'; these include humans, rhesus monkeys, and chimpanzees. Other land mammals having rather sharp aerial vision include the elephant (10'), antelope (11'), red deer (9.5'), and the domestic cat (5.5'). These figures can be compared to those of terrestrial mammals with relatively poor aerial visual acuity like rats that can only resolve lines subtending visual angles that are greater than 25' (see Schusterman & Balliet, 1970b, for a review of visual acuity in some land mammals).

In all of these visual acuity experiments, the *standard* grating consisted of 300 lines per inch, or 118 lines per cm (0.05 mm width). The lines were invisible to the human eye with normal visual acuity, appearing as a flat gray square. The *variable* gratings consisted of lines varying in width from 25.4 to 0.96 mm. In general, the psychophysical method of constant stimuli was used in the first phase of a study to obtain a range of variable gratings that the animal had to discriminate from the standard grating. During the final phase, the method of constant stimuli, or some variation on the method of limits, was used to obtain an acuity threshold, which was defined as the interpolated value of the MAR at which an animal responds correctly at least 75% of the time.
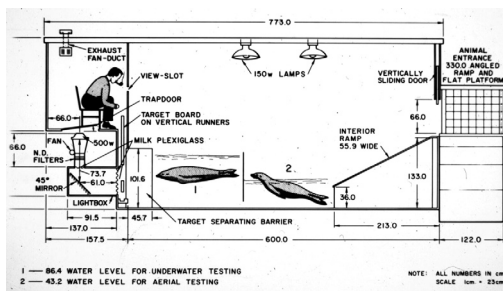
In one set of studies, which included all three pinniped species as well as the river otters, the variable and standard line grating targets were presented simultaneously. The animals were signaled to swim to them when both targets were in place and to press the appropriate target; however, a barrier extended out between the variable and standard targets, and the animals were trained to make their decision at this fixed distance from the targets, allowing the MAR to be calculated.

In another set of studies done only with *Zalophus*, conditioned vocalizations were used as an objective index of the fact that the California sea lion could discriminate between patterns—that is, variable gratings vs a standard (Schusterman & Balliet, 1970a). In the visual acuity experiments using a conditioned vocalization technique, the sea lion was trained to place its chin on a stationing device while looking forward and to emit a click vocalization when it saw a striped target and to inhibit clicking or remain silent for three to five seconds when it saw a gray square target of equal brightness. The two Ronchi ruled targets were presented successively, rather than simultaneously as I have previously described, for the first set of visual acuity experiments using target pressing as an indicator response. In the conditioned vocalization studies designed to measure visual acuity, I used what I then called the *frustration technique* in order to readily elicit clicking sounds from California sea lions. This was accomplished by withholding fish rewards while a sea lion worked at an underwater target pressing task, a response that hitherto had resulted in fish reinforcement. Steve Feinstein helped me to design these methods, and when the sea lion was shifted to a vocal conditioning task, we promptly reinforced the animal with fish for vocalizing when the target-pressing response did not "pay off." Next, the vocalization was brought under the control of the size of circular and triangular stimuli. A click burst emitted in the presence of a large or small target was reinforced, and silence in the presence of the opposite sized stimulus was also reinforced. Thus, vocalization or a "go" and silence or a "no-go" in the presence of the appropriate stimuli defined the correct response. In the acuity experiments, a correct response was defined as emitting a burst of clicks when the variable target was presented and remaining silent when the standard target was presented. Another way of putting this is that the sea lion's vocalizations were under the control of the size of the stimuli.

As a sidebar I should say that, to my knowledge, this was the first time a threshold determination for nonhuman animals, in this case measuring visual acuity in *Zalophus*, was accomplished by means of a conditioned vocalization technique, where an aversive stimulus like shock was *not* used as an unconditioned stimulus (UCS).

A few years later, in 1970, a five-year-old *Zalophus*, "Sam," who served as one of the subjects in the visual acuity experiments using conditioned vocalizations as the indicator response, had his hearing tested over a wide range of frequencies under water and over a more restricted range of frequencies in air by the same "unique" response paradigm. Sea lion Sam's task was to emit a click burst if a pure tone signal was heard or to remain silent until a trial light was extinguished; the tone was presented in about half of the trials. About 30 years afterward, Dr. Sam Ridgway, with the U.S. Navy Marine Mammal Program, used a similar response paradigm to obtain hearing thresholds in cetaceans; he required two beluga whales to emit a whistle upon hearing a pure tone signal.

In my experiment (Schusterman et al., 1965), both California sea lions, one Steller sea lion, and a harbor seal showed very sharp vision under relatively bright lighting conditions; the MARs were in the range of the visual acuity thresholds obtained for domestic cats—5' to 6' for *Zalophus,* 7' for *Eumetopius*, and 8' for *P. vitulina* These data strongly supported the notion that since pinnipeds forage almost exclusively under water, most species, at least during daylight hours, use vision to locate their prey items.

What about foraging and navigating at sea at night? The original data are rather conclusive, even though they come from only one study; one species, *Zalophus*; and one individual, a four-year-old male by the name of "Spike" (Schusterman & Balliet, 1971). My assistant on this very significant study was Richard Balliet, who at the time was an undergraduate in Psychology at California State University, Hayward (CSUH), where I taught a few classes during my early SRI days. Spike was tested in a light-tight tank, periodically inspected and corrected for light leaks; the background luminance to the plexiglass Ronchi Rulings was varied by a series of neutral density filters. The results of this experiment completely supported the early field observations by Bonnot and later those of Hobson (1966) on the nocturnal vision of *Zalophus*. Indeed, Spike's underwater visual acuity remained remarkably keen (8' to 13') even under very low light levels. These MARs matched those of some nonhuman primates like the rhesus monkey and baboon (in air, of course) at the same level of darkness. However, with further decreases in background luminance, the relative rate of decline in underwater visual acuity of the California sea lion is significantly less than that of human aerial visual acuity.

Now I understood why Edmund Hobson believed that he, and not Tom Poulter, had the

answer to the long-standing mystery of how sea lions and most species of seals managed to maintain themselves in a sleekly well-fed fashion, even though they do much of their fishing at night. Pinnipeds eat well because their nocturnal vision is so extraordinarily sharp even under extremely darkened conditions.

About a quarter of a century later, my graduate student, David Levenson, and I, at Long Marine Lab (LML) of UCSC, first studied pupillary adjustment in *Zalophus*, *P. vitulina,* and in a northern elephant seal (NES) (*Mirounga angustirostris*) as a function of different light levels. These pupillometric findings were followed by a behavioral psychophysical study on the *dark adaptation* and visual sensitivity of the same three pinniped species. The first study (Levenson & Schusterman, 1997) showed that the pupillary response is essential to maintaining appropriate levels of retinal or photosensitive stimulation during rapid changes in light levels by diving pinnipeds. The deepest diving pinniped, the NES, was found capable of an over 400-fold increase in pupillary size from bright to dark, while the shallower and moderately deep diving *P. vitulina* and *Zalophus* possessed considerably smaller ranges of only 25- to 200-fold changes over the same range of illumination. The second study (Levenson & Schusterman, 1999) showed that all three pinniped species have different but relatively swift rates of dark adaptation, and all three species are highly sensitive to light once they are completely dark adapted.

