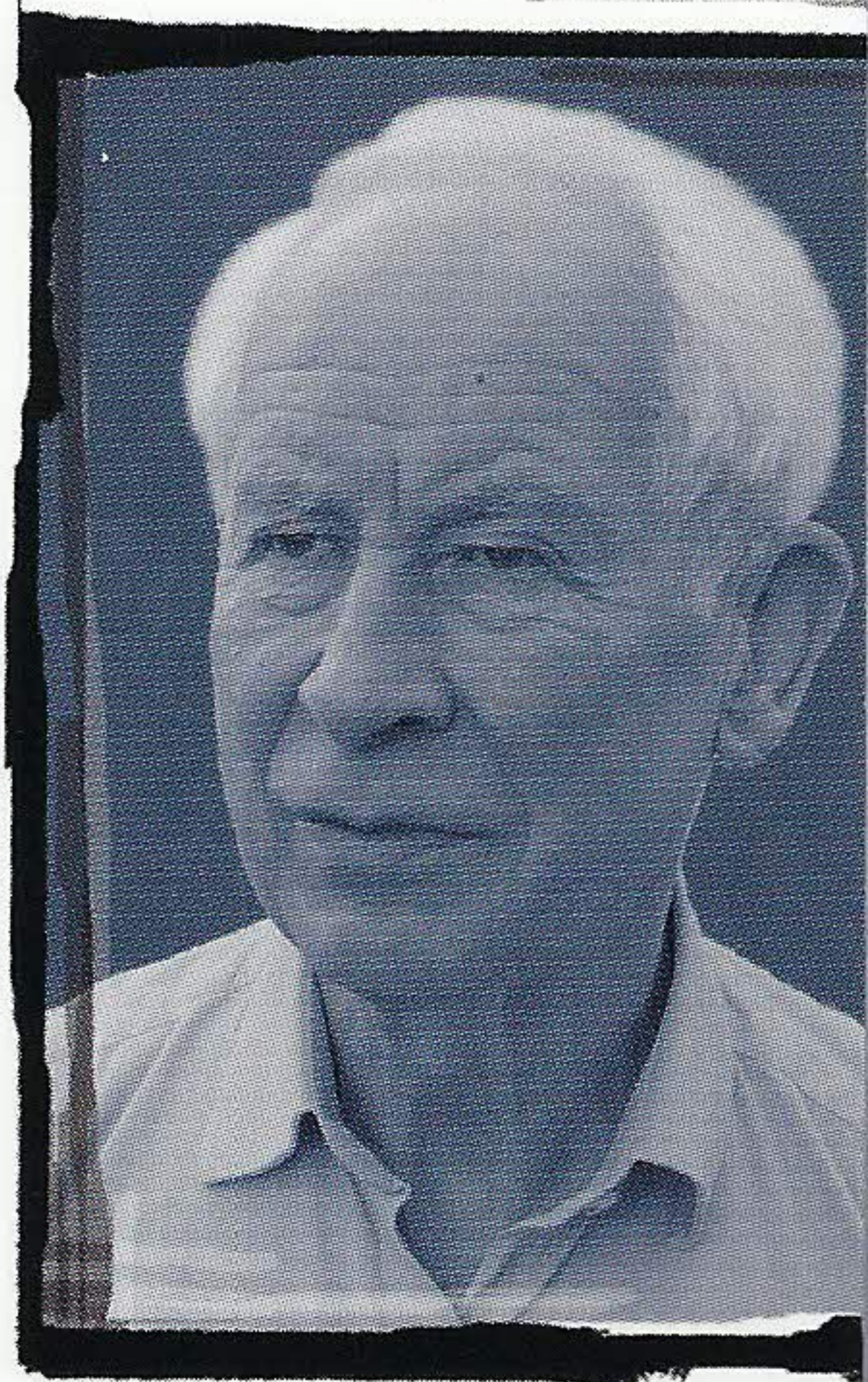
