



PAT RAND

Stan Rand recording Túngara Frogs (*Physalaemus pustulosus*) on Barro Colorado Island, Panamá, in the 1960s.

P R O F I L E

A. Stanley Rand (1932–2005)¹

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There is a hole in my chest where my heart used to be, and a chasm in tropical biology the size of the Panama Canal. Stan Rand died on 14 November 2005, and we are all the worse off for it, personally and professionally.

Dr. Austin Stanley Rand, Stan to all who knew him, was born on 29 September 1932. Perhaps destiny dealt him no choice but greatness in biology, as his father Austin was already a famous ornithologist at Stan's birth. Stan was never far from field biology or museums when he grew up — he published his first paper when he was 12!

Stan began his graduate studies with Dr. Ernest Williams at Harvard, where he became an early member of that awesome lineage of students of *Anolis* biology under Williams's tutelage. He received his Ph.D. in 1961, and remained at Harvard on a postdoc for a year. That year included an intensive period of study of Jamaican anoles at the University of the West Indies. He and his wife Pat then relocated in São Paulo, Brazil, for two years while Stan was a postdoc with Dr. Paulo Vanzolini. Initially, Stan was paid from royalties from a song that "Vanzo" wrote. That tune must have been quite a hit in Brazil — or maybe Stan just lived modestly (money was never a big issue to him). Regardless, the Rand's first child, Hugh, was born there and it appears he didn't starve.

In 1964, Stan received an invitation from Dr. Martin Moynihan to join a new cadre of impressive young scientists that Moynihan was assembling at the Smithsonian Tropical Research Institute in Panama. Stan joined the staff. He, Pat, and Hugh moved to Panama, where their two daughters, Margaret and Katherine, were born. They lived on STRI's Barro Colorado Island (BCI), where the forest was inhabited by anoles and iguanas during the day and the Rands were serenaded by choruses of Túngara Frogs at night.

Stan published early and often — over 100 scientific papers in 60 years of publishing. Note that he is not yet done; Túngara Frog papers with his data will continue to bear his name for some time, and I predict that one will appear in 2014 to mark Stan's 70th year in the scientific literature. Many of Stan's scientific contributions can be partitioned into studies of *Anolis* lizards, iguanas, and crocodiles, and, as a grand finale, his study of Túngara Frogs. Stan explored many fascinating tidbits of nature in addition to those projects, but I will briefly review only these contributions.

Stan published a series of studies on *Anolis* biology in the 1960s that had an immediate and lasting impact on tropical biology, ecology, and behavioral ecology. Prominent among those contributions was his notion of the "ecomorph." The genesis of this concept originated when his data showed that on each island of the Greater Antilles, different *Anolis* species had diversified and adapted to nearly identical niches on separate islands. During that time, Stan also investigated dominance interactions among lizards, showing that, if the size difference between males was sufficient, the larger male won, but, if the size difference was minimal, the resident won. He demonstrated the "residency effect" in 1967, well before this became an important issue in behavioral ecology. Stan also integrated physiological ecology into his studies. Critical to the ecomorph concept was the climatic, not just the structural, habitat the lizards occupied. At the behavioral level, he showed that lizards' responses to predators were strongly influenced by their body temperatures. All of this foreshadowed Stan's continuing emphasis on the organism's entire biology and the necessity of viewing it in its natural context.



Stan and Pat Rand in front of their house in Gamboa, Panama, in 2003.

¹ *Iguana* has not and does not plan to use obituaries as "profiles" again in the future. However, Stan Rand's contributions to herpetology were so monumental that we felt that we could not, in good conscience, let his death preclude the opportunity to feature him and his impact on our discipline. — The Editors

Stan made at least two other major contributions during his work with anoles. One was a paper with Williams in 1970 on signal redundancy in communication systems. They used information theory to estimate the quantity of information about species identity that potentially could be communicated in a lizard community. They calculated that the total amount far exceeded what was necessary. This study was a wonderful demonstration of how animals use multiple aspects of their displays to reinforce the same message, and it was one of the first applications of information theory to animal communication in the wild. Stan also considered the relationship between ecological space and predator-prey interactions in the context of “aspect diversity,” arguing that variation among species could result from predator-driven selection that causes species to diverge in the “escape space” available to them. This concept greatly augmented studies of apostatic selection and anticipated much of the work we see today in sensory ecology.

Another stage in Stan’s work dealt with social behavior in and between Green Iguanas and crocodiles. Much of this work was with Gordon Burghardt and his students, centered on the small island of Slothia, a mere stone’s throw from Barro Colorado Island. Female iguanas swim to Slothia from BCI and nest communally. Stan and his brother Will wrote an insightful paper on conflict resolution. It analyzed the competition between female iguanas over the burrows they dug for nesting. The analysis combined stochastic processes and energetic constraints and showed that females took into consideration the amount of energy they had expended in building the burrow.



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Stan Rand wearing his “Túngara team” hat during the field season in 2004.



