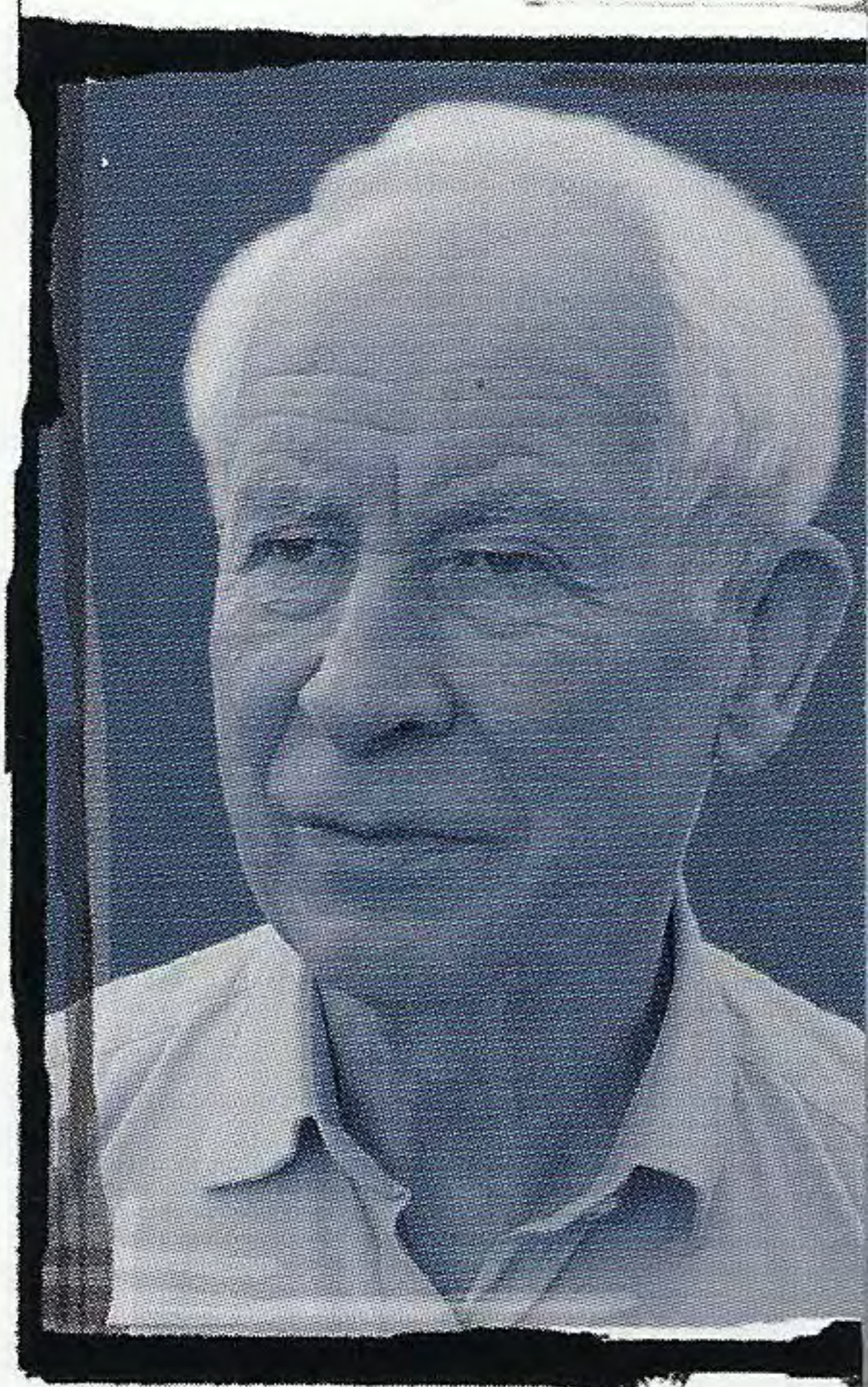
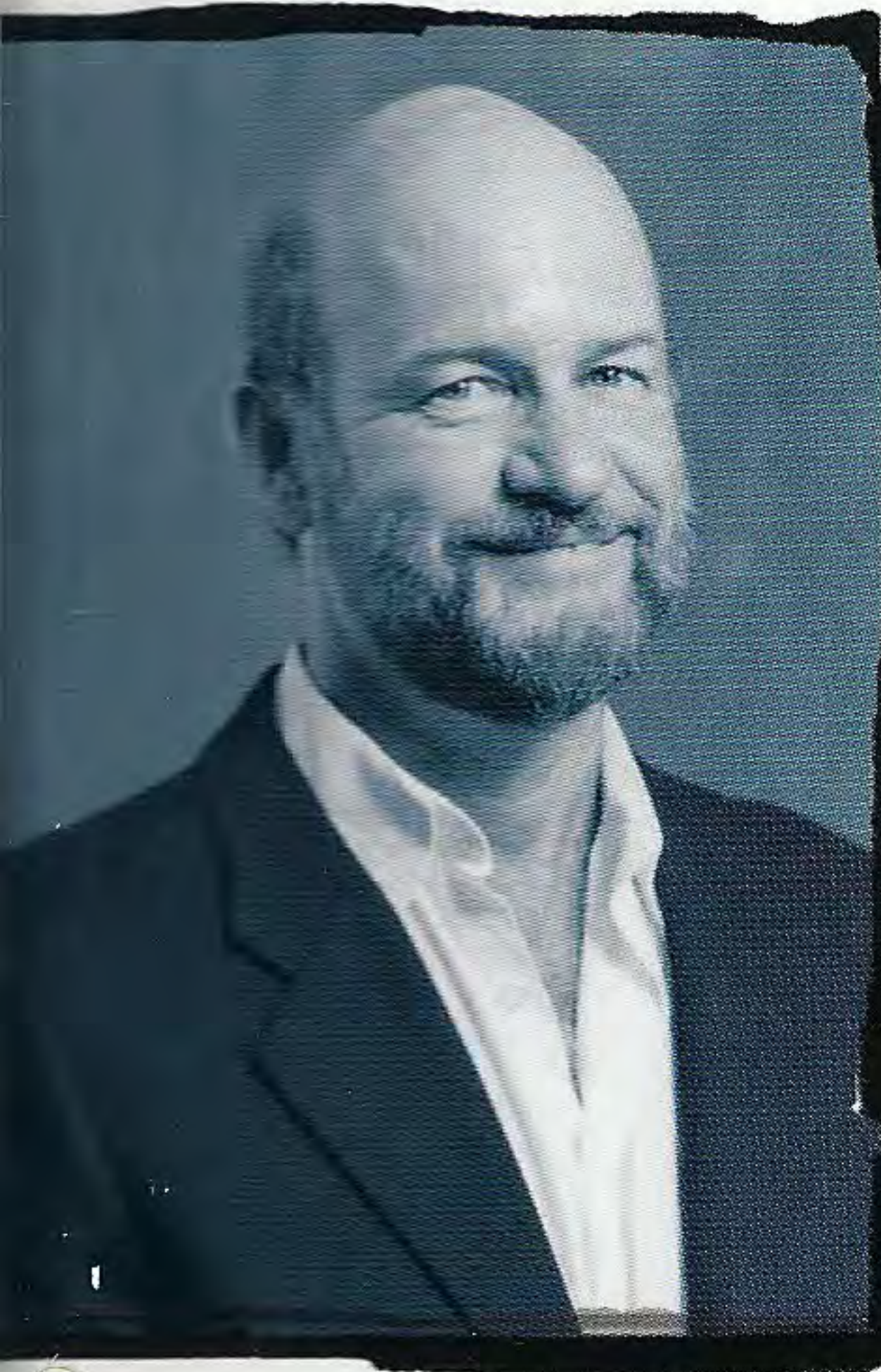