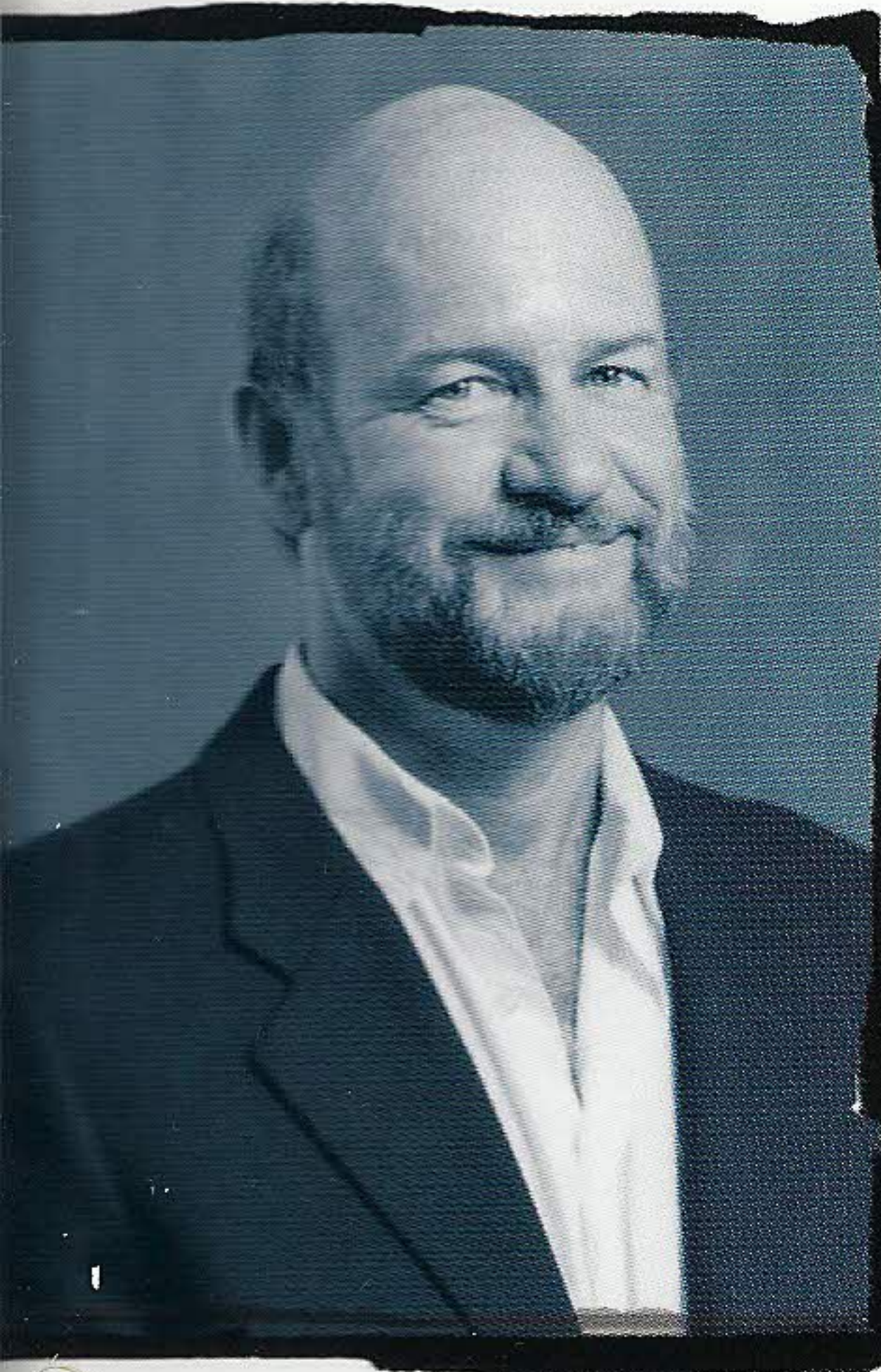