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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).

This study later led to some consternation among theoreticians interested in honest signals who were convinced that the “Concorde Effect” (adding more investment only because past investments have been made) should be maladaptive. I remember one night on BCI when, over some rather mediocre Panamanian rum, John Maynard Smith (who to me was always the “Stan of theoretical biology”) asked Stan just how this could be. Although Stan knew the theory about games, the data reigned supreme — this is what they do, he replied.

Some interesting interactions between crocs and female iguanas had been witnessed by few besides Stan. A female croc had earlier nested at the same site where the fecund iguanas sought shelter for their eggs. The female croc, Natasha, as the several-meter-long crocodile was affectionately known, rushed a nesting iguana, and grabbed the expectant mother in her mouth. Instead of devouring her, or at least dismembering her, as any protective maternal archosaur should do, Natasha delicately carried the iguana back to the water and released her. Crocodiles carry their newly hatched young to the water, so Stan thought that having a small squirming baby reptile in her mouth released Natasha’s maternal instincts. Some of this crocodile work is published, and much more is oral history on BCI. When great scientists such as Stan pass, we marvel at the accumulation of knowledge they left us, and we lament the untapped knowledge that went with them.

Stan began to study acoustic communication in frogs in the forest of Boracéia in Brazil while conducting his postdoctoral research with Vanzolini. That interest continued when he moved to Panamá. He immediately set out to document the vocal diversity of these gnomes of the Panamanian nights, but he also turned his considerable nocturnal skills towards one species, the Túngara Frog (*Physalaemus pustulosus*, which at the time had the more melodious generic moniker of *Engystomops*).

I went to BCI to begin my studies of sexual selection and communication in Red-eyed Treefrogs (*Agalychnis callidryas*) in 1978. These frogs proved intractable for the study I had planned, and I quickly switched my attention to Túngara Frogs. At this point, Stan had published one paper on their foam-nesting behavior, although nothing on their communication.

However, he gave me a manuscript that had been written in the late 1960s or early 1970s that described the complex calling of these frogs: a simple call, or “whine”, that could be produced alone or could be followed by one-to-many secondary components, or “chucks.” The manuscript was filled with incredibly interesting and detailed natural history as well as experimental studies of female phonotaxis. Among other things, Stan was interested in whether female frogs were more attracted to the complex call over the simple call. These experiments were conducted when the emphasis of mate recognition was focused at the species level and was concerned with how it contributed to speciation through behavioral isolation. In frogs, this work was being carried out in exemplary fashion by such luminaries as Murray Littlejohn and Carl Gerhardt, both of whom were inspired by the earlier studies of Frank Blair. So, at that time, Stan was working in the intellectual shadow of the Modern Synthesis and its emphasis on speciation, but instead he was addressing questions about female choice and sexual selection. This was some time before Robert Trivers (who also worked on *Anolis* and was advised by Williams during his Ph.D. studies) wrote his paper on parental investment and sexual selection in 1972. I added some to that early manuscript of Stan’s and we published it in 1981. I finished my thesis in 1982 while Stan was still concentrating on reptiles.

Stan and I remained in touch during the next few years, although neither of us worked on Túngara Frogs. In 1985, we met in the halls of the Smithsonian’s Natural History Museum in Washington, D.C. and I suggested we start up a joint project with those little beasts. In 1986, we began a now 20-year collaboration on what became known to some as the “Túngara Frog Project.” Our initial interests were modest as we began testing female phonotaxis in a carport using a plywood and burlap testing chamber in Gamboa, Panama. Stan and family had just moved from Panama City to Gamboa, and STRI was planning on having some laboratory facilities there soon. The first question we addressed was what aspects of the mating call made it attractive to females, and the first studies we published in 1990 argued that, in this system, sexual selection was generated by sensory exploitation. That idea, convergent with and inspired by others such as MJ West Eberhard at STRI, has generated some interest. Our interests in sexual communication in these frogs continued to expand in concert with the lab facilities in Gamboa, which in turn accommodated a more sophisticated approach to our own research questions.

Stan was always interested in the entire biology of an animal, and our studies soon grew to embrace additional aspects of communication, comparative studies of populations and related species, and, through our collaboration with Dr. Walt Wilczynski, the neural mechanisms that controlled mate choice. Memorable during those years was a 5000-km transect in which Stan and I sampled and collected Túngara Frog calls and tissues throughout the entire range of the species. Most of the data were collected when we departed from Austin, Texas after the meetings of the American Society of Ichthyologist and Herpetologist (ASIH) that was hosted there in 1993. We drove from Texas to Panama, collecting all the way. Those samples were supplemented by numerous trips to South America, where we studied



Holding a microphone and a Marine Toad (*Bufo marinus*) in place of the crucifix and the dove, Stan Rand impersonates Saint Francis of Assisi. Stan was passionate about fieldwork and deeply appreciated the beauty of toads. The picture was digitally modified at Stan’s request to create a monk’s hairstyle.

other populations of Túngara Frogs and their relatives. The data from that transect have already provided the grist for at least four separate studies, and their uses are still not exhausted.