For most mammals (including humans) and birds, the natural transition from daylight to night or from light to dark takes place gradually with dark adaptation being an increase in sensitivity as the eyes remain in the dark. Presumably, the mechanisms for human dark adaptation have evolved in this context. However, as a consequence of human technology, we can greatly speed up the transition from light to dark by the mere flip of a switch. For example, after entering into a darkened auditorium from a brightly lit lobby, most of us have experienced the incredibly awkward and embarrassing problem of groping strangers and tripping over things as we attempt to find an empty seat. Finally, we sit down and remain temporarily blinded for another 20 minutes or so until we can ultimately make out what our fellow moviegoers are doing. In contrast, for diving mammals like the pinnipeds, the natural transition from the light of day at the water's surface shifts quickly in the dark as the sea lion rapidly plunges to depths of 100 m or more, and in the case of the NES, to sometimes nearly a 1,000 m where they search for food prey. Presumably, the mechanisms for pinniped dark adaptation and sensitivity to light have evolved in this context. Sure enough, Levenson's findings

showed that a California sea lion dark adapts in about half the time (11 minutes) it takes for a human to dark adapt (20+ minutes), and an NES dark adapts about twice as fast (5 minutes) as a California sea lion. In addition, *Zalophus*'s sensitivity to light is about one half of a log unit greater than human sensitivity but about one half of a log unit less than an NES.

What makes the story of pinniped vision so utterly fascinating is that it is truly amphibious. As our original studies on visual acuity showed, their large eyes are suited primarily for vision in water rather than in air, enabling them to forage in a dark environment with enlarged pupils and enlarged, fish-like round lenses to compensate for the absence of corneal refraction under water. However, to facilitate acuity in air, the pupils in most pinnipeds are *stenopaic,* meaning that they are slit-like and are likely to function as a pin-hole aperture providing relatively clear vision in air as long as the pupil remains small as it does in relatively good light. However, as darkness comes, the ability of a sea lion or a seal to make out fine detail declines much more slowly under water than in air, where visual acuity falls off precipitously as the light level drops. In general, pinnipeds have sharp vision under good lighting conditions on land, but in low light or darkness, they are very near-sighted or *myopic.*

Indeed, until the mid-1960s, much of the available information on the visual performance of pinnipeds depended on anecdotal evidence from the field and had little basis in laboratory controlled psychophysical experiments. For example, several scientists researching the natural history and behavior of different pinniped species on land had noticed in their field studies that *Zalophus* shows little reaction to people, even at relatively close distances, whereas *P. vitulina* reacts strongly to people at much greater distances. On the basis of these informal observations, they concluded that with respect to their reaction to humans, the aerial visual discrimination in *Zalophus* in daylight is of a low order, while that of *P. vitulina* is significantly superior. Such a conclusion, however, is gratuitous and is probably due to the differing amounts of vigilance behavior of the species involved and therefore has little relation to visual acuity *per se*. Indeed, when I quantified vigilance behavior in a group of captive harbor seals (Schusterman, 1968), I found it to be more than 20 times greater than in a comparable group of California sea lions.

To close out the story of how well animals like sea lions, seals, and otters can resolve detailed features of their visual environment so they can see well both in air and water, I should briefly summarize our psychophysical experiments with the two Asian river otters named "Tom"

and "Jerry"; these were the critters that had been used earlier in size discrimination experiments by Paul Nachtigall (1969). These two were supposedly from the same litter; grew up together in the Kelly Park Zoo in San Jose; and any time they got frustrated, Tom and Jerry made these incredibly high-pitched squeaking sounds. In the first study done at SRI, Richard Balliet and I (Balliet & Schusterman, 1971) found that these two guys, when tested in relatively bright light, had aerial and underwater MARs ranging from 14' to 16'—a very respectable acuity score—but nevertheless, nearly three times inferior to the visual acuity scores of California sea lions Sam and Bibi under comparable lighting conditions. In collaboration with Barry Barrett, another undergraduate student at CSUH, it was found that, under very low light levels, simulating nocturnal conditions, visual acuity thresholds of the river otters were much inferior to those of sea lions under water (Schusterman & Barrett, 1973). This finding is consistent with the currently accepted notion that some mustelids (i.e., amphibious mammals belonging to the weasel family), like sea otters, that feed nocturnally as well as diurnally, mainly use their paws and vibrissae to locate and capture prey under water. At any rate, the comparative behavioral findings on the underwater visual acuity of pinnipeds and otters convinced me once and for all that many pinniped species, particularly *Zalophus,* depended on their keen vision to keep them well-fed at sea and not on an echolocation system as proposed by Tom Poulter. My hunch was that sea lions were like "cats gone to sea."

As I was first taught by Dr. Feinberg at CUNY, and then reminded of by his mentor, Dr. Kellogg, some animals have sensory equipment that in several ways is much inferior to ours but in other ways may be highly specialized and superior to ours. Human visual acuity under good lighting conditions is excellent in the atmosphere but very poor in the hydrosphere without goggles. On the other hand, sea lions have relatively good vision in air and under water, but it is inferior to human aerial vision. However, under water and in extremely dim light, the visual perception of sea lions in comparison to humans is reversed. Sea lion visual acuity under water, even under extraordinarily darkened conditions, is nothing short of phenomenal. Furthermore, sea lions dark adapt so much faster than humans, and they are so much more sensitive to light than we are. Indeed, the deepest diving pinnipeds—the elephant seals—are truly "creatures of the dark," and, not surprisingly, many of the prey items consumed by elephant seals are bioluminescent or associate with many of the bioluminescent organisms of the deep scattering layer.

For many of the pinniped species, including California sea lions and elephant seals, there is an entire underwater world out there in the bioluminescent dark and very dim light that is visually perceptible to them, even though we cannot perceive it and would not even know it exists without the help of our technical sensors such as man-made sonar and underwater light measurement devices.

Furthermore, there are some pinnipeds, like walruses, that characteristically forage for clams and other bivalves in the murky waters of the muddy sea floor; these pinnipeds have specialized whiskers and facial and oral structures used to detect, differentiate, and extract prey from the substrate. In some species, like *P. vitulina*, the extensive innervations of their whiskers can be up to ten times greater than that of terrestrial mammals. This makes the vibrissae of some pinnipeds well-suited as a displacement detection mechanism. For example, in 1999, Dr. Randy Davis and his associates attached miniaturized "crittercams" on foraging Weddell seals in the Antarctic and documented that after the seals detected their fish prey visually, their whiskers became erect as they closed in, suggesting that the whiskers were used during the final stages of prey capture (Davis et al., 1999). Dr. Guido Dehnhardt, a German marine mammalogist, demonstrated experimentally that a harbor seal is capable of detecting extremely weak hydrodynamic stimuli using its whiskers (Dehnhardt et al., 1998). These vibrations in water were several orders of magnitude below the particle velocities in the wakes produced by small swimming fish.

Following these first psychophysical experiments showing that the whiskers of *P. vitulina* function as a hydrodynamic receptor system, Dehnhardt and his colleagues published an article in 2001 in *Science* entitled "Hydrodynamic Trail-Following in Harbor Seals (*Phoca vitulina*)." In the experiments, a blindfolded harbor seal demonstrated that it could use its amazingly sensitive whiskers to detect and track trails as long as 40 m. These findings can explain how harbor seals can sometimes feed on prey in extremely dark and murky water without the aid of vision.