Leaders in Animal Behavior

The Second Generation

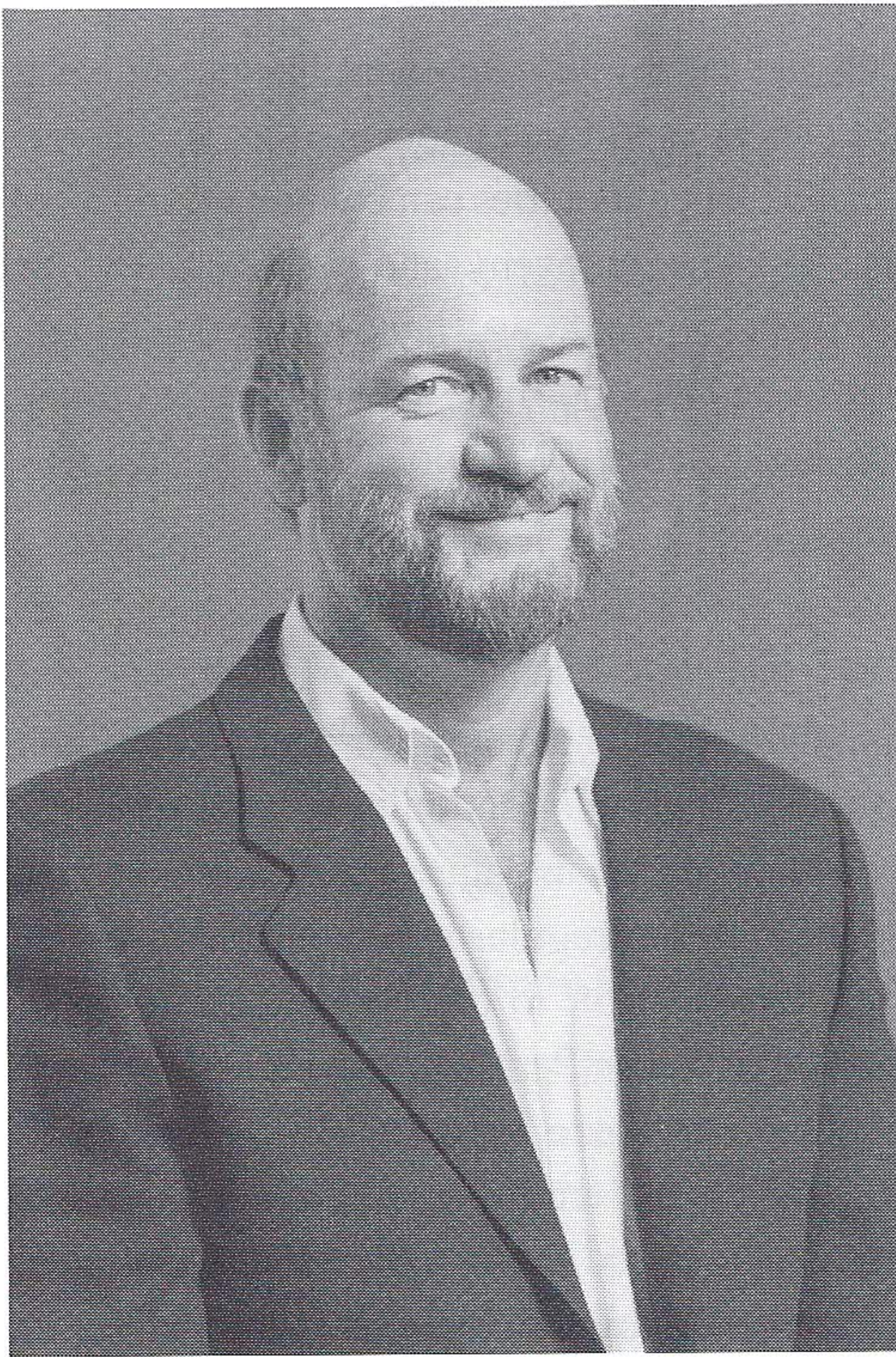


Edited by
Lee Drickamer and
Donald Dewsbury

CAMBRIDGE

An improbable path

MICHAEL J. RYAN



I know who I am and where I am, some idea of how I got here, but no inkling of why. The oldest of 11, the son of a truck driver, I was born in 1953 in the Bronx, born in a place and a time when, as Bruce Springsteen said, “you’re brought up to do what your daddy done”; my current station in life thus seems a most improbable outcome.

The purpose of this chapter is not to review my life. This is a scientific autobiography and the task is to review my science and how I came to do it. Of course, this includes the people and the circumstances that shaped what I do and how I do it. For me, this essay was a joy to write because it has helped me explore how I maintain my childlike fascination with basic

questions of our natural world, and why I am drawn to certain scientific questions. Thus this scientific autobiography is primarily one of interests and ideas.