Leaders in Animal Behavior

The Second Generation



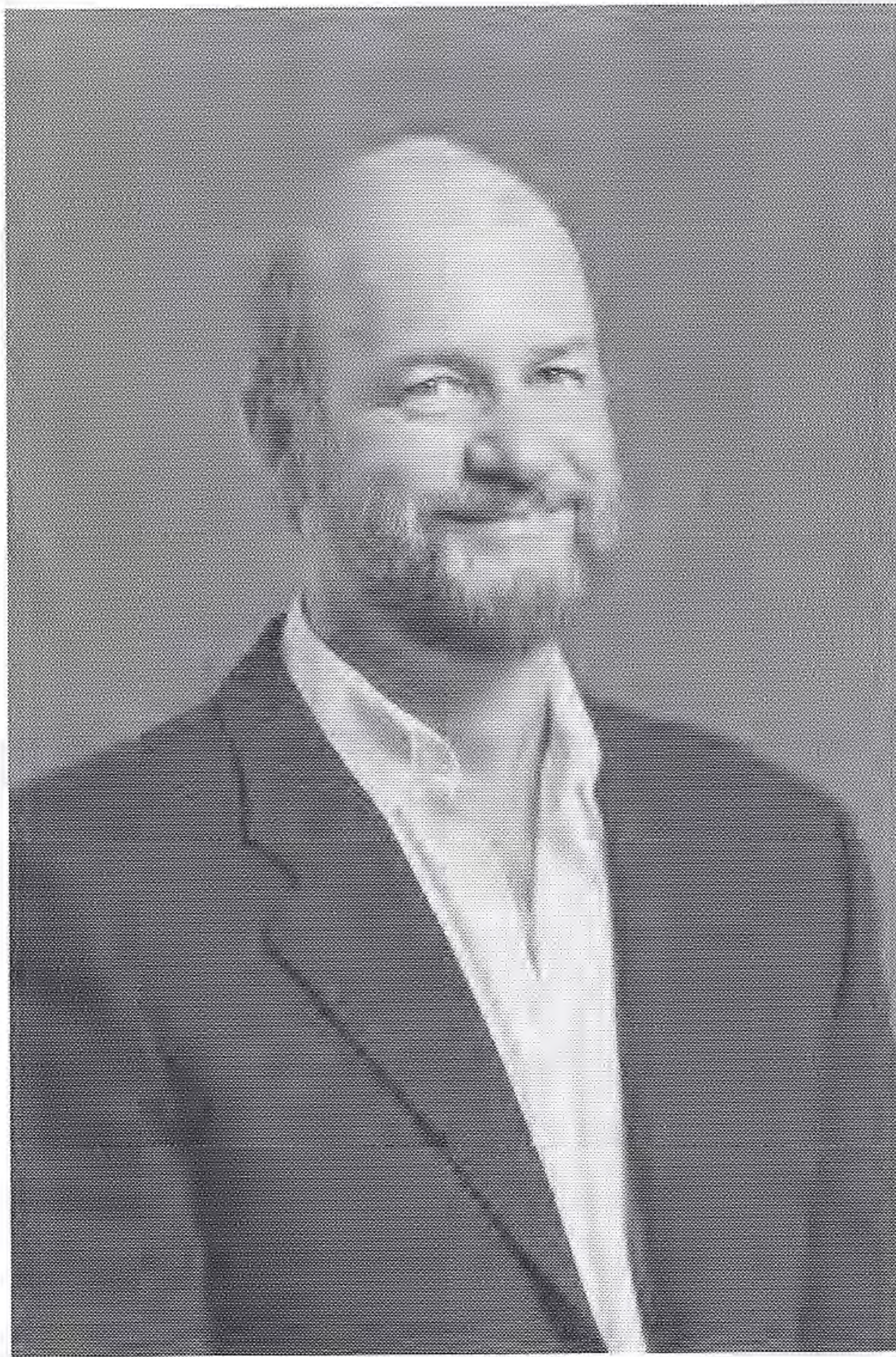
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CAMBRIDGE

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-asexual 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

special people, both faculty and other graduate students. We all wanted to show we deserved to be there but the competition was all directed inward. Students were always ready to help, discuss, and debate research, and most everyone was close.

There were two courses at Cornell that had an immediate and lasting impact on me. Bob Capranica and Ron Hoy taught *Animal Communication*. It was my first experience in having a course taught by some of the researchers who actually defined the field. The emphasis was integrative. It covered the physics of signals, signal production, and the neural decoding of signals as well as a few topics in behavioral ecology. But it was probably most memorable for its emphasis on Fourier analysis and information theory. This course made me aware of numerous research tools in the field of animal communication and for the first time made me aware of how important it was to have an understanding of mechanisms to truly grasp the totality of animal behavior. The animal communication course I teach today is modeled after that one. The other course that first year was *Vertebrate Social Behavior* taught by Steve Emlen. Steve had just published with Lew Oring a seminal paper in *Science* on the evolution of mating systems (Emlen & Oring 1977) and had made a number of other critical contributions to the fledgling field of sociobiology. His enthusiasm for the subject was contagious, he was an engaging lecturer, and, as if any of us needed to be convinced, he hooked us on the excitement of social behavior. There were other important courses for me that year as well. A symposium on animal communication had a series of invited speakers who gave public lectures and then attended a reception and spent a couple of hours in discussion with the students taking this course. Carl Sagan and Jane Goodall were among the stellar line-up of lecturers.

I also took a field course that introduced me to tropical biology. With Ruth Buskirk and Glenn Hausfater, a group of first- and second-year graduate students visited Guanacaste and Monteverde in Costa Rica, and Barro Colorado Island in Panama. Although I did a project on thermoregulation in an iguanid lizard (*Ctenosaura*) for my independent project, my most memorable experience was watching the diurnal mating behavior of the *Atelopus* frogs. Bright green and fearless, these frogs sat atop rocks in small streams in the forests of Monteverde, chirping their hearts out for females. I had never seen a diurnal frog nor one that was so accessible to the researcher; nothing at all like the bullfrogs I had studied. They are no more, however, having been among the early victims of the world-wide amphibian decline. On Barro Colorado Island (BCI) we hiked through the forest and were amazed by the capuchin monkeys who threw sticks at us from the canopy, the morpho butterflies that glided in front of us but seemingly could never be caught, and the red-capped manakins that flashed colors and clicked their wings as they flitted through their leks. At dusk we were about to hurry down the flight of 200-plus stairs to the dock to board the boat to Frijoles and then the train into Panama City. One of my friends came running from behind the Kodak House. She yelled, "Mike, come here, look, a frog lek!" It was a group of túngara frogs whining and chucking – this was even before they were widely known as túngara frogs. I had no idea what this was to portend (Figure 17.1).



Figure 17.1. A calling male túngara frog, *Physalaemus pustulosus*, with a small *Corethrella* fly. (photo by Santiago Ron).

STRI and túngara frogs

I had a pretty clear idea of what I wanted to study for my research. Robert Trivers' paper on parental investment and sexual selection (Trivers 1972) and Emlen and Oring's paper on the evolution of mating systems were bringing sexual selection into the forefront of sociobiology. Still, at that point there was scant evidence that variation in male display behavior had any influence on female mate choice. Darwin's notion of aesthetic preferences in females received little support from other evolutionary biologists, including his "bulldog" Thomas Huxley. Julian Huxley (1938) and that great herpetologist G. Kingsley Noble (Noble & Bradley 1933) bemoaned the lack of any evidence for female mate choice based on intraspecific variation in display traits. Darwin himself did not seem convinced that one could ever provide evidence of this phenomenon.

But then again, I thought, why did all these bullfrogs sound so different from one another? Variation in signals does not require that there be variation in their meaning, but this signal variation suggested that the males' calls might be perceived by the females as quite different from one another. Bullfrogs, however, did not seem to be the ideal species for such a venture. Their breeding season was too short and they seemed intractable for experimentation. I wanted to work in the tropics where the breeding seasons of many frogs extended throughout the long months of the rainy season, and to work with a smaller frog with whom I could do experiments. I scoured the literature and came across an account of red-eyed tree frogs, *Agalychnis callidryas*, which seemed to exhibit lekking behavior. I submitted an application for a short-term fellowship to the Smithsonian



Figure 17.2. Embarking for a 1990 field trip to the mountains of western Panamá (from left: Debbie Greene, Walt Wilczynski, Stan Rand, Mike Ryan, Kyra Mills, Ulysses [uncertain of last name], and Frederico Bolanos).

Tropical Research Institute in Panama to conduct this study on BCI. This was right before my Cornell trip to the tropics, and before I saw the *túngara* frogs on BCI.

I received the short-term fellowship. Before traveling to Panama to begin my thesis research I attended the meetings of the Herpetologists' League in Tempe, AZ. I presented a talk about my bullfrog studies, for which I received an award for the best student talk (the first of three I received), and I met Stan Rand, who gave a talk on vocal communication in *túngara* frogs, *Physalaemus pustulosus*. At that point, Stan had published only one paper on these frogs, on nesting behavior, and Stan was calling them mud puddle frogs (Figure 17.2).

I soon arrived on BCI and it was all I remembered it to be, except magnified: the overpowering green of the forest, the sounds of social interactions of innumerable animals, and the odors of the flowers advertising their goods. All of my senses were assaulted with diversity. It did not take long to find a sizeable population of treefrogs. I chose one in the lab clearing, near the small cement pond behind Kodak House that Stan had built years ago to study *túngara* frogs and where I had seen my first *túngara* frog lek. This would allow me to study the behavior of the treefrogs and have access to nearby facilities where I could do experiments. The problem was with the treefrogs. As their name might imply, much of their life is lived in the trees, often above 3 m or more above the ground. The frogs descended to the water to deposit their eggs as pairs already mated, and the act of mate choice was difficult to observe. And these damned cat-eyed snakes kept eating their eggs! (Much later, with no input from me, my graduate student Karen Warkentin made a wonderful career showing how the eggs detect such intrusions and how they fight back.) Red-eyed tree frogs were also a pitiful choice for a study of acoustic communication. Their calls are of fairly low amplitude, and the din of the then bothersome chorusing *túngara* frogs at my feet made it all but impossible to record the mating calls of the treefrogs.

I decided, with Stan's permission, to switch my study to túngara frogs. Stan had not studied them for many years and had not published his basic work on their calling behavior. At that time he was deeply involved in fascinating studies of iguana and crocodile behavior with Gordon Burghardt.