Thus, by the beginning of the second millennium, the only marine mammals known to have evolved the highly specialized ability of echolocation are the toothed whales (e.g., dolphins, beluga whales, sperm whales, beaked whales). Most of the well-controlled experiments that demonstrated echolocation in these marine mammals have been done with the small toothed whales like dolphins and porpoises. When Tom Poulter made his claims about the "fabulous" and "sophisticated" sonar abilities of California sea lions back in the 1960s,

I believe he was exaggerating beyond belief. He seemed quite unaware and insensitive to the potential of many pinnipeds being able to navigate, orient, detect, and capture food prey by relying during the nighttime on an eye that is perfectly adapted to vision in very dim light or on very sensitive vibrissae perfectly suited to a hydrodynamic reception system with spectral sensitivity well-tuned to the frequency range of prey-generated water movements in dark or very murky waters. However, as Poulter was informed more and more about these receptor systems in pinnipeds and that such sensory capabilities strongly argued against the idea that these critters had a biosonar system anything like that approaching sophisticated dolphin sonar, he put up even greater resistance.

At that time, Poulter not only refused to entertain ideas about the incredible potential that pinnipeds had for orienting in dark and murky waters without sonar, but he also refused to admit that the sounds emitted by pinnipeds under water, although superficially similar to dolphin echolocation clicks, did not have their essential nature. High-frequency biosonar, like that used by dolphins, is selectively advantageous because of the increased resolving power of a system using signals with wavelengths smaller than the objects being targeted. This is especially significant in water; since water is so much denser than air, sound waves travel almost five times faster in this medium. Thus, even back when Poulter was making his pretty outrageous assertions about sea lion sonar in the context of dolphin sonar, most of us already knew that the underwater sounds emitted by sea lions did not have the temporal or physical structure or physical characteristics of dolphin echolocation pulses. For example, during fine discriminations, where sight is impossible, Dr. Kenneth Norris reported in the early 1960s that a dolphin literally saturated the aquatic environment with 500 to 600 pulsive clicks per second (Norris, 1964). Source levels of some of the sonar clicks produced by dolphins and other toothed whales are extremely loud, being estimated at well over 200 dB. Dolphins generally emit broadband sonar pulses, which range from several tens of kilohertz up to 150 kHz (i.e., they employ very high-frequency signals when echolocating). *Zalophus*, on the other hand, normally produces click repetition rates varying from five to 70 to 80/second. The pulses are mostly of low intensity and cannot be heard far from the animal. Bill Schevill, working at Woods Hole and at the New York City Aquarium with Bill Watkins and Carleton Ray, reported that the main energy of *Zalophus*'s clicks was between 0.6 and 2 kHz (Schevill et al., 1963)—these are indeed low-frequency clicks and are unlikely to be of any value to a sea lion attempting to listen

for their returning echoes from the air-filled swim bladder of a fish it is trying to locate and track. Again, Poulter disregarded these unfavorable findings for his echolocation hypothesis in sea lions, and, undeterred, he blithely proceeded with his research program. In fact, in 1971, five years after he learned about my negative findings on sea lion echolocation, which I will describe in a moment, he published in the *Journal of Auditory Research* a paper confidently titled "Echo Ranging Signals: Sonar of the Steller Sea Lion, *Eumetopias jubatus*" (Poulter & del Carlo, 1971). So, despite conflicting evidence, Poulter's ego would not allow him to modify his hypothesis, suggesting, perhaps, that it may be more realistic to assert that sea lions use their click reverberations for simple, close-range spatial orientation. Instead, he stuck to his original notion: that there is "overwhelming" evidence in sea lions for the degree of sophistication present in dolphin echolocation.

At this point, it became crystal clear to me that Tom Poulter would never be receptive to critical reviews even if they were well-considered. He had his mind made up, and he did not want to listen to opposing viewpoints. He was convinced that he was right and did not even want to be exposed to any information that did not fit his preconceptions.

In 1962, when I was at Yerkes Lab in Orange Park, the director, Art Riopelle, sent me to a wonderful, richly informative meeting of the New York Academy of Sciences, which was hosting a symposium on the evolution of nonhuman primates. There were several outstanding scientists attending, including a very young, tall, and handsome blond woman by the name of Jane Goodall. But the speaker who most caught my attention was Richard J. Andrew, and his talk was entitled "The Situations that Evoke Vocalizations in Primates" (Andrew, 1962). It turns out that Dr. Andrew, who at the time was at Yale University, had a theory about the causes of vocal behavior, not only in monkeys and apes, but in many other species, including most birds and mammals. One of his points was that perhaps the most pervasive situations for evoking calls in social animals is the "perception of a desired object like food." When Poulter first began describing his studies of echolocation clicks in *Zalophus*, I thought about Andrew's ideas about vocalizations elicited by the sight of food, by stimuli signalling food, by greeting a fellow, or by a novel object. Andrew added that whenever intense attention to a stimulus situation is aroused, there is a good likelihood that vocal behavior will ensue, particularly when autonomic nervous system responses are involved (i.e., emotions), which are typical of *conflict* and *frustration*. He concluded his talk by saying that

there is some evidence, at least in chickens, suggesting that it may be possible to condition these calls—that is, to increase the probability of their occurrence by making a reinforcing event contingent on the chick's calls.

So in 1965, armed with R. J. Andrew's model, I tried to design and conduct experiments that would help to identify the causes of *Zalophus*'s sound production under water, particularly its emission of clicks. I saw this as a logical approach to the general problem of sound production in sea lions rather than a causal analysis of the first stage of a highly sophisticated and efficient bio-sonar system. To this end, I also began a series of studies to test the echolocation capabilities of *Zalophus*. One could say that I was taking a dual approach. Behaviorally, I was testing predictions from an *echolocation hypothesis* against those from a *communication hypothesis*.

Several animal behaviorists from UCLA and UCSC, including Dr. George Bartholomew, Dr. Nicolas Collias, and Dr. Richard Peterson, had noticed that *Zalophus*, along with NESs and the northern fur seals (*Callorhinus ursinus*), vocalize in air, emitting sounds that often have a pulsed structure. These calls are valuable in these polygynous breeding pinnipeds for understanding the role played by vocal communication in their social organization throughout the reproductive season. The aerial sound emissions by seals and sea lions are related to, among other things, social play, female-female competition, male-male competition, sexual activity, mother-pup interactions, disturbance from a resting state, and exploratory or investigative behavior. For this reason, it seemed quite reasonable to me to think that because the pinnipeds are amphibious, the underwater click vocalizations by *Zalophus* are a counterpart to their aerial vocalizations and are, therefore, related to a general arousal phenomenon as well as to a specific, more focused arousal such as *questioning reaction* or *orienting reflex*. Since the click vocalizations are likely to convey information regarding the mood of the animal, these pulsed calls may function as part of its underwater communication system.