Asking questions

June 18, 2007, Gamboa, Panama

“Why are the frogs calling so much right now? Why don’t the females call? Why are túngara frogs always in puddles? Why don’t the red-eyed tree frogs make chucks? Why do they leave their children”? I am being bombarded by these “Why, Daddy?” questions from my daughters Lucy and Emma, 11 and 8, as they are once again enthralled by these little calling machines we call túngara frogs. Although this is their first night in Panama this year, it is hardly their introduction. Their joining me for my research here has become a yearly tradition, but their captivation with nature, in general, and these gnomes of the night, in particular, has not waned, nor have their questions ceased. Their inquiries can bounce around all of Tinbergen’s (1963) four questions: causation, survival value, ontogeny, and evolution. The “whys” change to “wows” when they scoop up a foam nest in order to watch the eggs hatch and the tadpoles develop in our apartment. But all of their questions, and mine as well, center around the one larger question Tinbergen proposed in that same paper, “Why do animals behave like they do?” (p. 411).

Starting out

There was no single epiphany sparking my interest in animal behavior, but rather a series of smaller acts of revelation. (Some of this section is taken directly from Berreby (2003) and Ryan (2006b).) I was always interested in nature and in animals. I lived in New York City, in the Bronx, until I was 10. My mother regularly took us to the American Museum of Natural History and my dad often carted us off to the Bronx Zoo; dinosaurs and snakes were the biggest lures at each. I watched Marlin Perkin’s *Mutual of Omaha’s Wild Kingdom*, and this motivated my friends and me to organize our own “safaris”. We would go into the basement of our apartment building and collect empty whisky bottles left there by homeless persons; we ignorantly but affectionately called them hobos. We would become quite familiar with these basements during the air raid drills associated with the Cuban Missile Crisis. We then scavenged the nearby vacant lots hunting grasshoppers. We imprisoned our quarry in the newly acquired ‘collection jars’, counted and then released them. I am embarrassed to say that it never dawned on us to do a mark-recapture study.

In the fifth grade my family moved to rural Sussex County in northwestern New Jersey, and I experienced what was akin to “ecological release”. We were surrounded by forests, and those forests were inhabited by creatures we never encountered in alleys of the Bronx. My brothers, friends and I almost lived in the forest, spending all day hiking, looking for animals, and sleeping under the stars as we were serenaded by the nocturnal choruses of insects and frogs. Hunting and fishing were big parts of those years. When I first encountered a formal biology course in high school my interests were well primed.

I attended a Catholic high school and had a wonderful biology teacher, a Benedictine monk, Father Patrick Bonner. From there I attended a small state college in Glassboro, New Jersey, to become a high school biology teacher. Reading and criticizing the primary literature in an ecology class taught by Roger Raimist revealed that the scientific process was accessible to mere mortals. I had two other classes that had an important influence on me, herpetology and animal behavior. The professor was Andy Prieto, who became a good friend and who steered me toward graduate school before I had ever even seen a graduate student. While at Glassboro I also joined the 'biology club'. This was shortly after Earth Day was founded, and to many of my friends in this club, biology was synonymous with environmentalism. We spent most of our time outdoors learning the flora and fauna of the serene and somewhat odd environment of the nearby Pine Barrens. I also was one of three students chosen to accompany Prieto on a trip to the Galapagos Islands. It was my first time out of the country, my first time on an airplane since I was two, and my first time in the tropics. That trip left a lasting impression; how could it not?

My senior semester of student teaching high school biology could not have been more rewarding. I loved teaching and I had an excellent rapport with the students. I had the good fortune of being assigned to a high school near the campus, within walking distance of my house and, critically, where discipline was not a problem. This made it more difficult to choose between graduate school and high school teaching. What made it more even more tempting was an offer from my old high school, Pope John XXIII, to teach biology and coach baseball. When I turned down the teaching job they offered me part-time of just coaching baseball. That was even more difficult to walk away from.

Trying out graduate school

I decided to enter a Master's program in graduate school. If I decided that graduate school was not for me, the MS degree would still contribute to my teaching credentials and ensure a slightly higher salary. I entered Rutgers University, Newark (NJ), in 1975 under the mentorship of James Anderson.

I did not receive any financial support when I began. Newark was a commuter's campus and still devastated from the race riots of the 1960s. It was an awful place to live and I had little luck finding affordable housing anywhere near by. So I lived with a friend in the peace and serenity of the forests of Sussex County, which I have always loved. It meant a 40 mile commute to campus along interstate 80, a main thoroughfare into New York City. But I found that if I left my house by 5 AM, eating my breakfast as I drove, I could avoid much of the traffic. Gas prices at that time were much lower, and I have my father's truck driver's genes, so driving was never a challenge.