Stan's earlier unpublished studies provided a critical foundation for my work. He had shown that males produce a call with two components, a whine to which chucks could be added. Males added chucks, up to six of them, in response to calls from other males. Females preferred whines with chucks to whines without chucks.

The studies of the túngara frogs posed other challenges but soon began to proceed fairly smoothly. By summer's end I had data showing that females choose their mates with little interference from males, larger males were more likely to be chosen as mates, and there was a significant negative correlation between male body size and the fundamental frequency of the chuck. This latter effect was known in some frogs, has since been shown in numerous others, and is simply due to larger males having a larger vocal apparatus that vibrates at a lower frequency.

Before leaving Panama at summer's end I talked to Stan about continuing my studies of túngara frogs for my Ph.D. thesis and he was quite supportive. I presented my preliminary data to my Cornell committee and they approved it, and I remember being especially pleased that Capranica and Emlen were enthusiastic. If I could have paused at that point 30 years ago and peered into the future I would have seen that the associations I was to now solidify with STRI, with Stan Rand, and with the túngara frogs would be the center of my scientific life for decades to come.

I spent the next year at Cornell writing grants to return to BCI. I received both a long-term STRI predoctoral fellowship and a dissertation improvement grant from the National Science Foundation. I was on my way.

Túngara frogs, tractability, and technology

Túngara frogs were a near-perfect system for my study of sexual selection and communication. It is a bit easier to quantify male mating success in frogs than in many other animals. Birds were then and still are now the paradigmatic taxon for behavioral ecology. In birds the mating act is a "cloacal kiss". The male mounts the female, their cloacas touch, and males transfer sperm. In some species this takes but a few seconds. In most frogs, the male clasps the female from the top and they usually remain in this state, amplexus, for hours. In túngara frogs, the pair also constructs a foam nest. The process takes about an hour, they usually begin nest construction towards the end of the night when chorusing has begun to subside, and they frequently do so out in the open in conspicuous places.

Túngara frogs are also quite tractable when it comes to marking and monitoring the behavior of males, recording their calls, and conducting preference tests. The frogs are small, about 30 mm in length, and they call in pools of water often in clear view, their calls are loud, and their vocal sac makes them quite conspicuous. After some practice in the dark, it is easy to locate a microphone on a stand within about half a meter of a frog and

have it resume calling fairly quickly. Thus recordings of frog calls are very clean; the caller is easily identified compared to others with whom he is chorusing, and the signal:noise ratio is high. The greatest advantage of studying frogs, however, is the ability to test experimentally female preferences for male signals using the phonotaxis paradigm first used by Martof and Thompson (1958). In these experiments, a reproductively primed female is placed between two speakers that are opposite one another, each broadcasting a stimulus antiphonal to the other speaker. The female usually begins the experiment under a cone in which she can hear the calls and is allowed to acclimate. The cone is then lifted and the female approaches one of the speakers. In nature, females only approach a male's call when searching for a mate. Furthermore, frog calls, compared with bird song, are relatively simple and thus can be more easily synthesized by the addition of various sine waves, a type of reverse engineering in which the call is deconstructed into sine waves with a Fourier analysis and then analogous sine waves are synthesized and combined to synthesize the call.

When I returned to Cornell after my first summer on BCI I talked to Capranica about synthesizing calls. I wanted to test the hypothesis that the large-male mating advantage derived from female preferences for lower-pitched calls. He had his research associate Ann Moffat help me. We did the synthesis in a large room filled with sine wave generators, wave shapers, and a variety of other machines I couldn't identify. They were all linked together with cables, and it was hard to fathom at first sight how all these sounds combined through this spider-web-like network could deliver a synthetic whine-chuck call onto the tape recorder. Ann, however, was as expert in explaining call synthesis as she was in doing it. The usefulness of the knowledge I gained was short-lived, however, as the affordable computing age dawned. This was brought home a few years later when I saw Capranica give a talk on animal communication methods. He showed a slide of that same room filled with sound equipment, the walls teeming with wires and blinking oscilloscopes, and a large Kay Sonograph dominating one of the corners of the room. The next slide was of the same room but it was nearly bare. In the center of the room was a small table with an Apple computer. This was the future. All of the signal analysis and synthesis which was the purview of only large and rich labs was now available on a much smaller, cheaper scale to anyone with a few hundred dollars.

The technology, or lack of it, at STRI then is still hard to imagine. STRI had one computer in the entire Institute. It was in Panama City, part of an environmental science monitoring project. STRI generously let me use it for a few hours on Sunday afternoons. There was no software; I had to write programs in BASIC for all the statistics I used. There was no screen, just an LCD panel that displayed one line at a time, so I would have to print out the entire program to debug it. There were no floppy disks; all the data had to be entered on punch cards. So each Sunday morning, I would fill my backpack with punch cards, a BASIC manual, and a statistics book and take the boat across Gatun Lake and wait for the train into Panama City. The train almost never arrived on time, and sometimes didn't arrive at all. But waiting by the lake, in an open field surrounded by tropical forests and everything that came with the forests, made a late train seem like a treat.

Technology has been a blessing in recording signals. At that time, I used a Nagra tape recorder. Even now when I occasionally use one, to digitize some old reel-reel tapes, I am amazed by their incredible precision and smooth operation. But they weigh 17 lbs! I recorded calls of most of the frogs and numerous other animals on BCI those three years; the frog calls constitute much of the CD that accompanies Ibanez *et al.* (1999). More than once in the pursuit of a sloth or monkey vocalization I unintentionally rode down a muddy hill on my back in the rain clutching a Nagra to my chest. Those are rugged machines – more rugged than me, I hate to admit.

Back to BCI

... it is obviously probable that [females] appreciate the beauty of their suitors. It is, however, difficult to obtain direct evidence of their capacity to appreciate beauty.

(Darwin 1871, p. 111).

Female choice and male mating success

I spent the next three years or so on BCI. I continued to monitor female choice and male mating success, this time for most of an entire breeding season. On each of 152 consecutive nights I measured, toe-clipped, and marked with observation tags all new males and females that were present, remarked any frogs that had lost their tags, and determined who mated each night. Over that time I marked and observed 617 males and documented 751 matings. At the same time I began to conduct female preference tests. I tested the hypothesis that the large-male mating advantage, which was even more strongly supported by the second and larger data set, resulted from preference for chucks having lower fundamental frequencies.

In the first series of experiments I gave females a choice between synthetic calls, courtesy of Moffat and Capranica, which had chucks of fundamental frequencies near the two extremes, indicating small and large males. There was a preference for lower calls of larger males, offering strong support for sexual selection by female choice. As far as I knew, this was the first experimental demonstration that female choice could generate sexual selection. I wanted to be sure the manuscript was strong, thus I asked a large number of key people in the field to read it for me: Kraig Adler, Steve Emlen, Carl Gerhardt, Hank Howe, Bert Leigh, Stan Rand, Bob Trivers, Kent Wells, and Mary Jane West-Eberhard. The care was worth the effort. It was accepted by *Science* and published in 1980 (Ryan 1980).

The rest of the time studying túngara frogs concentrated on quantifying variation in mating success during the longer sampling period, conducting more female choice tests to titrate the range over which females discriminate, and doing various experiments, some successful but with many failures, to determine what benefits accrued to females choosing larger males.

Energy costs of calling and the inspiration of George Bartholomew

When túngara frogs add chucks to their whines the calls become more attractive. When they are calling in a chorus pretty much all of them produce chucks, but when a male is by himself he usually only produces a whine. If complex calls are more attractive, why not always make them? I knew there must be a cost, and I began to explore this question.

One advantage of working at STRI is the constant stream of visiting scientists who work at the various field sites and labs. A regular visitor to BCI during my time there in the late 1970s was George Bartholomew. Bart was one of the founders of the field of environmental physiology. He was also one of the most integrative of the biologists I had known, and he defined the terms of gentleman and scholar.

Bart's work on moths had hit some stumbling blocks during his visit. I approached him and his graduate student Terri Bucher and asked whether they would be interested in measuring the energetic costs of calling in túngara frogs, and specifically to test the hypothesis that complex calls incur an additional energetic cost. Stan had planted this bug in Bart's ear previously, suggesting that they measure the cost of visual displays in anolis lizards. We showed that there was a substantial increase in the rate of oxygen consumption, and thus energy expenditure, during calling but it was no more expensive for a male to make a chuck than not. This was the first direct estimate of metabolic cost of a sexual display in a vertebrate. Although we did not pursue this line of research much further, measuring the energetic cost of calling in frogs became a small cottage industry for some time.

Predation costs, Trachops, and Tuttle

It seemed crucial that we continue our attempts to understand why males do not always make the most attractive call. In 1976 Robert Jaeger published a short note in *Copeia* in which he reported that large marine toads, *Bufo marinus*, were dining on túngara frogs in Kodak Pond on BCI. He suggested that the túngara frogs' calls were luring the toads. Jaeger did not comment on the simple versus complex calls of the túngara frogs, but in light of Peter Marler's paper about the relationship between call structure and function (Marler 1955), Stan and I both thought that chucks made advertisement calls easier to locate – for both females and potential predators. I tried and failed with experiments to show that marine toads were attracted to túngara frog calls. Then an amazing thing happened. Stan Rand received a letter from Merlin Tuttle, a bat researcher. The year before Tuttle had captured a bat, *Trachops cirrhosus*, with a frog in its mouth (Figure 17.3). Merlin was returning to BCI in the dry season (January) to begin a study to determine if the bats were homing in on frog calls. He wanted to know if there was a herpetologist on BCI who might be interested in helping.