Social, novel, and other important stimuli like the presence of food, strongly induced behavioral and physiologic arousal, and the concept of arousal, as I had learned from one of my mentors at Yerkes Lab, Bill Mason, is useful in the interpretation of investigative behavior and in patterns of social behavior. If clicking vocalizations under water are related to the emotional character of *Zalophus*, then they may be expected to play a leading role in its behavior in situations considered arousal-producing. In order to test this hypothesis, three California sea lions (one male, Sam, and two females, Bibi and Cathy, between three and four years old) were presented with a social situation (another *Zalophus*) and a novel situation (a mirror) in our redwood tank filled with water (Schusterman et al., 1966).

The amounts and types of underwater vocalizations were compared in the presence and absence of the stimuli. Sea lion behavior was quantified by means of a time-ruled checklist; event frequency was recorded at 30-second intervals. Both underwater vocal behavior as well as investigative behavior was scored. We observed the sea lions from the testing platform. Roger Gentry, who after leaving Poulter began working for me at SRI, monitored and scored the occurrence of underwater vocalizations. Jim Schmook, a graduate student from San Jose Sate University, observed the animals. He activated a stopwatch only when an animal's head was submerged, and he scored behavioral categories and made quantitative notes on the activities of each animal. Vocalizations were scored only during "running time"—that is, when at least one sea lion had its head under water.

Each sea lion was paired with each of the other two on separate occasions. Testing was done daily, and the three pairs received a total of four test sessions, with one individual of each pair alternately introduced into the pool individually or as a "partner." The procedure was as follows: (1) a sea lion was introduced into the tank and swam freely for one hour, with observations being made during the first 10 minutes of this period; (2) the underwater vocalizations of the single free-swimming animal was recorded for 20 minutes; (3) a second animal, the "partner," was introduced into the tank, and the vocalizations emitted under water by both animals were recorded for 20 minutes; and (4) the partner was removed from the tank and recording of underwater vocalizations by the first animal was repeated. Each session was conducted in daylight in clear water for 12 days.

The underwater vocalizations recorded during the experiment included "whinny" sounds, barks, and a buzzing sound as well as varying patterns of click trains similar to those described by Poulter in his sonar experiments with *Zalophus*. Clicks were the most prevalent vocalizations emitted by these *Zalophus* while under water. On average, the percentage of time Sam and Cathy produced clicks while they were socially interacting was 35%; for Sam and Bibi, the score was 15%; and for Bibi and Cathy, the score was 52%. These scores can be compared with the pre- and post-baselines, which showed individuals clicking hardly at all—less than 5% of the time. Although "other" vocalizations, which included buzzing, whinnying, and barking, occurred less frequently than clicking, the combined scores of three pairs of *Zalophus* was
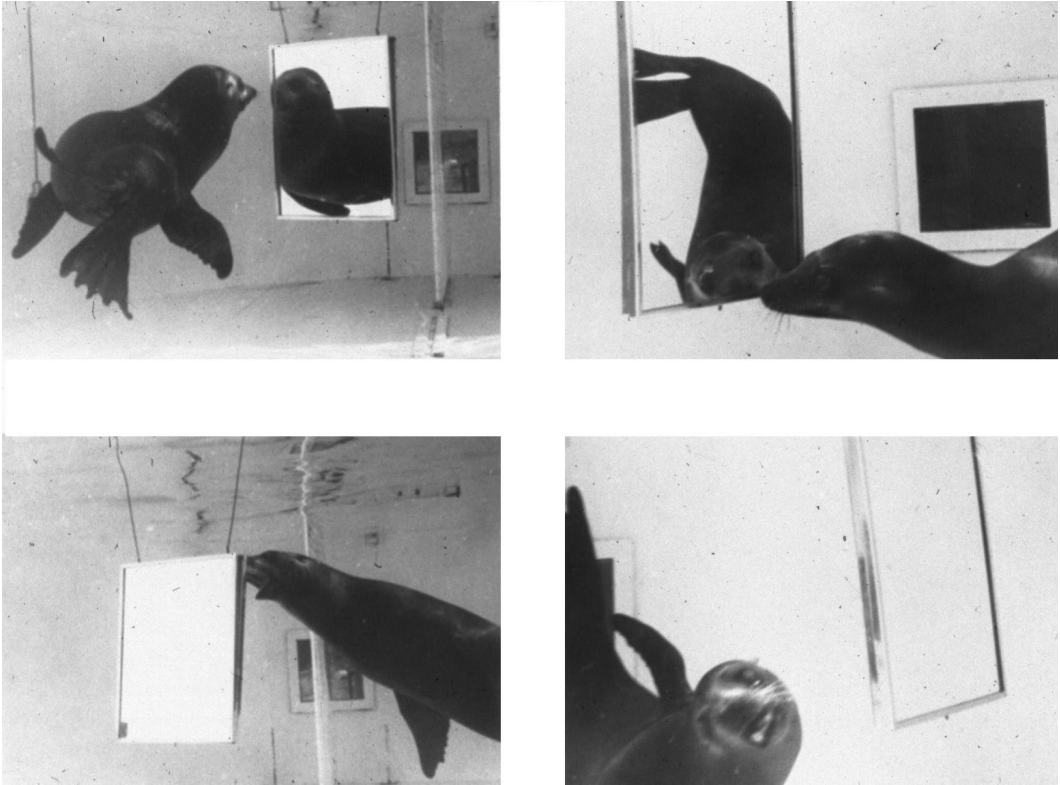
Figure 19. Orientation of a sea lion to back-to-back mirrors in the testing tank; in one photo, the sea lion is about to bite the mirror; and in another, it is in the act of turning sharply away from the mirror after making a "threatening" run at it.

10%, whereas during baselines, "other" underwater vocalizations did not occur at all.

Although clicking was the predominant underwater vocalization, Bibi frequently whinnied, especially when interacting with Sam. Sam and Cathy never emitted this underwater sound. Play-fighting (characterized by chasing, gentle biting, pushing, and "porpoising" together and over one another) was the most frequent social activity observed in the pool. Although clicks were produced frequently during social encounters, especially during extensive chases, they were also produced when the sea lions were together but not necessarily swimming close to one another. Barking and whinnying were specific to social encounters, usually occurring when play appeared to shift to aggression (chasing, hard biting, and lunging).

These results are certainly *unsupportive* of echolocation as the probable function of *Zalophus*'s emission of underwater click trains. Instead, they *support* the notion that these pulsed sounds, as well as others such as barks, function as part of *Zalophus*'s vocal repertoire, which is used amphibiously as part of their social communicative process. In fact, a few years later, in 1969, Richard Balliet and I published a paper in *Nature* entitled "Underwater Barking by Male Sea Lions (*Zalophus californianus*)" (Schusterman & Balliet, 1969). We showed that, when taken in conjunction with field observations by Peterson and Bartholomew, our laboratory observations support the hypothesis that barking by *Zalophus* is probably the most widespread underwater vocalization by males (we used six males ranging in age from 4 to 7 years old) and that barking serves the same function under water as it does in air, mainly as territorial and dominance displays, which tend to discourage overt physical aggression. Reproductive male *Zalophus* bark incessantly in air when they are on their territory, but they also produce barks under water when the bull's territory is submerged during high tide. In 1990, years after my original work on sea lion barking, I dropped a hydrophone among mostly male *Zalophus* during their first invasion of San Francisco's Pier 39 and heard many of them barking and clicking under water. I also had students from CSUH observe and record *Zalophus* begging for food at the pier in Monterey as the sea lions emitted barks, clicks, and growls

both in air and under water during these frustration and conflict situations. It was obvious, even in these simple observations of wild sea lions, that it was easy for individual sea lions to learn to emit vocalizations for fish reward under frustration and attention-getting conditions.