In the year 2000, Stan, Walt Wilczynski, David Cannatella, and I were PI’s on a multidisciplinary grant. This grant, which involved collaborations among more than a half dozen labs, addressed issues from phylogenetics to molecular neurobiology, all emanating from the basic biology of the Túngara Frog that Stan first glimpsed in 1964. As the grant ended in 2004, we were asked to organize a two-day symposium on “Sexual Communication in Túngara Frogs” at the Animal Behavior Society meetings in Oaxaca, México. To kick off that symposium, numerous attendees, many with little or no interest in frogs, sexual selection, or communication per se, packed the room to hear Stan Rand present what ended up being his last scientific presentation: “Natural History of the Túngara Frog.” When Stan finished that talk, I detected in the sustained applause a tone of reverence and appreciation for someone special.

The work on Túngara Frogs will continue unabated, serving as a scientific legacy to Stan, but it also will be a continuing collaboration from the grave. Although no longer with us, we will never outlive Stan’s inspiration or exhaust his insights.

Having now provided a most cursory summary of Stan’s scientific career, I would like to end by saying more about Stan the person, which is the real reason why so many of us mourn his passing. Above all, Stan was a naturalist. His eyes, ears, and mind were focused on the organism in its environment. He was well schooled in theory, but not terribly impressed by it. He was

a great experimenter, but was always a bit cynical about how such results might apply in the wild. Once we were waiting out a drought in a small dusty town in the bush in Brazil. We went to see a movie, “Edward Scissorhands.” An old woman narrates the story in which, as a youth, she befriends a boy who has scissors for hands. Afterwards, I asked Stan how he liked the movie. He said it was totally unrealistic, the chronology didn’t match, and the old woman could not have been a youngster when she first met Edward. I said, “Stan, for chris-sakes, the boy had scissors for hands! How realistic is that? So what if the chronology was off.” He wouldn’t budge. The opening of the movie was built on a house of cards and he would contemplate no farther.

For most, Stan is intricately associated with STRI. The Smithsonian Tropical Research Institute is a great institution, and Barro Colorado Island is its crown jewel. We celebrated Stan’s retirement from STRI with a symposium in his honor at the 1998 meetings of the ASIH in Guelph, Canada, the proceedings of which are published in *Anuran Communication* (Smithsonian Institution Press, Washington DC, 2001). All of the more than 20 authors I first invited to participate said yes; so much for a list of back-ups! When I introduced the symposium, I said that, but perhaps for BCI, Stan was STRI’s most valuable resource. An institution’s greatness is defined, of course, not just by its physical facilities but also by its humanity — and that is where Stan made by far his greatest contribution. Because of his immense knowledge of tropical biology, Stan was often called upon for advice, especially to initiate novices to this land of plenty. His generosity knew no bounds, and his humor, warmth, and enthusiasm were contagious. He readily extended this generosity into the personal realm. He and Pat formed the social hub of Gamboa for the last 20 years, and their house was a scientific salon. Pat’s famous “frog dinners” for many of the visiting researchers in Gamboa (regardless of whether or not the



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When a student asked Stan about chemical defenses of Túngara Frogs (*Physalaemus pustulosus*), he volunteered to lick some to find out if he could detect any chemicals. Stan had a humorous disposition and enjoyed making people laugh in the lab.



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Stan getting ready to fly in an ultralight plane in 2003 over the area of Chilibre, Panamá. Stan was an adventurous man always looking forward to new experiences.

scientists worked on frogs) were the social highlights of our summers. These dinners were also an incubator of scientific ideas. Stan was not a “science nerd,” he was broadly informed and could entertainingly engage guests with a broad array of topics, but his insights and wit were always sharpened and ready to be applied to the next scientific question.

I remember once bemoaning that, because Stan was not at a university, numerous students missed out on all that he had to offer. Wrong, wrong, wrong! STRI offers a wide array of fellowships for researchers at all stages of their careers. They all need STRI sponsors. I have counted more than 50 students that Stan sponsored before 1990; surely I have missed many. In addition, since 1986, Stan acted as sponsor to more than 70 interns and associates who have worked with us on the Túngara Frog project. He visited my lab in Austin twice a year for a long time; those visits were so heavily booked that I had to sequester Stan at a local pub to have time with him — but even that hiding place was discovered all too quickly. Finally, literally hordes of students owe Stan deeply. Two now rather famous biologists, one studies monkeys and the other ants, told me long before they were famous that Stan was crucial to the early development of their research forays on BCI. When I informed by mass e-mail numerous colleagues of Stan’s death, I received a plethora of responses in which the word “love” was used much more than one might associate with “macho” (and “macha”) field biologists.

So, now we say good-bye, Stan. Thanks for all that you shared, the family, the friends, the tropics, and the frogs. You will not be forgotten. Next rum’s on me.

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