Like most frogs, túngara frogs do not breed in the dry season. Instead of returning to Cornell for the dry season, as I had originally planned, I decided to stay and work with Merlin. This was a collaboration made in heaven. Merlin's interest was from the prospect of bat foraging, not surprisingly since I always thought Merlin was part bat anyway. My

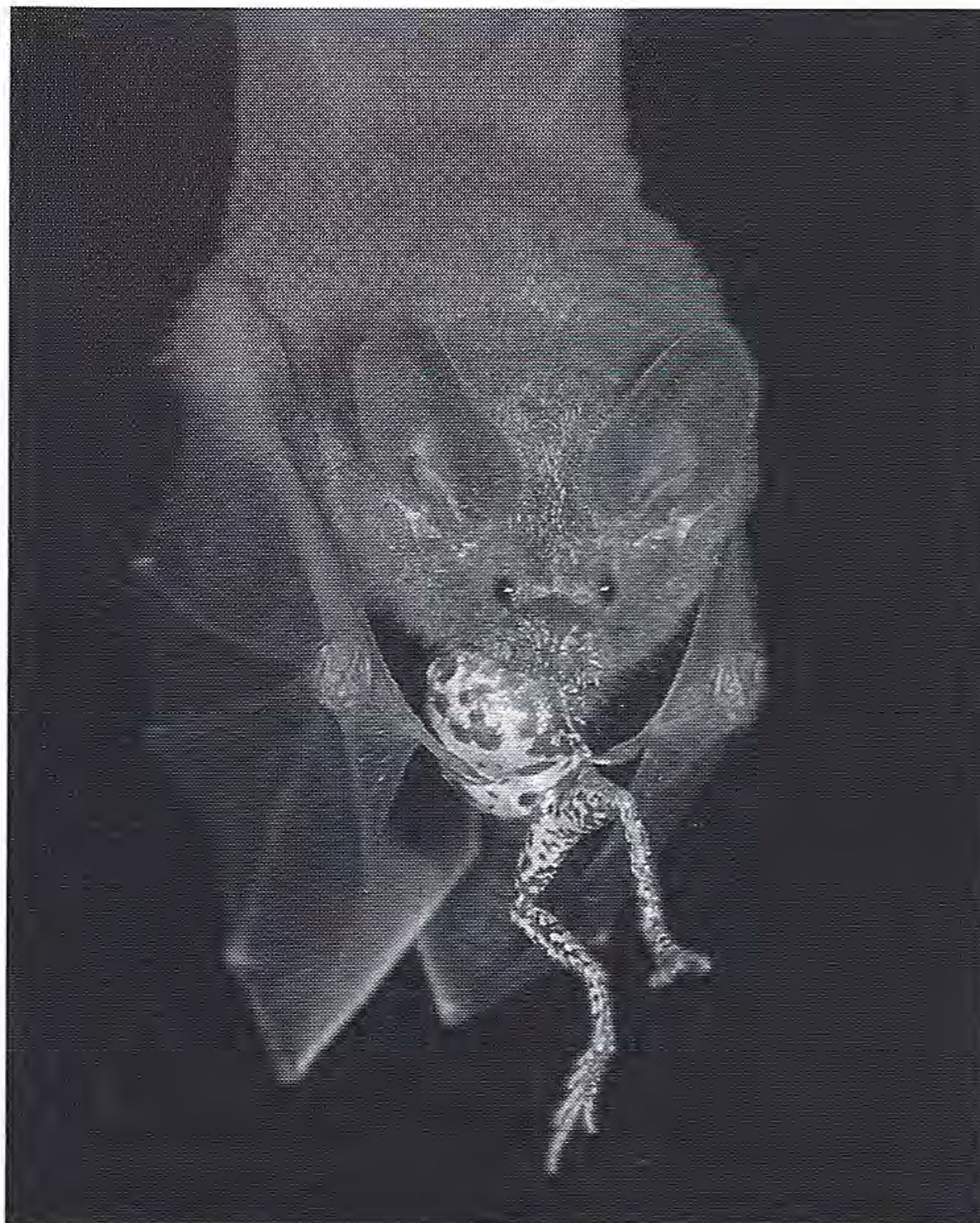


Figure 17.3. A frog-eating bat, *Trachops cirrhosus*, with a túngara frog (photo by Alexander T. Baugh).

interest, of course, was from the frog's point of view, especially the túngara frog's point of view. Merlin is an incredible bat field biologist, and I have rarely met anyone with such a feel for their study animal. Joined with my interest in the frogs, animal communication, and sexual selection, we formed a good team.

In a week or so we had successfully netted some *Trachops* on BCI and had them in a flight cage. Merlin taught me how to net bats and how to train *Trachops* so they would eat from my hand, and introduced me to most of that incredibly diverse chiropteran fauna on BCI. After the *Trachops* became habituated we tried our first experiment. We placed two speakers in opposite corners of the flight cage and played a túngara whine from one side and a whine-chuck from the other. The bat immediately left its perch and landed on the speaker playing the whine-chuck! We were elated. But that was the last bat to respond for weeks! We kept changing details of the experiment and the flight cage but the bats would not leave their perch. Ernst Mayr, who was on BCI at the time, suggested that we might be feeding the bats too much. We are not sure why, but the bats again began to respond and hardly ever stopped. Our first publication, in *Science* in 1981 (Tuttle & Ryan 1981), was on the general phenomenon of bats responding to frog calls and their ability to discriminate between palatable and non-palatable frogs and between small and large ones. We then published a paper in *The American Naturalist* the next year showing that the bats preferred the túngara frogs' complex calls over simple ones (Ryan *et al.* 1982). So it was now clear that when males add chucks to increase their attractiveness to females they do so at the risk of increased predation by what we now refer to as frog-eating bats.

Almost not leaving STRI, and leaving STRI, for a time...

I began to get ready to leave BCI in the summer of 1981 after almost three years on the island. That was a heady time to be on BCI. The number of scientists working there was impressive enough, but STRI would often bring other visitors solely for the purpose of enhancing the intellectual climate there. Mary Jane West-Eberhard and Bill Eberhard were doing pioneering work in sexual selection. Although STRI staff they lived in Costa Rica but regularly visited Panama. Ernst Mayr, John Maynard Smith, Amotz Zahavi, and Robert Trivers all visited the island for various lengths of time. As I said, Mayr was interested in our *Trachops* work and offered some good advice on keeping the bats motivated. Maynard Smith wrote his Game Theory book on BCI. I was in charge of the beer machine, so needless to say he and I became quite close. Zahavi was quite clever in how he could explain much of the behavior of túngara frogs in terms of the handicap principle, and he had me chasing one of those ideas with experiments for some time. Trivers was at STRI for a year to write his social evolution book and was always quite encouraging. If these intellectual giants were to visit a university, graduate students might be able to join them for a lunch and ask a few questions. But being on BCI they were a captive audience.

For many who work on BCI the dream is to never leave. That dream almost came to fruition. Ira Rubinoff, the Director at STRI, was away on sabbatical and Mike Robinson, who later became the Director of the National Zoo, was the Acting Director. I received a message that he wanted to see me in his office in the city. I had no idea what it was about. After asking me how I liked it at STRI he offered me a job there. The idea was that I would be the staff scientist on BCI once I received my Ph.D at Cornell. It was a total shock, and even Stan Rand seemed to have no inkling of the job offer. I immediately accepted. But due to a variety of bureaucratic issues and hiring freezes the offer had to be withdrawn. So off I went back to Cornell.

Finishing a thesis and starting a book

While on BCI I received a letter from an editor at the University of Chicago Press, Susan Abrams. She said that she had heard about my work with túngara frogs and suggested that I write a book. I had given this some thought. I was doing some very different kinds of studies with túngara frogs and I thought there might be some advantage to putting all of this work together in one place. Not everyone thought this was a good idea at this stage in my career. Some members on my thesis committee thought that I should be concentrating on primary research and publishing papers, not rehashing research in a book form. Steve Emlen was one of the few who recommended that I go ahead with the project.

Another goal that year was my research on neurophysiology. My plan was to characterize the auditory sensitivity of the túngara frog by recording from the eighth auditory nerve. I had become interested in what I was calling a "neuro-neutral" theory of sexual selection, which I will return to later, and these data would be helpful in exploring that concept. Capranica was on leave that year and my work in his lab just didn't go well. But as I learned years later from

Walt Wilczynski, these frogs are small and it is a real chore to record from their auditory nerves. Even an expert such as Walt retreated from the eighth nerve to the bigger target of the mid-brain to get some insight into what these frogs were hearing.