The next experiment that we did at the Coyote Hills Lab in 1965 dealt with the effects of a mirror on underwater vocal and investigative behavior (Schusterman et al., 1966). A mirror may be thought of as a novel stimulus having some of the properties of a social stimulus once the animal orients to it and perceives its reflective image. Niko Tinbergen, a well-known Dutch ethologist and colleague of Konrad Lorenz, reported that a sexually active stickleback fish assumes a threatening posture when it sees itself in a mirror.

Two mirrors were hung vertically back-to-back over the center of the tank and well below the water's surface. Vocalizations and visual orientation to the mirrors were scored. The design and procedures of this study resembled those of the previous study on social factors influencing underwater sound emission except that the mirrors replaced the "partner" during the test phase.

None of the three sea lions emitted sounds before or after the test periods—that is, when the mirrors were not available—but all three immediately oriented and produced underwater clicks upon initial exposure to the mirrors. After the initial burst of clicks, while approaching the mirrors, sea lion Sam remained silent and showed no further interest in the back-to-back mirrors. The two female *Zalophus*, Bibi and Cathy, however, showed a great deal of interest in their reflected images from the mirrors by continuing to orient and emit click vocalizations. Orientation and clicking continued to occur, but at a decreasing rate, both within and between test sessions. For both sea lions, orientation scores were at 100% at the beginning of the first session and dropped to 90% for Cathy and 50% for Bibi by the end of the session. By the fourth day of testing, orientation scores for Cathy began at 60% and declined to 20% over a five-minute period, while Bibi's comparable orientation scores were 70% and 0%. Click bursts for these sea lions showed the same pattern. In the first session, Cathy emitted clicks 50% of the time initially, which decreased to 10% at the end of the session; and for Bibi, the comparable scores were 40% and 0%. During the last session, Cathy clicked 20% of the time at the beginning and not at all at the end, while Bibi emitted no clicks on the last session. There are several prominent features that tend to characterize play and investigative behavior: *response to novelty*, *habituation,* and *recovery*. Habituation refers to the tendency of an animal to become less responsive to stimuli that become familiar. Following a period of time after short-term habituation, the response recovers to a strength usually less than its original level and the animal again gets used to the stimulus so that long-term habituation may persist over some time period. Our results show that *Zalophus*'s underwater investigative behavior toward mirrors, as indicated by measures of visual orientation and click emissions, also conform to these principles. In fact, the curves I just described for underwater clicking by *Zalophus* to a novel/social situation resemble those reflecting novel object-contact curves obtained with common chimpanzees, and the frequency of investigative behavior displayed by *Zalophus* appears to resemble those of other modern carnivores when they are exposed to novel objects.

Overall, the change in rate of underwater calling in response to an increased likelihood of real, simulated, or novel conspecific presence argues strongly in favor of a predominantly communicative function of clicking and other call types by *Zalophus*.

Next on my agenda was a series of performance tests required to study how *Zalophus* assess near-range objects in their surroundings by using echo information. I conducted three experiments in order to measure various aspects of *Zalophus*'s echolocation performance. In the first experiment, sea lions Bibi and Cathy were trained to press one of two targets with their noses: Bibi was required to press the larger of the targets (736 cm^2) and Cathy the smaller (16 cm^2). The targets were black discs made of 20-gauge steel and were presented side-by-side with a barrier between them. The distance between the centers of any two targets was 57 cm. The barrier extended out from the plane of the circular black targets by a distance of from 1.5 to 2 m. This configuration forced the sea lions to make their decision to go to one or the other target from distances never any closer than the extent to which the barrier extended out from the plane between the targets and usually about a half a meter farther away. Both Cathy and Bibi performed the task perfectly in clear water. However, when the water was made extremely turbid or cloudy by introducing a harmless vegetable dye, attenuating visibility to a distance of about 2.7 to 2.8 m (the maximum distance at which a diver wearing goggles could see the largest target), performance levels by both animals fell to chance. They clearly showed that they could not perform this gross size discrimination task without their vision intact, definitely indicating the lack of any sonar discrimination ability. What is more, one sea lion, Cathy, never emitted clicks in the turbid water condition (nor, for that matter, in the clear water condition). Bibi produced click bursts on almost every trial despite

correct choices remaining at chance during turbid conditions, while she only occasionally produced clicks while performing perfectly in clear water. In an earlier experiment, using mostly the same set-up, Bibi was tested at night, when five 150-W lamps could be used to illuminate the testing tank. We found that by alternating light and dark conditions quickly so that she did not have time to dark adapt, her correct responses were at a 100% in the light and about 50% or chance in the dark. However, Bibi's click emission on discrimination trials was inversely related to her performance—that is, when she could see the targets and perform the task correctly, she produced clicks much less frequently than when she was selecting the incorrect target about as frequently as she selected the correct target. When this occurred, Bibi gradually began acquiring the habit of clicking on all of the trials that were presented in the dark. However, Bibi's underwater clicking was of no help at all in her attempts to perform the easy size discrimination task. Apparently Bibi had expected fish reward in both of these experiments, and when the tank was dark or the water was made cloudy, her disappointment and frustration in not obtaining a fish reward was reflected by her underwater vocal behavior—clicking. These results with *Zalophus* are reminiscent of Tinkelpaugh's food substitution experiments with monkeys and chimps. In both cases, the animals are "disappointed" because a reward is expected and is either switched, with its value being lowered, or the S+ (the stimulus associated with reward) is difficult to discern. In either case, there is disappointment, frustration, and a *questioning reaction*. It is in such a motivational/emotional *cognitively dissonant* state that animals, including humans, often emit vocal and/or verbal behavior. Indeed, it was observations such as these which led Steve Feinstein and me to come up with the *frustration technique* to facilitate underwater click emission in California sea lion Cathy and then bring her vocalization under the control of different size stimuli.

I considered the possibility that the sea lions were not able to perform the size discrimination task with metal discs in the dark or in cloudy water because of being required to make their decisions at a distance of 1.5 or 2 m from the disks, and that perhaps *Zalophus*'s sonar may be functional only at very close distances from the targets. Therefore, this time, in clear water during daylight hours, a second experiment was conducted with sea lion Bibi. In this case, two flat circular plexiglass targets with a 33-cm diameter were used in a discriminative echolocation task. One target had a gap, or an *airspace*, 0.32-cm thick between two plexiglass sheets of 0.32-cm thickness to yield a total thickness of 0.96 cm; we called this the

"air-plexiglass sandwich." The other target had the same diameter but was constructed of a solid piece of plexiglass 0.96-cm thick; we called this target the "solid plexiglass" target. The reason for using such targets was that when a sound pressure wave moving through water hits an air interface like the air-plexiglass sandwich, it can barely make the leap into the new medium. Instead, the air acts as a mirror, reflecting most of the sound energy back into the water. Thus, the plexiglass with the air space would have a much stronger acoustic reflection than the solid plexiglass target. Both targets were painted black and appeared to be visually identical (more on this point later). Sea lion Bibi was first trained with only the air-filled disk present in the clear water, and she was also trained to emit broadband clicks and swim toward and press the air-filled target. Eventually, "sonar" discrimination test trials were run in which the air-plexiglass sandwich and the solid plexiglass were presented simultaneously and the sea lion was required to press the air-plexiglass sandwich only. Bibi's performance remained at a chance level (51% correct responses) throughout the course of 2,050 trials. This chance performance occurred despite the fact that Bibi emitted broadband clicks on each and every trial. Clicking continued as the sea lion approached to within 15 to 61 cm of a target. Frequently moving back and forth at this distance between targets while producing a continuous train of clicks, Bibi finally made a choice between the air-plexiglass sandwich and the solid plexiglass by pressing one or the other, activating a microswitch and producing a light signal, which the experimenter used as a response measure. However, on the basis of Bibi's chance performance, it would appear that this sea lion's behavior was an attempt to visually sample the targets and was unrelated to auditory or echo sampling. In other words, Bibi apparently persisted in a futile attempt to differentiate visually between these identical appearing targets but paid no attention to the potential echoic differences between the two disks.

