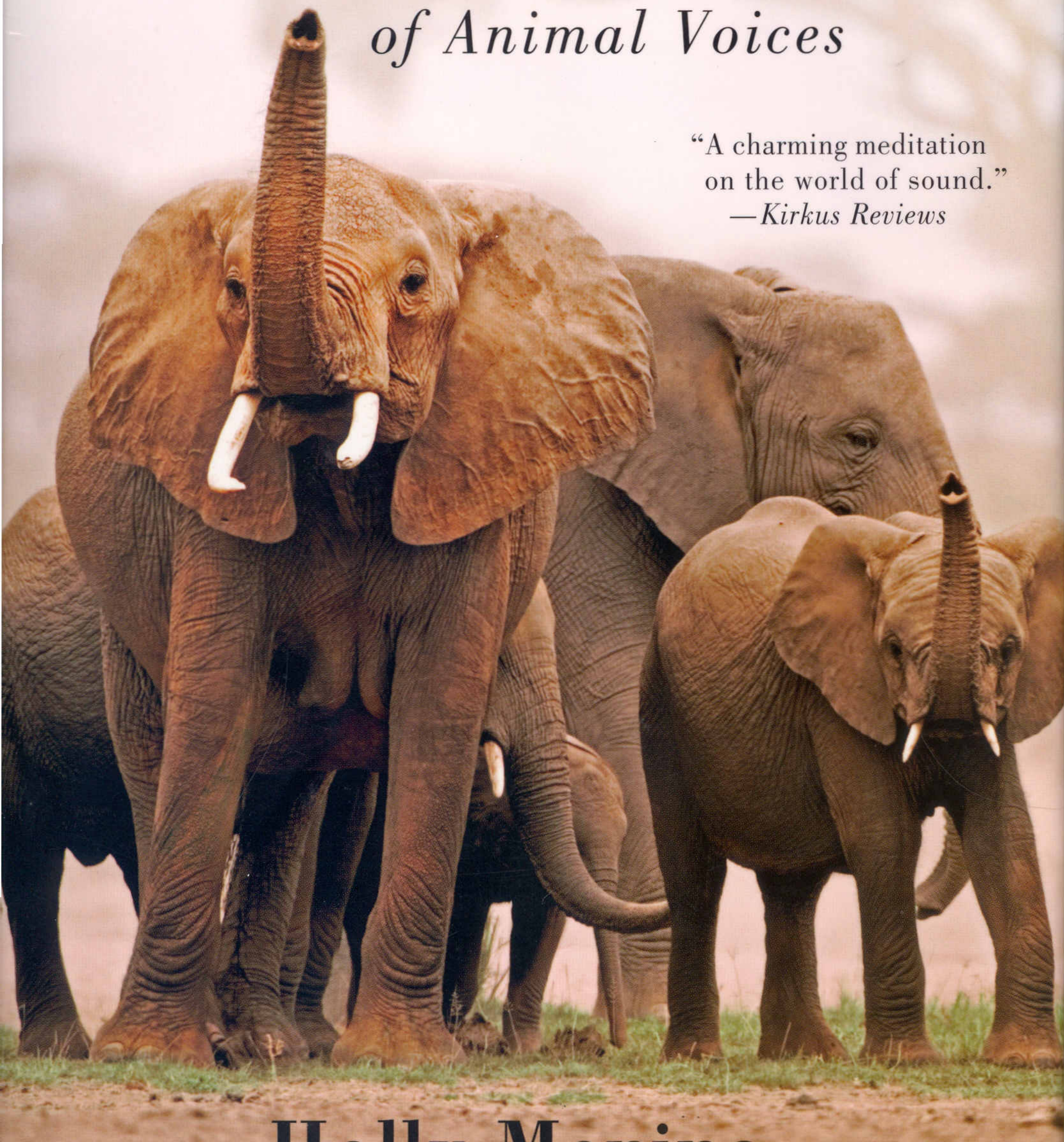
CALLS BEYOND OUR HEARING

Unlocking the Secrets of Animal Voices



"A charming meditation on the world of sound."
—*Kirkus Reviews*

Holly Menino

2

Don't the Girls Get Prettier at Closing Time?

On my first night in Gamboa, I ride out on the main road to Panama City with Mike Ryan and his two summer research assistants, Jenny Saunders and Sasha Ozeroff. This is my second trip to visit scientific research in Gamboa, and so I am not surprised by the intense humidity that clings to you all day and persists after dark. Even the Smithsonian's mini-truck moving through the night doesn't stir much of a breeze. A couple of miles from Gamboa, Mike pulls the mini-truck off the road. The rest of us strap on headlamps and follow him into a thicket of edge-growth forest, down an embankment through a fine mist of mosquitoes, and into a dark tunnel of leaves and roots.

The four of us emerge in a clearing, where there is a pond. Ocelot Pond is a flat, glistening piece of water standing in the dark and the heat. It is less than a foot deep and its total area isn't much larger than the aboveground swimming pool that adorns many backyards. Sometimes the pond isn't here. The area is just a low place in the clearing. But it is the wet season in Panama, when there seems little difference between water and the air we breathe. Enough rain has collected to draw a congregation of tropical frogs. They call intermittently, each with a distinctive voice. This is the chorus.