In addition to writing my thesis and working in Capranica's lab, I needed to find employment for the next year. I had three potential avenues. One was to do a postdoctoral fellowship with Eugene Morton at the National Zoo. Gene had been one of the founders of the field of habitat acoustics in animal communication. He had shown that the songs of many birds evolved to match the acoustic features of the habitat to enhance signal transmission over long distances. I wanted to ask similar questions about frogs. I didn't receive that postdoc; years later Gene told me that as the ornithologist at the zoo he was expected to sponsor students working on birds, not frogs. My second option grew from my interest in a fellowship from the Miller Institute for Basic Research in Science at the University of California, Berkeley. These fellowships were quite prestigious and well salaried and provided the opportunity to be mentored by one of the science faculty at Berkeley. The fellowships also came with great independence and freedom. Dr David Wake is a well known evolutionary biologist at Berkeley who had done classical work on evolution with salamanders, mostly from a morphological and developmental perspective, and he agreed to sponsor my application.

The third avenue for employment was to apply for faculty positions. In January of 1982 (I was 28), I interviewed at the University of Texas in Austin. They were filling five jobs that year and I was the first of many to be interviewed. There was an ice storm while I was there. While I was in Austin, Dave Wake called to let me know that I would be awarded a Miller Fellowship. So at least I had employment for the next two years, and that removed some of the pressure of the interview. I think it also upped my ante there. With the hiring of five new faculty in one year, they seemed to welcome a potential hire who would not come for another two years; they told me if I were hired I could first spend two years at Berkeley. Eventually I was told that I had the job. When I gave that news to George Bartholomew, he told me not to make a decision right yet as I was going to be interviewed at UCLA. I was then offered that job as well. The chance to have Bart as a colleague was a huge temptation, but I thought that the quality of non-academic life for me, given my life style, would be better in Austin than Los Angeles. I might have been right about that choice, but I'll never know. I have been very happy in Austin and in the course of my career, and I have also been honored to have offers from the University of Chicago, the University of California at Davis, and another offer at STRI. All of those institutions are of very high quality and peopled with outstanding researchers in my field. Whether each decision was the best one doesn't really matter; what matters is that life has been good for me in Austin.

As soon as my thesis was defended I started to work on my book, and made substantial progress during the summer. The main purpose of the book was to weave together the various studies on mating systems, communication, and costs of calling, much of this already published in specialty journals and some not yet published. A new idea in the book was what I awkwardly termed the "neuro-neutral model". The idea was fairly simple. Females preferred calls with lower fundamental frequency chunks. The lower the fundamental the closer in frequency the

harmonics, thus these calls might squeeze more energy into the frequency window to which the inner ear is sensitive. Greater acoustic stimulation should lead to greater neural stimulation and perhaps increase the attractiveness of the call to females. The general notion was that males are under selection to find ways to increase the sensory stimulation of females. If mutations arise that increase call attractiveness, this could lead to the evolution of more effective displays that might not be related to other components of male fitness, such as overall survivorship. That is, attractive displays need not be reliable indicators of good genes or other attributes of survivorship. The females mating with these males would produce “sexy sons”, and it is possible that this process could initiate runaway selection. But it also seemed clear that runaway selection would not be required either. This idea is a derivative of West-Eberhard’s sensory trap and was the beginning of the idea I later called “sensory exploitation”.

I sent the first draft of my book to Peter Marler and asked him to write a foreword. I didn’t know him well, having only talked to him at any length only once when as a grad student I gave a seminar at the Rockefeller University field station in Millbrook. But I considered him the preeminent animal behaviorist of his time. Needless to say, I was thrilled when he agreed. Peter wrote a wonderful essay on how recent changes in the field of animal behavior towards evolutionary biology were critically important, but unfortunately this paradigm shift also led to the abandonment of studies of mechanisms at the field’s own peril. He thought the túngara frog system was an example of how one could integrate evolutionary and mechanistic topics.

I finished my book while I was at Berkeley and *The Túngara Frog, A Study in Sexual Selection and Communication* was published by the University of Chicago Press in 1985 (Ryan 1985), right after I arrived at Texas. The elation of having the book published was followed by substantial trepidation waiting for the first review. All scientists receive peer reviews of the manuscripts they submit to journals, but these are private and not published, which is not true of book reviews. That first review appeared in *Science*, and gave high praise: “this is a careful, creative, and informative study that is likely to become a classic of its kind” (Andersson 1986). Other laudatory reviews followed.

As with many things, writing a book took longer and was more work than I had imagined. But it was a smart decision to do this. It brought together otherwise disparate studies to make clearer the links between them. It highlighted the usefulness of integrative studies, and made the túngara frog system well known for studies of sexual selection and animal communication. Because of policies of The University of Chicago Press, I was not allowed to acknowledge the support and friendship of their science editor, Susan Abrams. She was a superb editor, interested in everything, and had wonderful maternal instincts. Until she died a number of years ago she was a fixture at many meetings and seemed to be everyone’s friend. She certainly was mine.

It’s Miller time!

It is hard to imagine a better postdoctoral situation for me than my time at Berkeley. My sponsor, Dave Wake, believed that Miller Fellows should have total intellectual freedom and

not tied to the research or lab of the sponsor. And what a place to be free! The Museum of Vertebrate Zoology (MVZ), where Dave was the director and I had my office, was a wonderful community where most everyone met for coffee each morning and had their own seminar series once a week. I became friends with all of the scientific faculty, including Dave Wake, Harry Greene, Jim Patton, Bill Lidicker, and Ned Johnson, and many of the graduate students, especially Claudia Luke. The Department of Zoology, housed in the same Life Sciences Building, was packed with outstanding scientists. George Barlow was a well-known behaviorist and I attended behavior seminars that included him, Thelma Rowell, Frank Pitelka, and Roy Caldwell.

The intellectual emphasis at Berkeley, and especially in the MVZ, could not have been more different than Cornell. Sociobiology had just been birthed and Cornell was one of its birthing places. Most of the graduate students and faculty in behavior at Cornell were focused on understanding the adaptive significance of behavior. As Emlen often pointed out, the field was young and theory outstripped data. Many of the faculty at Berkeley, especially Dave Wake, were interested in another new field, evolutionary development, or "evo-devo," and were extremely cautious about accepting hypotheses of adaptation that did not consider the importance of constraints. Rather than being on the bandwagon of sociobiology with Wilson, Trivers, and Hamilton, they seemed more impressed with the criticisms of sociobiology being sounded primarily by Stephen Jay Gould and Richard Lewontin. For me, this led to no intellectual discomfort but a healthy dialectic. Although at Cornell I was schooled by some of the luminaries in sociobiology, such as Steve Emlen and Paul Sherman, I was also exposed to neural mechanisms of behavior by folks like Bob Capranica and Ron Hoy. So I appreciated the need to consider constraints on adaptation.

Another development that was paralleling the field of sociobiology was the rebirth of phylogenetics. Publication of Hennig's *Systematics* book in English gave rise to the push for cladistics on the North American continent. There were some students at Cornell (John Rawlins and Jim Carpenter) who were doing this on their own, but they were in entomology and our intellectual circles intersected only briefly. In NB&B we knew little of any of this. At the MVZ, however, phylogenetics reigned supreme. I began my Miller with a firm foundation in behavioral ecology and the mechanisms of animal behavior. I left with an appreciation for phylogenetics and its techniques, and I began to understand how I would apply this approach to studies of behavior. Although I didn't realize it at the time, the last link to what would become my interest in integrating studies of brain, behavior, and evolution was in place.

I made good use of my freedom at Berkeley. I finished up my túngara frog book, I took a course in quantitative genetics, read some books on phylogenetics, attended numerous lectures, and taught a sexual selection seminar with Frank Pitelka. I returned to bullfrogs briefly with Paul Licht and one of his graduate students, Mary Mendonca, studying the hormonal basis of alternative mating behaviors. I did some work in Panama studying habitat acoustics of a large number of species of frogs, and with Eliot Brenowitz reanalyzed

Morton's classical study of habitat acoustics in birds, emphasizing, perhaps not surprisingly, the importance of morphological constraints and phylogenetic history.

I also spent nearly half a year in Kenya with Merlin Tuttle on a memorable trip studying *Cardioderma cors*, a bat that was reported to eat frogs. This is a microchiropteran bat in the family Megadermatidae, a different family from *Trachops*. We thought that, like *Trachops*, they might be using frog calls as localization cues; if so, it would be a wonderful example of convergence and allow for a series of interesting comparative studies. We did most of our work on the coast, south of Mombasa, where these bats were numerous.

We had a fantastic field assistant in Kenya, Paul Koboche. He was a well-rounded naturalist, could speak most of the languages there, and was incredibly educated about African history. I learned much from him and we became very close friends. I met some of his children and we talked about how when I had my own children I would return and we would all go on safari. We had some adventures in Africa. One was a very close call in the Tsavo when we were charged by an elephant. Paul was driving our Land Rover while Merlin and I were standing in the back as the elephant charged. When the elephant got close, too close it ended up, we yelled for Paul to take off. He popped the clutch and stalled the truck. The elephant pushed the truck and Paul thought that its "nudge" push-started the stalled vehicle, allowing him to speed away just in time to avert disaster. Paul later went on to become a well known conservationist in Kenya.