The position of the sea lion while she was still emitting clicks and just prior to indicating her target choice was such that the signal (echo from the air-plexiglass sandwich) to noise (tank reverberation) ratio should presumably have been favorable for accurate detection and discrimination. Since one of the crucial aspects of any biosonar system is the degree of attention paid to the potential echo information, Bibi's results suggest that *Zalophus* does not, either habitually or instinctively, "pay attention" to such available echo information. On the other hand, it may be argued that since these tests permitted the sea lion its full visual capabilities, reliance or the seeking

of visual cues interfered with the animal's echoic/auditory attention processes. For this reason, 500 additional test trials were given with underwater visibility reduced to a distance of about 1.8 m. Again, unfortunately for Pouter's echolocation hypothesis for sea lions, Bibi's performance remained unchanged at a chance level with 47% correct responses.

A few months later, Steve Feinstein did a series of experiments in which he used the same targets that we used with sea lion Bibi, placed in the same position under water within the tank. First, Feinstein developed an artificial clicker simulating *Zalophus* click emissions, which produced broadband pulses ranging in frequency from 85 Hz to 8 kHz at a rate of 27/second. Feinstein then placed the speaker emitting the clicks 30 cm in front of the air-filled plexiglass disc, the solid plexiglass disc, or no target in the water. His sonograms of these three conditions clearly showed that the air-plexiglass sandwich caused a dramatic increase in the intensity of the sound-reflected energy at about 8 kHz as compared to the other two conditions. In the final phase of Feinstein's study, two human divers with no previous training were instructed to indicate whether or not they heard a target (Feinstein, 1966). At a distance of 30 cm, the divers reported "hearing" the air-plexiglass sandwich with perfect or near perfect performance on each of 30 trials, but they did not hear the solid plexiglass target. The subjects reported that the solid plexiglass (a poor sound reflector) sounded the same as when there was no target available in the tank, while the air-plexiglass sandwich (a good sound reflector) sounded very distinctive, and was immediately obvious. Thus, human subjects who are not only relatively deaf under water but also have difficulty localizing sound can perform a relatively simple sonar task, while *Zalophus*, given a comparable sonar task, failed to show any signs of echolocation capability.

Even though the Navy Marine Mammal Program was clearly showing that dolphins could detect and discriminate between a variety of inanimate objects, it could be, and indeed was, argued by Poulter that *Zalophus*, although not capable of differentiation between the sound reflection characteristics of different inanimate objects, could detect and quickly find food fish by means of its "fabulous" sonar. For this reason, I began to conduct several tests by which a sea lion was shown a whole dead herring being thrown into the test pool filled with clear water and was allowed immediate entrance into the pool (Schusterman, 1967); Sam, Bibi, and Cathy were used in this experiment. In 10 trials per sea lion, each one showed the same action; the animal swam directly toward the herring (about 25 cm in length) and ate it. After this,

the visibility was reduced by a cloudy substance to a distance of about 10 to 20 cm, and each animal received ten more trials in cloudy water. After draining the pool, from six to nine untouched fish were recovered for each sea lion.

Underwater acoustic monitoring by means of a sensitive hydrophone during clear and cloudy water testing revealed a complete absence of click sounds and other calls by all three sea lions. Additional tests with live fish yielded similar results. In this case, thirty live mudsuckers (about 13 to 15 cm in length) were thrown into a tank of perfectly clear water while sea lion Sam watched the process. Then, the animal immediately entered the tank and caught and ate 18 fish during the first 15-second period, nine during the next 15 seconds, and three during the last six seconds, thus consuming 30 live fish in 36 seconds. The procedure was repeated in turbid water (visibility being reduced to about 20 cm), and when the pool was drained 135 seconds later, 17 untouched mudsucker fish were found, indicating that even though the sea lion foraged more than four times as long in the turbid water than in the clear water, it was far less efficient in the turbid water. To control the sea lion's food satiation in the turbid water condition, the pool was refilled with clear water, nine live fish were thrown into the pool, and sea lion Sam caught and ate them all within 10 seconds. The same experiments with live fish were replicated with two other sea lions and yielded practically the same results. These findings show rather conclusively that *Zalophus* is considerably better at catching live fish in clear water than in extremely cloudy or turbid water. Nevertheless, two of the three sea lions were able to find nearly 50% of the fish without emitting click trains. I presumed that because these live prey are primarily bottom dwellers that the sea lions made an exhaustive visual, tactile, and perhaps chemical search of the bottom of the pool and were able to eliminate the water column in their search for mudsuckers.

Taken together, these combined findings, derived from carefully controlled experiments, demonstrate that the principle function of underwater vocalizations by *Zalophus*, including clicks, is communicative. Moreover, it is demonstrably clear that these sounds are not part of an active biological sonar system used by *Zalophus* under conditions that would logically motivate its use. *Zalophus* has failed to use sonar to discriminate between inanimate objects or when seeking live or dead food fish.

Since my research at SRI on *Zalophus* in the mid-1960s, the notion that amphibious pinnipeds, like the echolocating odontocetes (or toothed whales) or insect-eating bats, also have evolved

a sophisticated biosonar system has been largely discounted. Today, several pinniped species have been observed and studied carefully at research centers, oceanariums, aquariums, zoos, and in their natural habitats. These pinnipeds have been studied by some very bright and highly motivated scientists for almost half a century but to no avail. The behaviors and vocalizations under water have been described, discussed, and analyzed repeatedly. Nevertheless, no researchers have come up with any behavior that appears to fit the sonar model characterized by either odontocete cetaceans or insect-eating bats. Even though one cannot prove the *null hypothesis* (a negative), in order to make scientific progress, one is obliged to ignore possibilities, no matter how enticing, for which there is little or no evidence. Finally, in 2000, my colleagues and I wrote a paper entitled "Why Pinnipeds Don't Echolocate," published in *The Journal of the Acoustical Society of America* (Schusterman et al., 2000). The key points made in this paper are as follows: (1) the retention of aerial hearing abilities for airborne vocal communication by pinnipeds has limited their sensitivity

of hearing under water, where all pinnipeds must forage; and (2) instead of using active biosonar, pinnipeds depend on other sensory capabilities, such as underwater hearing or passive biosonar, enhanced vision, and acute hydrodynamic reception, to orient in the marine environment. These sensory channels have been refined and merged into overlapping perceptual systems that allow different species of pinniped to forage and navigate at sea without the use of active sonar.