Together with another graduate student, Clark Keller, I did some contract work cleaning out abandoned houses in Newark to support myself. Soon afterward, however, Anderson received a contract to determine the reptiles and amphibians that should be granted protected

status by the State. He hired several of us on this contract and my job was to determine the range and status of the blue spotted salamander, *Ambystoma laterale*, which was known from only one small area in the northwestern part of the state. Any rainy nights that winter and spring were spent 'road running', driving up and down roads to intercept the salamanders as they migrated from the woodlands where they usually reside to the wetlands where they breed.

During that work Jim Anderson and I discovered a salamander previously unknown to the State. *Ambystoma tremblayi* is an all-female gynogenetic species associated with *A. laterale*. These two taxa and another sexual-aseexual pair, *A. jeffersonianum* – *A. platineum*, are sometimes considered a hybrid swarm. Gynogenetic species are usually of hybrid origin and are clonal. But they have an odd "sexual" requirement: they need sperm to trigger embryogenesis. I could not wrap my head around this odd system. Why would these species not become extinct? Why would males of the sexual species waste their time, energy, and sperm on a clonal female? I didn't study these questions in the salamanders, but I pestered my advisor by not letting go of them. It would be 20 years before I did some research on this topic.

When I began at Rutgers it was clear that I wanted to do a thesis that combined herpetology and animal behavior. Lizards seemed the most social of the herps, but Anderson took me to the Great Swamp National Wildlife Refuge, in the area where we found the *Ambystoma* salamanders, to see a chorus of bullfrogs. It was a stunning experience. Large males with bright yellow throats were emitting a near-deafening call that sounded like "jug-a-rum". They were vigorously defending their territories and when another male intruded they would clasp each other face to face and have a wrestle off. Females were smaller and without yellow throats, but a lot of the frogs lingering on the territories that we thought were females were actually mature but younger males adopting an alternative "satellite" mating strategy. I had found my MS thesis topic.

I studied the bullfrogs for two seasons, 1976 and 1977. I received my first grant, from the Theodore Roosevelt Memorial Fund of the American Museum of Natural History, one of the places that nurtured my early interests in biology. Most of the money went to purchasing a more reliable flashlight and a box of batteries; research was simpler then. My main goal was to document the relationship between territoriality, mating strategies and mating success. What really caught my interest, though, was the frog's mating calls.

There are about 5000 species of frogs. Typically, males produce mating calls that females use to identify and evaluate mates and which also serve in male-male interactions. The Modern Synthesis of Evolutionary Biology put a great emphasis on speciation, and the role of mate recognition as a premating isolating mechanism was a prominent contribution of behavior. Frank Blair's research had demonstrated how the species-specific nature of the anuran mating call resulted in reproductive isolation between species, and Robert Capranica's studies had begun to show how the frog's auditory system decoded conspecific calls. All of this being the case, I was impressed with how different the males all sounded from one another. These males are territorial and males tend to be in the same place each night. As I checked the location of the males I had marked with numbered bands I placed around the waists, I realized that I often could identify a male by his voice. I had decided that

after my study of territoriality in bullfrogs I would investigate their communication system, and I would specifically ask whether variation in the males' mating calls influenced their attractiveness to females. I was not yet aware of the intriguing notion of sexual selection.

The Zoology Department had an interesting group of faculty for students interested in herpetology. Jim Anderson was a field biologist, ecologist and evolutionary biologist; Dan Wilhoft a physiologist; and Sam McDowell an anatomist and taxonomist who could draw diagrams of anatomy with both hands simultaneously. There was also a new faculty member from Cornell University, Doug Morrison, who brought sociobiology and behavioral ecology to the department and instantiated in me an early fascination with bats that would later reach fruition.

Another great resource for me was the Institute of Animal Behavior (IAB). The Institute had gained a large degree of fame at this time under the leadership of Danny Lehrman, who passed away shortly before I arrived. Lehrman was well known for his studies of the hormonal mechanisms underlying courtship behavior in ring doves, and for his influential critiques of Konrad Lorenz's theories of instinct. At my time Jay Rosenblatt, who studied behavioral development in rats, was the Institute's director, and there were two faculty in field behavior, Monica Impeken and Colin Beer. The Institute was a different sort of place; it had both the air and the reputation of elitism. There were only a small number of students; all of them received full fellowship support for their entire graduate school career, and they seemed to have little interest in interacting with those in zoology – or so I was warned. The Institute could only be reached through a private elevator to which only IAB members had keys, and there were no classrooms, just a lounge with a kitchen where their informal classes were held.