Paul and I had often talked about my returning to Kenya in the future and we would revisit many of the places we worked with our families. Tragically, a number of years ago he was killed by an elephant in Tsavo.

Merlin moved to Austin, Texas, in 1985, a year after I started at the University of Texas. He became the full-time director of an organization he had founded, Bat Conservation International, which also goes by the acronym of BCI. So one BCI brought us together and another BCI kept us together. Unfortunately, Merlin and I have become so busy with our respective jobs that our paths do not cross as much as either of us would prefer.

At Berkeley I also met Ted Lewis in the engineering school. I knew his work on neuroanatomy of one of the frog's inner ear organs, the amphibian papilla. This organ had a frequency-place map, and its size varied drastically from a simple patch of tissue in the most primitive frogs to a much larger horn-shaped structure in the more modern anurans. If the sensory epithelium is larger then there should be more room to sense sounds of different frequencies. Thus these frogs should be able to hear a greater range of frequencies or there should be more frequency resolution. Capranica had some data suggesting it was the former. With these data in mind, I wrote a paper for *Proceedings of the National Academy of Sciences* suggesting that neuroanatomy can influence speciation. The idea is simple: the range of sensitivity of a receiver can limit the amount of meaningful mutations in a signal. Since the divergence of recognition systems usually occurs with speciation, then speciation should be more likely when divergence of recognition systems is more likely. The paper was accepted in *PNAS* (Ryan 1986).

Beginning at Texas

During my time at Berkeley I was already looking forward to interacting with scientists at the University of Texas, in part because of Mark Kirkpatrick's arrival as a Miller Fellow at Berkeley. He was working on theoretical models of sexual selection, and has always had a knack for simplifying mathematical explanations, so he was a great help in furthering my understanding of the population genetics of sexual selection. He arrived during my second year as a Miller Fellow and was immediately interviewed for a job in the Zoology Department at the University of Texas. He was offered it and accepted. So for the year we overlapped at Berkeley we knew we would both be at Texas. We are both still here.

I was hired with a group of four others in the Zoology Department at the University of Texas. Jim Bull, an evolutionary biologist, and Harold Zakon, a fellow graduate student from Cornell and a neurobiologist who works on electric fish, are still there. Matt Winkler is a molecular biologist who eventually left to found the company Ambion. John Rawlins, also a fellow graduate student from Cornell, who eventually left to join the Carnegie Museum, introduced systematics to much of the department. To me, having just come from Berkeley, he was preaching to the choir.

In general, our teaching was one course a semester, an undergraduate course and a graduate course. My undergraduate course was *Vertebrate Natural History*, which was a wonderful way to be introduced to Texas and to spend lots of time in the field with students. Eventually I traded that course for *Animal Behavior*. For my graduate course I developed one in *Animal Communication* with Harold Zakon. The course was modeled on the one that both Harold and I took with Capranica and Hoy at Cornell. Eventually Walt Wilczynski and I taught that together for a few years. I then changed it into an undergraduate course with a full lab and a requirement for independent projects. This has been a popular course with a full enrollment each time I teach it. For me the teaching has two important values. The first and most important is the interaction with students. The second is the rather clichéd feeling that you don't understand something until you teach it.

Swordtails

At Berkeley, George Barlow had told me about a thesis from Stanford University in which the researcher manipulated the sword length in swordtail fishes (*Xiphophorus*) to examine its influence on mate preference. The basic idea was that male displays seem to be supernormal sexual stimuli, and the swordtails might offer a way to investigate the phenomenon. This rung true in its relation to the neuro-neutral model I had considered for túngara frogs, and I became increasingly interested in incorporating these fish into my research at the University of Texas. Swordtails and platyfish (*Xiphophorus*) are an important model for studies of melanoma. As luck would have it, the UT Cancer Research Center was within an hour's drive and one of its scientists, Don Morizot, was an evolutionary geneticist who worked with these fish. I drove out to meet him and he told me that amazing story of the *P* gene.

Breeding studies by Klaus Kallman showed that in several *Xiphophorus* there were polymorphisms in male body size, and size was genetically passed from father to son. In one species, *X. nigrensis*, there were three body size classes: small, intermediate, and large. In a close relative, *X. pygmaeus*, there were only small males. This raised a number of obvious questions for a behavioral ecologist: Did the size classes differ in their mating behavior? Were small males sneakers and large males courters? Were there genetically determined mating strategies? How was this genetic polymorphism maintained, and how did female mating preferences figure into all of this? And what about that species with only small males?

At that point there had been no studies of the behavioral ecology of swordtails. There were some excellent laboratory studies done in Germany on dominance hierarchies. This suggested that there might be some difficulties in studying these fish, but Morizot assured me that was not the case, and he and Klaus Kallman had wondered why this system had evaded the interests of behavioral ecologists. They invited me on a trip to Mexico and introduced me to these fish in the wild.

Although I was now intrigued by the role of *P* genes in the swordtail mating system I still wanted to pursue the role of the sword in mating preferences. A graduate student of mine, Bill Wagner, spent some time attaching false plastic tails to males but we could never show that it influenced female preference in *X. nigrensis*. It seemed we had chosen the wrong species, as another graduate student, Gil Rosenthal, later showed that *X. nigrensis* only had a very weak preference for swords. At the same time, however, there was another graduate student, Alex Basolo (who later married Bill Wagner), studying sex ratio evolution in *X. helleri*. Alex tried these same experiments attaching false tails to species with and without tails and was quite successful (Basolo 1990). In fact, she has made a career of such studies.

In *X. nigrensis* we showed that small males chased females, large males courted them, and females preferred the latter. But what about *X. pygmaeus*, the species with only small males? These males exhibited the “alternative” mating strategy of sneaking even though there are no large courting males. And the females? They prefer large courting males of the closely related but allopatric *X. nigrensis* to their own small non-courting males. Thus they retain the preference for large size and courtship that was lost in this species. We published this work in *Science* in 1987 (Ryan & Wagner 1987), and it made clear to me how important it was to consider the evolutionary history of a species to really understand its current behavior.

Studies of swordtails continue to be a part of my research program, especially as researchers are getting closer to sequencing the *P* gene and understanding its functional significance. The behavioral ecology of swordtails has also become the main focus of a former graduate student and two former postdocs of mine. Gil Rosenthal, a leading expert on the behavioral ecology of these fishes, is now working on olfactory communication and hybridization. He also bought his own field station in prime swordtail habitat. Molly Morris is continuing to work on signaling behavior as well as phylogenetics in swordtails, and Molly Cummings brought her intricate knowledge of visual ecology to bear on these fishes. Another former postdoc, Deborah McLennan, still works occasionally on this system, and always with intriguing results.

Mollies

Since I had worked with gynogenetic salamanders I had been intrigued by their maintenance. Gynogenetic females mate with males of other species. If they cannot do so, they become extinct. If they are too good at it, they could drive the other species to extinction and follow them closely into oblivion. A gynogenetic fish that faces the same challenge is the Amazon molly. They associate with the sailfin molly in the northern part of their range, which includes Texas.

I met a German undergraduate, Ingo Schlupp, at the first International Herpetological Congress in Canterbury, England, in 1989. I had just started to study mollies; Ingo planned to do his thesis on mollies and needed lab space in Texas. I offered him space. He later did a postdoc with me, and he continues to use both my lab and my house as a base for this research, which he continues as a faculty member at the University of Oklahoma. He is one of my closest friends.

Ingo and I walked across the UT campus one day in 1994 reviewing the basic assumptions of the gynogenetic mating system. One was that males of the sexual species did not receive any benefit from mating with asexual species since there was no fertilization. It then struck me that there might be a partial solution to this dilemma. Lee Dugatkin had shown mate-choice copying in guppies: females alter their mating preferences upon observing the mate choice of other females (Dugatkin & Godin 1992). If this were to happen in mollies, then a male sailfin molly mating with an Amazon molly might obtain delayed benefits if this seemingly wasteful act made him more attractive to his own females. We teamed up with Cathy Marler, one of my postdocs. In a matter of a few weeks we conducted the experiments, which did indeed show mate-choice copying, and the paper was accepted in *Science* (Schlupp *et al.* 1994). It was the fastest time from idea to publication in which I had ever been involved.

Cricket frogs

I was hired at UT to replace Frank Blair. He had made fundamental contributions on the role of frog mating calls to species isolation, but his health was in decline then and we had little opportunity to converse. After he passed and I moved into his office, I found a manuscript by Evitar Nevo and Bob Capranica. I had been meaning to read it when I got a call from Walt Wilczynski. Walt had been a postdoctoral associate with Capranica while I was finishing up at Cornell and was hired by the Psychology Department at UT while I was at Berkeley. I thought Walt would be a valuable colleague at UT but I never envisioned how critical a collaborator and close a friend he would become over the next two decades. Walt was calling me to say that Capranica sent him a manuscript he wrote with Nevo on geographic variation in cricket frogs (it was eventually published (Nevo & Capranica 1985)). It was mostly an analysis of cricket frog calls throughout its large range in North America. There were some phonotaxis tests and no neurobiology. In that paper they pointed out that there are two subspecies of cricket frogs in Texas that meet at the border of the grasslands and piney

woods in east Texas. They referred to the subspecies as “incipient species”. Usually, studies of species recognition compare well established species. But there has been a lot of evolution that can affect mate recognition once speciation is complete. Differences between species now might have played little or no role in the process of speciation. Studying an ongoing process might add some insights.