In the winter of 1965, I received a letter from Dr. Rene-Guy Busnel, Professor-Director of the Laboratoire de Physiologie Acoustique in France, who, as the director of the organizing committee of a symposium on *Bionic Models of the Animal Sonar System*, was inviting me to present a one-hour paper on my two years of research to determine whether *Zalophus* possesses an active sonar system. I was delighted beyond belief. I could tell a group of highly enlightened scientists in a completely open forum that my tests designed to show the use of active sonar in *Zalophus* had provided only negative results and suggest that, if sonar is operational, then it is rather primitive

Figure 20. Attendees at the *Bionic Models of the Animal Sonar System Symposium* at the Villa Falconieri in Frascati, Italy, 1965

Figure 21. Attendees carefully listening to simultaneous translations of papers at the Frascati Symposium, 1965

Figure 22. Ken Norris as well as some others in our field initially believed that pinnipeds used echolocation. He changed his mind in September 1966 after he heard the author's presentation in Frascati, Italy. As was characteristic of Ken, he saw humor in the presentation and in Poulter's hasty retreat following it and proceeded to draw this cartoon, which he shared with the author in private at the meeting.

compared with that of the dolphin. My story would be pitted against Poulter's in the glaring sunlight of objectivity, and the experts on biosonar, including Ken Norris, Don Griffin, F. P. Mohres, and W. B. McLean, would make their judgment.

The symposium was held at the Villa Falconieri in Frascati, Italy, a suburb of Rome, from 26 September

through 3 October 1966. The lectures and debates would be written in English or French, and there would be simultaneous translation service during the symposium in English, French, and German. It was the first and last international symposium that I attended in which there were simultaneous translations. The scientists I met there were to become some of my closest intellectual buddies during the course of my professional career and included Bertl Møhl of Denmark; Uli Schnitzler and Gerhard Neuweiler of Germany; and Bill Evans, Ken Norris, Don Griffin, Forest Wood, and Scott Johnson of the United States. The days and evenings were chock-full of lectures and discussions, but by 9:00 PM each night, some of us were drinking the wonderful dry white wine of Frascati, and by midnight, we were singing, dancing, telling ribald stories, and generally having a great time at the Villa. There were some 50 invitees, and although Busnel warned us against partying too much, a core group, myself and my wife Roberta included, paid little heed to his admonitions. The Villa's architecture was Etruscan, with an elegant façade and a central portico consisting of three arcades. Much of the wild partying activity occurred at the reflecting pond, surrounded by the giant cypress trees that encircled the Villa Falconieri. At these "pool parties," we frequently dipped into the water and splashed one another with great frivolity. Occasionally, we snuck out of the Villa and went to Frascati. Some of us spoke a little Italian or Spanish, so we got along fine with the town folks. The core group of revelers included Bertl Møhl and Søren Andersen with their wives, as well as Ken Norris, Bill Powell, Scott Johnson, Uli Schnitzler, Gerhard Neuweiler, and Allan Grinnell. One night, when Ken Norris and I were snookered and locked out of the Villa, we ended up throwing

Figure 23. Whitlow Au, Gerhard Neuweiler (seated), Pat Moore, and the author at the Third Animal Sonar Symposium in Helsingor, Denmark, 1986
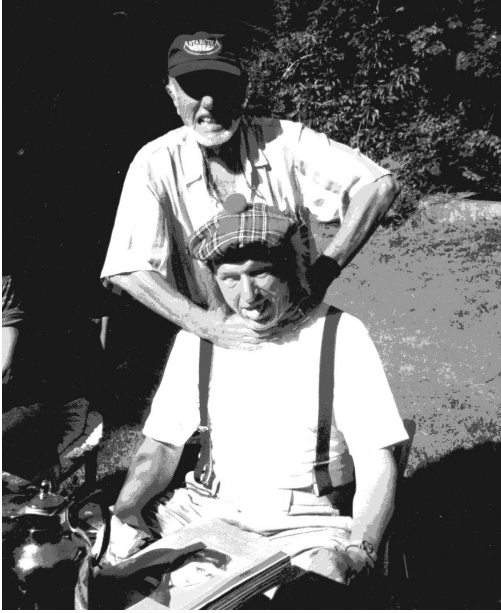
Figure 24. The author jokingly strangling his good friend Bertl Møhl at Bertl's home in Denmark in August of 1999

rocks at Forest Wood's window until he came down and allowed us into the building. At first, "Woody" acted furious about our intrusion, but then Ken and I realized it was just a bluff, and the three of us began laughing uproariously.

Soon after my return from the Symposium in Frascati, I received a stern memo from the VP of SRI Dale Huchison. The note accused me of performing scientific studies that were invalid. Attached to his memo was a letter from Poulter stating that he had inspected my plexiglas targets and noted that they were "identical," and it was therefore impossible for a sea lion to differentiate between the two targets. I was both thrilled and flabbergasted! I explained to Huchison that I used a *paradoxical technique* to test sea lion sonar. Even though the targets appeared visually identical, in reality, one target was solid, while the other contained a pocket of air, the latter thus offering a much stronger acoustic reflection in water. I further noted that, apparently, my efforts to make the two targets visually indistinguishable had been wildly successful, considering Tom Poulter had been unable to tell them apart. I went on to say that if Poulter had bothered to tap the targets with

Figure 25. Francie and Ron Schusterman after ten years of married life, pictured here with "Sprouts," the harbor seal, in their version of a ménage à trois

his finger, he would have heard that one was solid and the other hollow. Poulter was a great scientist in many ways, but he had little humility and could not admit to making a scientific mistake. Perhaps if he had taken a course in Experimental Psychology with either Mort Feinberg or Winthrop Kellogg, he could have compensated for or even overcome his giant character flaw. Deep down, I experienced a wonderful feeling of triumph—tinged with irony—at the role I had played in advancing this fascinating domain of empiric knowledge.

Acknowledgments

Literature Cited

Andrew, R. J. (1962). The situations that evoke vocalizations in primates. *Annals of the New York Academy of Science, 102,* 296-315.

Balliet, R. F., & Schusterman, R. J. (1971). Underwater and aerial visual acuity in the Asian "clawless" otter (*Amblonyx cineria*). *Nature, 234*(5327), 305-306.

Berkson, G., & Schusterman, R. J. (1964). Reciprocal food sharing of gibbons. *Primates, 5,* 1-10.

Bonnot, P. (1951). The sea lions, seals and sea otters of the California coast. *California Fish and Game, 37,* 371-389.

Davis, R. W., Fuiman, L. A., Williams, T. M., Collier, S. O., Haey, W. P., Kanatous, S. B., et al. (1999). Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science, 283,* 993-996.

Dehnhardt, G., Mauck, B., & Bleckmann, H. (1998). Seal whiskers detect water movements. *Nature, 394*, 235-236.

Dehnhardt, G., Mauck, B., Hanke, W., & Bleckmann, H. (2001). Hydrodynamic trail following in harbor seals (*Phoca vitulina*). *Science, 293*, 102-104.