I took two classes at the Institute, Rosenblatt's course on behavioral development, and Impeken's course on social behavior. Regretfully, my teaching duties kept me from taking Beer's ethology course, but I was able to use his Kay Sonograph to start quantifying variation in the bullfrog's mating calls. I also attended many of the seminars at the Institute, and spend some time there socially. I was always welcome, and at one point I was, in a sense, invited to the high table – I was given my own elevator key! Many years later, when I returned to the Institute to give a seminar, it truly warmed my heart when Colin Beer introduced me as "one of our own".

Things could not have gone better at Rutgers. I eventually received a TA and I was excited as much about teaching as about research. Jim Anderson and I became very close friends, and when I decided to transfer to the Ph.D. program in my second year he gave me his full and enthusiastic support. That all ended quickly, however. Jim and the students who were working on the endangered species project all attended a town meeting of citizens concerned with planned development in the Great Swamp region. We were hoping that the presence of threatened *Ambystoma* salamanders in the area might cause the State to halt the development. Anderson gave a wonderful presentation of island biogeography theory as an argument against habitat fragmentation. When the meeting ended we all went our separate ways. It was the last time I saw Jim. He died in a car crash on the way home. Ironically, the NY Times reported the next day on conservation easements in California that were being made

to allow salamanders to pass under highways during their migrations. They credited Anderson's studies while he was a student at the Museum of Vertebrate Zoology at the University of California, Berkeley, in motivating these improvements.

Anderson's death was devastating to all of us, not just his students but the entire biology community at Rutgers. He was only in his 40s when he died, full of life and energy, and the most respected person in our department. I had never lost someone so personally close to me, and I was at a loss what to do next, refusing even to discuss it for weeks on end. Doug Morrison became my sponsor, my mentor, and also a close friend. He convinced me that I needed to go to Cornell to be at one of the epicenters of the new sociobiology and behavioral ecology.

Starting graduate school, again

After some delay on their part, I was finally accepted at Cornell into the Section of Neurobiology and Behavior (NB&B). My advisor was Kraig Adler, who was studying amphibian orientation. Kraig is a herpetologist and, luckily for me, was willing to take students who used reptiles and amphibians for subjects for a variety of studies. For that I am eternally grateful. Cornell was a wonderful place, and NB&B an exciting and initially intimidating department. In that small faculty of 15 or so, there were three members of the National Academy of Sciences: Tom Eisner, Bill Keeton and Dick O'Brien.

Cornell was a perfect match for my interests. There were two key faculty members whose research complemented my interests in animal communication and mating behavior. Robert Capranica was a neuroethologist with a lab full of grad students and postdocs trying to understand how the frog's brain decoded acoustic signals. Steven Emlen, one of the founding figures of behavioral ecology, is best known for his studies of avian social behavior but he had also just published a seminal paper on lek organization in bullfrogs. Adler, Emlen, Capranica and Bill Brown, who years before with E. O. Wilson published a groundbreaking paper on reproductive character displacement, would come to constitute my doctoral committee. Cornell was a different place than Rutgers and a different species from Glassboro State College.

I had never been around graduate students like those at Cornell. As with most programs, that is where most of your learning takes place. Adler had three other graduate students at the time: Gordon Rodda, who was working on alligator orientation and went on to do conservation biology with US Fish and Wildlife; Bruce Waldman, who initiated an entire research field with his discovery of sibling recognition in tadpoles, a general topic that he continues to study today; and John Phillips, who initiated a quest he still follows, understanding how animals use the earth's magnetic field in orientation. Other graduate students at that time were Eliot Brenowitz and Steve Nowicki, who both study the neurobiology and behavior of bird song, Gary Rose and Harold Zakon, who now both study the neural basis of communication in electric fish, and Pepper Trail and Doug Lank, who were students of bird behavioral ecology. In retrospect, Cornell offered a very competitive but a very cooperative atmosphere. We all knew we were in a special place, at a special time, and surrounded by