In our first study, which appeared in *Science* in 1988 (Ryan & Wilczynski 1988), we showed that there was geographical variation in call dominant frequency, some but not all of this variation was due to variation in body size, and this was correlated with tuning of the frog’s inner ear. The correlated variation among populations resulted in local mate preferences which could provide grist for the mill of speciation.

The cricket frog work also led to interesting Ph.D. theses by Bill Wagner and Nicole Kime. Bill showed that males can alter their call’s dominant frequency during male-male encounter as a bluff of body size. Nikki showed that the graded series of call complexity in which initial calls of the call bout were shorter and subsequent ones increasing in duration were not, as we had thought, a gradation from male aggressive to more attractive calls. Much still remains to be learned here.

Back to túngara frogs

I had not worked with túngara frogs for a few years since I had finished my Ph.D. thesis, but Stan Rand and I remained close friends. In 1985 I was in Washington, D.C., at the Smithsonian Institution’s Natural History Museum and went to visit Stan, who was on a sabbatical leave there. Studies of the acoustic bases of mate preferences were only a small part of my thesis work. I had continued to be interested in what mechanisms of mate choice could tell us about sexual selection: the neuro-neutral model with the túngara frogs, the effects of neuroanatomy of speciation in frogs, the preference for phenotypes long lost in swordtails. I had been thinking of returning to work on túngara frogs and concentrating on understanding the details of how and why females were more attracted to acoustic variation. I told Stan about this and he said he had moved to Gamboa, a small town on the Panama Canal, and suggested we work together there.

We did the first experiments in 1987. This was before STRI acquired the joint lab/living quarters, Building 183, in 1988. We performed phonotaxis experiments in the same small portable chamber that Stan used in the 1960s and that I used for my thesis work. We conducted the experiments on a concrete slab under the apartment I was staying in. It worked most of the time, but whenever a bus rumbled past, the frogs leapt wildly and we had to scratch the experiment.

In 1988 STRI began slowly turning Gamboa into a research site. The first move was to acquire a building that had labs downstairs and apartments upstairs. Stan had an acoustic chamber built in his frog lab where we could conduct our experiments under well controlled conditions, and we repeated all the experiments we had done the year before. The “frog lab”; to which I still have access even after Stan’s passing thanks to the immense generosity of

STRI, has been upgraded considerably and has been the control center for our túngara project for two decades now.

Sensory exploitation in 1990

When male animals utter sounds in order to please the females, they would naturally employ those which are sweet to the ears of the species; and it appears that the same sounds are often pleasing to widely different animals, owing to the similarity of their nervous systems.

(Darwin 1872, p. 91)

The study we began under a garage in Gamboa in 1987 was published in *Evolution* in 1990 (Ryan & Rand 1990). The gist of that study was that details of the frog's auditory biology can predict acoustic components that are going to be more attractive. Frogs have two inner ear organs that are sensitive to air-borne sound, the amphibian papilla and the basilar papilla. Walt Wilczynski had shown that in túngara frogs the AP is tuned to about 500 Hz and the BP to about 2100 Hz. There is substantial processing of signals by the brain, of course, but in most frogs the inner ears act as filters that initiate call analysis.

With this knowledge in hand, we were able to synthesize calls that were much simpler but just as attractive as the real male call. The first point was that the details of the female's sensory system, through their influence on female choice, generated the selection under which male calls evolved. If males could evolve display components that were more stimulatory to the female, they were perceived as more attractive and thus favored by sexual selection. Rephrased, male display traits can evolve under sexual selection for sensory exploitation. This is what I was getting at with the "neuro-neutral" model in my túngara frog book. Another point we made is that there are alternative pathways to making attractive signals. We were able to synthesize stimuli that were attractive to females but that males did not produce. The particular response of the male to sexual selection should be biased by their evolutionary history, and especially by the types of sounds their larynx can produce.

The tuning of the BP tends to match the chuck's dominant Hz. The match is not perfect. The average tuning of the BP is a few hundred hertz below that of the average chuck's dominant Hz. In my thesis work I had shown that females choose larger males based on their lower-frequency calls. One of Walt's students, Jim Fox, made a computer model of the filtering properties of the BP and showed that chucks with lower frequencies should elicit more stimulation of the BP, and this might be the neural mechanism that ultimately explained preference for larger males.

Not all frogs use both of the inner ear organs in communication; perhaps most do not. The túngara frog and its sister species, *P. petersi*, both add very distinct suffixes, chucks in túngara frogs and squawks in *P. petersi*, to their whine-like advertisement calls. All of the frogs in the *P. pustulosus* species group, nine or so, produce whine-like calls whose dominant frequencies tend to match the tuning of their AP. It is possible in some of these species the BP is recruited in decoding some of the higher harmonics in the whine, but for other species this seems unlikely. Did the tuning of the BP evolve to match the chuck

because of benefits accrued to females in choosing larger males or did the male's evolve a chuck that happened to match? In 1989 Stan and I made a short trip to Ecuador to begin studies of the close relatives of túngara frogs. I followed up with a six month stint there in 1990, and we then pursued these frogs in Peru, Venezuela, and Brazil over the next seven years. The neurobiology showed that the BP tuning of these close relatives was quite similar to that of the túngara frog. Thus there was no evidence that females evolved their tuning to favor the frequencies produced by larger males. These data on the tuning of the túngara frogs and *P. coloradum* was the second paper we published on sensory exploitation in 1990, this one in *Nature* (Ryan *et al.* 1990).

I also did female phonotaxis experiments with *P. coloradum* and showed that these frogs, which lack chucks, prefer their own calls to which chucks are appended. More recently Santiago Ron, while a graduate student at UT and now a faculty member at Universidad Catolica in Quito, Ecuador, has delved deeper into this class of frogs west of the Andes and has discovered more species and more types of calls than had been previously known. This is a story that is continuing to be developed.

I published a third paper on sensory exploitation in 1990 in *Oxford Surveys In Evolutionary Biology* (Ryan 1990). Earlier, Doug Futuyma visited UT and I told him about these ongoing studies. He urged that I write a more general paper outlining the arguments for sensory exploitation. Here I reviewed data from neurobiology and sexual selection that made a more general argument for this phenomenon.

At about the time these studies were being published, Steffan Ulfstrandt invited me to give a plenary lecture at the third International Conference of Behavioral Ecology in Uppsala, Sweden. The congress was memorable for me, and the talk was well received – I was immediately asked to visit Zurich, Bern, and Basle to talk about this idea in Switzerland. John Maynard Smith later gave a plenary lecture at the same congress. I had come to know John quite well on BCI as a grad student, and like everyone else who knew him, I was struck by his brilliance and his insights, as well as his most generous personality. His talk was memorable because he offered a public apology to Amotz Zahavi, who I happened to be sitting next to at the time, for his criticisms of Zahavi's handicap principle. At one point near the end of his talk John stopped, paused and said, "now about that stuff that Mike Ryan was talking about ... I don't know. I'll have to think about it". (Later at that meeting he tried to arrange for me to meet Magnus Enquist who was working on artificial neural networks because he thought Enquist's studies offered strong support for what I had just talked about. How right he was. I will return to this topic later.)

Brain, behavior, and evolution in túngara frogs

The notion of sensory exploitation made it clear that to have a deep understanding of behavior we needed to integrate an understanding of the neural mechanisms with the past phylogenetic history. Specifically, we wondered how the past history of the receiver influenced how it responded to signals today.

The study published in *Evolution* in 1990 convinced us of something Tinbergen made clear, the sign stimulus. Not all aspects of a signal are salient to the receiver. We are now able to measure many types of signals in excruciating detail, and we sometimes forget that our ability to obtain these quantitative measures does not always inform US about the receiver. That study also showed us that there might be various signal forms that are equally attractive to a receiver. For example, only the fundamental frequency of the whine is needed to elicit phonotaxis from females; the other harmonics do not even increase the attractiveness of the call, and a single tone that excites the basilar papilla is as effective as the full harmonic spectrum of the chuck. The question we began to ask was not whether signals and responses to signals are adaptive, but why is it that signalers use those particular signals and why do receivers show those particular responses? The ideal resolution would be to visualize the evolutionary history of signals and receivers. That wasn't possible. Nor could we compare signals and receiver between daughter (derived) and founder (ancestral) species as in Hawaiian *Drosophila* (Kaneshiro 1980). For most extant species their ancestors are extinct.

Felsenstein wrote an important paper in 1985 in which he introduced the notion of independent contrasts (Felsenstein 1985). He provided a method to estimate quantitative characters at ancestral nodes and control for phylogeny when comparing sister taxa. We used this and some similar methods to estimate the calls of ancestral nodes.

At that time a colleague in my department, David Cannatella, had begun to resolve the phylogenetic relationships of the species in the *Physalaemus pustulosus* species group. He had first worked on this group in 1984 (Cannatella & Duellman 1984). His study provided me and Stan with a phylogenetic background against which to examine the evolution of the communication system.

