

OBITUARIES

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AUSTIN STANLEY RAND 1932–2005

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 November 14, 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 September 29, 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' tutelage. He received his Ph.D. in 1961 and remained at Harvard on a postdoc for one year, which included an intensive period of study of Jamaican anoles at the University of the West Indies. He and his wife Pat then relocated to Sao 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 must have been quite a hit in Brazil—maybe, Stan always lived modestly and 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, and Stan and Pat had two daughters, Margaret and Katherine, 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 done yet: Túngara Frog papers with his data will continue to bare his name for some time, and I predict there will be one in 2014 which will mark Stan's 70th year in the scientific literature.) Much 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 between these projects, but I will briefly review only these contributions here.

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 with his data showing that on each island of the Greater Antilles, different *Anolis* species had diversified and adapted to nearly identical niches among 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 there were a smaller size difference, 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 concept of the ecomorph was the climatic habitat, not just the structural, which the lizards occupied. At the behavioral level, he showed that lizards' response to predators was strongly influenced by their body temperature. 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 made at least two other major contributions from his work with *Anolis*. 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 could potentially 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 uses of information theory applied 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 (thanks to both Ray Huey and Jonathon Losos for their thoughts on Stan's *Anolis* work).

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 BCI. Female iguanas swim to Slothia from BCI and communally nest. Stan and his brother Will wrote an insightful paper on conflict resolution. It analyzed the competition between female iguanas over 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. 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"), asking Stan just how this could be. Although Stan knew the theory about games, the data reigned supreme—"This is what they do", he replied.

There were also some interesting interactions between crocs and the female iguanas that few besides Stan had witnessed. 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 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 Panama. 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 then had the more melodious moniker of *Engystomops*.

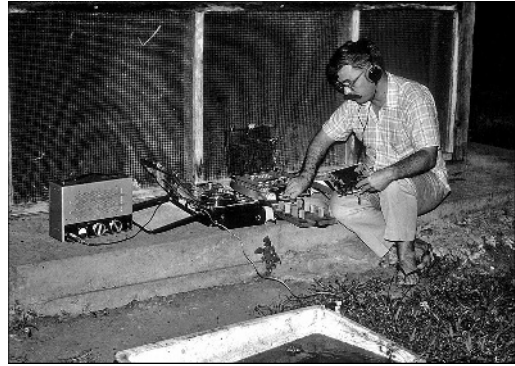


Fig. 1. Stan recording Túngara Frogs in the 1960s.

I went to BCI to begin my studies of sexual selection and communication in red-eyed tree frogs 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. But he gave me a manuscript that had been written in the late 1960s or early 1970s. It 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. thesis) 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, while neither of us worked on these



Fig. 2. Experiencing the sensory biology of a Túngara Frog (*Physalaemus pustulosus*).

frogs. In 1985, we met in the halls of the Smithsonian's Natural History Museum in Washington D.C. and I asked, "Why don't 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 car port using a plywood and burlap testing chamber in Gamboa, Panama. Stan and family had just moved from Panama City to Gamboa, and STRI was figuring to have 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 M. J. 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 the 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 that Stan and I sampled in which we collected Túngara Frog calls and tissues throughout the entire range of this species. Most of the data were collected when we departed from Austin, Texas after the ASIH meetings that were 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 other populations of Túngara Frogs and their relatives. The data from that transect has provided the grist for at least four separate studies, and its uses are still not exhausted.

In the year 2000, Stan, Walt Wilczynski, David Cannatella, and I were PIs 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



Fig. 3. A. Stanley Rand, 1932–2005.

organize a two-day symposium on “Sexual Communication in *Túngara* Frogs” at the Animal Behavior Society meetings in Oaxaca, Mexico. To kick off this 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, there was a sustained applause in which I detected a tone of reverence and appreciation for someone special. The work on *Túngara* Frogs will continue unabated, and it will be a scientific legacy to Stan but more than that. It will be a continuing collaboration from the grave. Although no longer with us, we will never outlive Stan’s inspiration nor exhaust his insights.

Having now provided a most cursory summary of Dr. Rand’s scientific career, I would like to end saying more about Stan as a person; this 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. As an anecdote, 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 S. 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 could contemplate no further.

For most, Stan is intricately associated with STRI. The Smithsonian Tropical Research Institute is a great institution, and BCI is its crown jewel. We celebrated Stan’s retirement from STRI with a symposium in his honor at the 1998 ASIH meetings in Guelph, Canada, the proceedings of which are published in “Anuran Communication” (Smithsonian Institution Press, Washington D.C., 2001). All of the more than 20 authors I first invited to participate said yes—so much for a back up list! 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 by its humanity. And it is here that 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 were the social hub of Gamboa for the last 20 years and their house a scientific salon. Pat's famous "frog dinners" for many of the visiting researchers in Gamboa (regardless of whether or not the scientists worked on frogs) were the social highlight of our summer. These dinners were also an incubator of scientific ideas. Stan was not a "science nerd," he was broadly informed and could entertainingly engage one with a broad array of topics, but his insights and wit were always sharpened and ready to be administered 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! The Smithsonian Tropical Research Institute offers a wide array of fellowships for researchers at all stages. 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 has 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 that hiding place was found too soon. Finally, there are literally hordes of students who owe Stan deeply. Two now rather famous biologists, one who 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 goodbye, 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.

MICHAEL J. RYAN, *Section of Integrative Biology, University of Texas, 1 University Station C0930, Austin, Texas 78712-0253; E-mail: mryan@mail.utexas.edu.*