Evans, W. E., & Haugen, R. M. (1963). An experimental study of the echolocation ability of a California sea lion, *"Zalophus californianus." Bulletin of the Southern California Academy of Science, 62,* 165-175.

Feinstein, S. H. (1966). Human hearing under water: Are things as bad as they seem? *The Journal of the Acoustical Society of America, 40*, 1561-1562.

Gentry, R. L. (1967). Underwater auditory localization in the California sea lion (*Zalophus californianus*). *Journal of Auditory Research, 7,* 187-193.

Gentry, R. L., & Peterson, R. S. (1967). Underwater vision of the sea otter. *Nature, 216*(5114), 435-436.

Hobson, E. S. (1966). Visual orientation and feeding in seals and sea lions. *Nature, 210*(5033), 326-327.

Kellogg, R. (1959). Size discrimination by reflected sound in a bottle-nose dolphin. *Journal of Comparative and Physiological Psychology, 52*(5), 509-514.

Kellogg, W. N. (1961). *Porpoises and sonar*. Chicago: University of Chicago Press.

Kellogg, W. N. (1962). Sonar system of the blind. *Science, 137*, 399-404.

Kellogg, W. N., & Kellogg, L. A. (1993/1967). *The ape and the child.* New York: Hafner Publishing.

Kellogg, W. N., & Kohler, R. (1952). Responses of the porpoise to ultrasonic frequencies. *Science, 116*, 250-252.

Kellogg, W. N., & Rice, C. E. (1966). Visual discrimination and problem solving in a bottlenose dolphin. In K. S. Norris (Ed.), *Whales, dolphins and porpoises* (pp. 731-754). Berkeley: University of California Press.

Kellogg, W. N., Kohler, R., & Morris, H. N. (1953). Porpoise sounds as sonar signals. *Science, 117,* 239-243.

Levenson, D. H., & Schusterman, R. J. (1997). Pupillometry in seals and sea lions: Ecological implications. *Canadian Journal of Zoology, 75*, 2050-2057.

Levenson, D. H., & Schusterman, R. J. (1999). Dark adaptation and visual sensitivity in shallow and deep diving pinnipeds. *Marine Mammal Science, 15*, 1303-1313.

Nachtigall, P. E. (1969). Visual size discrimination in the east Asian clawless otter (*Amblonyx cineria*) in air and under water. *Proceedings of the Sixth Annual Conference on Biological Sonar and Diving Mammals, Stanford Research Institute Press, 6,* 83-86.

Norris, K. S. (1964). Some problems of echolocation in cetaceans. In W. N. Tavolga (Ed.), *Marine bio-acoustics* (pp. 317-336). New York: Pergamon Press.

Poulter, T. C. (1963). Sonar signals of the sea lion. *Science, 139*, 753-755.

Poulter, T. C. (1966). The use of active sonar by the California sea lion, *Zalophus californianus*. *Journal of Auditory Research, 6,* 165-173.

Poulter, T. C., & del Carlo, D. G. (1971). Echo ranging signals: Sonar of the Steller sea lion, *Eumetopias jubatus*. *Journal of Auditory Research, 11*, 43-52.

Poulter, T. C., & Jennings, R. A. (1969). Sonar discrimination ability of California sea lion (*Zalophus californianus*). *Proceedings of the California Academy of Sciences 36*, 381-389.

Rice, C. E., Feinstein, S. H., & Schusterman, R. J. (1965). Echo detection of the blind: Size and distance factors. *Journal of Experimental Psychology, 70*, 246-251.

Schevill, W. E., Watkins, W. A., & Ray, C. (1963). Underwater sounds of pinnipeds. *Science, 141*, 50-53.

Schusterman, R. J. (1963). The use of strategies in two-choice behavior of children and chimpanzees. *Journal of Comparative and Physiological Psychology, 56*(1), 96-100.

Schusterman, R. J. (1967). Perception and determinants of underwater vocalization in the California sea lion. In R. G. Busnel (Ed.), *Les systemes sonars aminaux, biologie et bionique* (pp. 535-617). Jouy-en-Josas, France: Laboratoire de Physiologie Acoustique.

Schusterman, R. J. (1968). Experimental laboratory studies of pinniped behavior. In R. J. Harrison, R. J. Peterson, C. E. Rice, & R. J. Schusterman (Eds.), *The behavior and physiology of pinnipeds* (pp. 87-171). New York: Appleton-Century-Crofts.

Schusterman, R. J., & Balliet, R. F. (1969). Underwater barking by male sea lions (*Zalophus californianus*). *Nature, 222*(5199), 1179-1181.

Schusterman, R. J., & Balliet, R. F. (1970a). Conditioned vocalizations as a technique for determining visual acuity thresholds in the sea lion. *Science, 169*, 493-501.

Schusterman, R. J., & Balliet, R. F. (1970b). Visual acuity of the harbor seal and the Steller sea lion under water. *Nature, 226*(5245), 563-564.

Schusterman, R. J., & Balliet, R. F. (1971). Aerial and underwater visual acuity in the California sea lion (*Zalophus californianus*) as a function of luminance. *Annals of the New York Academy of Sciences, 138*, 37-46.

Schusterman, R. J., & Barrett, H. B. (1973). Amphibious nature of visual acuity in Asian "clawless" otters. *Nature, 244*, 518-519.

Schusterman, R. J., Balliet, R. F., & Nixon, J. (1972). Underwater audiogram of the California sea lion by the conditioned vocalization technique. *Journal of the Experimental Analysis of Behavior, 17,* 339-350.

Schusterman, R. J., Gentry, R., & Schmook, J. (1966). Underwater vocalizations by sea lions: Social and mirror stimuli. *Science, 154,* 540-542.

Schusterman, R. J., Kellogg, W. N., & Rice, C. E. (1965). Underwater visual discrimination by the California sea lion. *Science, 150*, 1743-1744.

Schusterman, R. J., Katsak, D., Levenson, D. H., Reichmuth, C. J., & Southall, B. L. (2000). Why pinnipeds don't echolocate. *The Journal of the Acoustical Society of America, 107,* 2256-2264.

Tinklepaugh, O. L. (1932). Multiple delayed reaction with chimpanzees and monkeys. *Journal of Comparative Psychology, 13,* 207-243.

Walls, G. A. (Ed.). (1942). *The vertebrate eye and its adaptive radiation.* New York: Hafner Publishing.

Post-Script
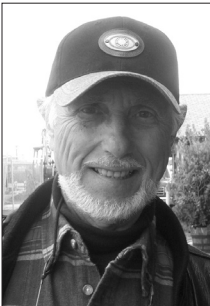
Ron Schusterman passed away on Thursday, February 11, 2010, during the final editorial work on this manuscript. He had suffered from heart disease for most of his life but remained strongly committed to his ongoing writing, research, and other professional commitments through his last days. The material presented in this article was partially drawn from writings for a book that he was working on about his life in science and with animals.

Ron is survived by a loving family, including his wife Francie; his three daughters Marisa, Nikki, and Lesli; his grandchildren Max, Nacho, Danielle, and Alyssa; and his children and grandchildren by marriage, Sarah, Jacob, Isabella, Shawn, and Talia. He leaves behind a close community of friends, colleagues, and students upon whom his influence was immeasurable. He will be dearly missed.

–Colleen Reichmuth, UCSC, Long Marine Laboratory