We measured the average call parameters for the fundamental frequency of the whine of the túngara frog, the other four known species in the species group, and three other congeners. For each call parameter we estimated the value at each of the ancestral nodes and then took all of the estimated parameters for each node and synthesized the call. We then determined whether females (falsely) recognized each of the heterospecific and ancestral calls as a potential mate and to what degree females preferred their own conspecific call to each of the other calls. The main result was that females made lots of recognition errors, and even some discrimination errors. One might predict that the similarity of the heterospecific/ancestral call to that of the túngara would determine the recognition errors, but the phylogenetic distance, which was not strongly correlated with the call similarity, was even a better predictor of when such errors occurred.

Why would phylogeny predict recognition errors? When an ancestor gives rise to two daughter species the calls and the responses to them diverge. They are not designed from scratch but more likely result from some tweaking of the ancestral signal and receiver systems. A simple prediction was that if one could change the calls that the brains of ancestors had to recognize, this should change how current brains recognize their calls.

This brings us back to Magnus Enquist. I was impressed by the work that he and Antony Arak published on sexual selection and artificial neural networks in *Nature* in 1993 and 1994 (Enquist & Arak 1993, 1994). They trained networks to recognize arbitrary signals and

showed that certain well-known effects, such as supernormal responses and preference for symmetry, emerged in the absence of selection but as byproducts of network design. That approach seemed to embrace some of the contingency of real brains and how they might evolve that seemed to be missed in population genetic modeling. I was thinking of starting to use networks to approach the historical contingency idea when Steve Phelps, a graduate student, entered the picture. After some discussion and a computer science class, Steve switched to my lab and, with the joint sponsorship of Walt Wilczynski, began his study using networks to simulate brain evolution in túngara frogs.

Steve trained neural networks to recognize túngara frog calls. Once trained, he gave the artificial neural networks other calls with which we had tested real frogs but that he did not use in training the neural networks. The response biases of the networks predicted that of the frogs. Next he varied history. One population of nets were trained with the most ancestral call that we had estimated and then its immediate descendent, etc., on the way to the tungara call. Other populations of neural networks were given histories that differed from the real one in various ways. History did not constrain the nets from being able to evolve to recognize the túngara call. But it did influence how the nets did so. This was revealed by the ability of the nets to predict the response biases of the real frogs. Only if the nets had the real history could they predict the behavior of the frogs (Phelps & Ryan 1998; Phelps *et al.* 2001).

Steve continued some of this work as a postdoc at STRI with me and Stan. He had an important influence on our túngara frog work that continues today, and he remains a sounding board on many ideas, even though he now studies rodents.

Family

This was about the time that my family came to be. I married Marsha Berkman in 1994. My daughter Lucy was born in 1995 and Emma in 1998. Marsha and I divorced in 2002, but the girls remain the center of my life. The joy they bring me each and every day is unmatched, and that joy keeps everything else in life in perspective. Whether we are watching monkeys on BCI in Panama, driving cross-country, or swimming in the creek behind our house, their constant inquisitiveness also reminds me of why I am a scientist (Figure 17.4). I am often asked whether I want my daughters to become biologists. I don't really care. What I do want is that they grow up to maintain their fascination with and respect for the natural world around them. It seems that will be the case.

Large collaborations

This winding path of research experiences eventually led to an incredible opportunity for collaborative research. In 1998 a group of four PIs, David Cannatella, Walt Wilczynski, Stan Rand and I, received a grant from an NSF program, Integrative Challenges in Environmental Biology. Others involved included Cathy Marler at the University of Wisconsin, and Robert Dudley who during the granting period left our department for the University of California



Figure 17.4. Lucy Ryan, Emma Ryan, Rachel Page, a frog-eating bat, and the author.

at Berkeley. The purpose of this grant was to integrate studies of brain, behavior, and evolution in túngara frogs toward a deeper understanding of the function and evolution of socio-sexual behavior.

My initial feeling was that if funded the grant would provide funding for our separate labs to continue our own research. Although we hoped for synergism I was skeptical. I could not have been more wrong. We made remarkable progress. David Cannatella and his students, especially Santiago Ron from Quito, Ecuador, discovered new species doing new things in the *P. pustulosus* species group in western Ecuador. A graduate student of mine, Kathy Boul, discovered two populations of *P. petersi* only 20 km apart in Amazonian Ecuador in which one produced complex calls and the other didn't, and which failed to recognize each other as conspecifics. Together with population genetics work by Chris Funk, another postdoc on the grant, they offered what I think is one of the strongest examples of sexual selection driving speciation (Boul *et al.* 2007.). Two of my other graduate students, Rachel Page and Ximena Bernal, added layers of complication to the communication network of túngara frogs. Rachel documented how the frog-eating bat, *Trachops cirrhosus*, learns to associate the palatability of frogs with their calls and how this information is culturally transmitted among bats (Figure 17.4) (Page & Ryan 2005). Ximena studied blood-sucking flies, *Corethrella* spp., which exhibit phonotaxis to the túngara frog calls and, like the female frogs and frog-eating bats, prefer complex calls to simple calls (Figure 17.1) (Bernal *et al.* 2006). Even the famed insect neurobiologist, Ron Hoy, is stymied as to how these flies can hear the call, although he and Ximena are sure to figure this out in due time.

Another student, Beth Dawson, addressed an issue that had long been an assumption in anuran biology, that frogs don't learn their calls. Although Beth showed that this is basically

correct, early acoustic experience does influence some details of the acoustic structure of a túngara frog's call and has a strong influence on the types of sounds that will elicit his calling. We made other advances in neurobiology. Kim Hoke, with the encouragement of Sabrina Burmeister, who was a student of Walt's and now also works on túngara frogs, came to work with me and Walt. Kim uses gene expression to map neural responses in the brain. She has made great progress in showing how the brain analyzes call variation and has also uncovered areas of the brain that seem responsible for differences in how the sexes respond to signal variation (Hoke *et al.* 2004, 2005).

Perhaps the most rewarding aspect of the grant was the forum for interactions it provided. Each year we had a meeting in Austin for everyone associated with the grant and anyone else who cared to listen. Usually about 20–30 attended and we often invited an outside observer and ended with a dinner or a party. The party after the last meeting was at my house and included some local musicians (“Braless” they called themselves) whom Walt and I had followed for some time. It was bittersweet, as the party also served as a *bon voyage* for Walt and his partner Debbie, both of whom I had known since I was in grad school at Cornell. Also, this was the first meeting that Stan missed; up to then he had visited Austin at least once a year for two decades. His health was beginning to decline. We called him and passed the phone around to all in attendance. He knew everyone there, and he could even recognize the music of Braless, whom he had heard on his past visits to Austin.

The official end to this grant was a symposium that I organized for the forty-first Animal Behavior meetings in Oaxaca, Mexico, in 2004 on Sexual Selection and Communication in Túngara Frogs. There were 17 papers by 19 presenters. One of the first talks was by Stan Rand on the natural history of túngara frogs. Stan's health had hardly been worse. The auditorium was packed; I think many realized they were hearing Stan's last talk.

Stan died on November 14, 2005. My last conversation with him was a couple of days before he died. I called him just before I left to give a talk in our engineering department about how túngara frogs produced complex calls. I was talking about Stan's early ideas on this topic while he was undergoing surgery and as I talked I realized Stan would soon be gone. When I returned to my office some of my students were trying to be upbeat, saying that Stan sounded stronger. I told them we had just talked to him for the last time. Stan's influence on tropical biology and the hundreds of students he mentored in more than four decades at STRI will never be forgotten (Ryan, 2006a). He certainly was one of the most important people in my life. That is another story in itself.

The research that I began with Stan continues unabated. The number of students, undergraduate and graduate, male and female, latin and anglo, who cut their scientific teeth on this system continues to grow, as do our insights into why these animals behave as they do.

50 years and going...

A good place to end this rant is at my half-century mark. My dear friend Ingo Schlupp organized a party and symposium at UT celebrating my fiftieth birthday in October, 2003. A logistical nightmare for anyone, Ingo was able to do this from overseas without me having a



Figure 17.5. The author near Boquette, Panama (photo by Ximena Bernal).

clue. He was worried, however, that I might not be in town so he broke the news to me while we were drinking beer with students in an outdoor café in Leiden in The Netherlands on a temperate September night. I was incredulous, and of course, grateful. A number of former postdocs, graduate students, and close friends arrived from various places in North America and a few countries overseas. I was grateful to see all of them. Ingo moderated the symposium and Stan Rand, Peter Marler and Gil Rosenthal all gave presentations that were mixtures of lyrical, insightful, and hilarious. My daughters Lucy and Emma got a big kick out of the event, especially Gil's depiction of me as a bald and bearded toddler roaming the landscape with dinosaurs. We then migrated to another room for a reception and my friend, Andrew "AJ" Johnson, who had come from England for the event, serenaded the crowd from an overhanging balcony with a somewhat inebriated version of Danny Boy.

Yes, a good place to end, to leave the past and get back to the future (Figure 17.5).

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LEADERS IN ANIMAL BEHAVIOR

The Second Generation

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