We don't pay any attention to most of the calls because we are listening for one in particular. The insects, especially the mosquitoes, are bad, but we don't have to stand around and wait for long. In fact, we have barely reached the edge of the pond before the call comes across the water more penetrating than the combined sounds of the insect noise and the calls of other frogs. The sound begins with the whine of a futuristic bullet through outer space, like something from a *Star Trek* sound track, and it ends with a light clunk as the bullet hits home. The túngara's name is Panamanian onomatopoeia for its downsweeping bullet-whine call–you can approximate the call by sounding a tone about an octave higher than the note you want to land on and letting your voice slide in a downhill glissando to the syllable *chuck*. Science has a fairly flat-footed name for the frog, *Physalaemus pustulosus* or, more familiarly, *P. pustulosus.*

It is hard to believe an animal can make a sound so clear and technological, but this is the signature call of the tiny male túngara frog. It is also hard to believe that what this sound is all about is desire and attraction, but I learn from Mike that this is so. The space-age whine-chuck is the sexual solicitation, the advertisement call, of the male túngara. Although the male is only the size of a teaspoon, soft and slippery, and, no matter what your sex, wouldn't hold much appeal, he has irresistible sexual draw for túngara females, which are appreciably larger. The females do not call or respond. Both have brown warty skin.

"They look like toads," I observe. "Why aren't they túngara toads?"

"The Panamanians do call them toads–*sapo túngara*. But in fact, there is no scientific difference between frogs and toads," he says, "except in our own popular thinking about the animals." Apparently, this distinction is one made by people like me, who happen to believe that a frog is a smooth- and slippery-skinned water dweller and a toad has dry warty brown skin and lives on land.

Because it is so mouthy, the tiny túngara frog of Central America is one of the most intensely studied amphibians in the world. The frog's singing and sex life have made it a species of interest for herpetologists, animal behaviorists, and now neurobiologists–and the darling of three generations of scientists who have migrated to Gamboa to work under the auspices of the Smithsonian Tropical Research Institute. Mike is the current patriarch. He has been coming down to Gamboa to listen to the whine-chuck of the túngara for about thirty years. He is a good-humored, sharp-thinking mentor to an ever-rotating bevy of graduate students, and he resembles Charles Darwin. Mike is blockier, more muscular, and the hair around his pate and his beard haven't begun to turn white, but still, he would be believable cast in the role of the grand old man. The resemblance ends with physical attributes. Unlike Charles Darwin, Mike is gregarious, and he has a playful mind and a social network within behavioral ecology as robust as his person.

The path to Gamboa opened up when he was studying the calls of bullfrogs in New Jersey's Great Swamp for his master's degree. He was interested in the differences in their calls, and at that time there was no evidence of sexual selection by females. He began work on a doctoral dissertation, and when his adviser died, Mike moved to Cornell

University and a study of an animal called the red-eyed tree frog. This was the frog that took him to the Smithsonian Tropical Research Institute and its famous biological reserve, Barro Colorado Island.

The red-eyed tree frogs were hardly cooperative subjects. They live up in the canopy of the rain forest and emit rather weak calls. These calls were hard enough to detect even without interference, and on Barro Colorado there was plenty of din. The frog choruses on the ground threatened to drown out the red-eyed tree frog, and the keening whine-chuck of the túngara was a particularly insistent interruption. Since he couldn't lick the túngaras, Mike wondered about joining them. The noted herpetologist Austin Stanley Rand was a senior scientist at STRI in Panama City, and having done some preliminary investigations of the túngara in the 1960s, Stan Rand had the research rights to the species. Mike's question "Would you mind if I looked at the túngaras?" was the beginning of a long, productive collaboration and a close friendship. A few years after Mike had earned his doctorate, he resumed his túngara research with Rand in Gamboa. In the meantime, Mike published "Female Mate Choice in a Neotropical Frog" in *Science* in 1980. His finding that the females determined which matches were made went undisputed because the choreography of the nightly rituals at the pond edge was such clear proof. The males sit still and call. The females listen and then vote with their feet.

Simple enough, and I have come down to Panama because I want to start with the fundamentals of vocalizing, with a simple, short-lived animal and then go on to look at increasingly brainy animals, longer-lived animals, where the questions would undoubtedly be more complex. But when I first contacted Mike with the idea of starting with a simple animal, a simple call, a simple sound, I didn't consider the fact that I was inviting myself into a research agenda with a thirty-year history.

Mike returns to Gamboa for a month every summer to patrol the ponds and puddles and gutters. While some of his students remain in Texas, a few of the others come down to Panama and ensconce themselves for the entire summer. This year the Ryan team consists of Amanda Lea, a graduate student focusing on the male froggies, as she calls them, and managing Mike's lab; Ryan Taylor, a former postdoc under Mike who now teaches at Salisbury State University in Maryland; and the two undergraduates, Jenny from the University of Texas at Austin and Sasha from Simon Fraser University in Canada.

What Mike and his team are focusing on this summer is the brief chuck or series of chucks that round off the call. While the male's whine is blatantly audible, it is just the introduction to the most potent attractant in his call. What comes after it is what really gets the females going, what hits the sonic G-spot, the chuck. They know this. But how do these snippets of sound work?

The night we spend at Ocelot Pond repeats itself. Just after dark every night, we drive out by twos and threes to catch frogs for the experiments in Mike's lab. We go to the same places we went before, because our containers are full of frogs we caught the night before and we need to take them home before we look for new subjects. These returnees are relocated in the very same place where they were caught in order to avoid disrupting the genetic makeup of the various populations around Gamboa–remember, this is a community where scientists keep close tabs on just about every aspect of rain-forest life. There are multitudes of túngara populations here and all over Panama–for that matter, multitudes of them from southern Mexico down through northern South America–in shallow ponds, puddles, and gutters. In spite of this abundance, we are hearing only a few sparse volleys of space-age bullets across Ocelot Pond on this particular night.

Catch frogs implies a good deal more sport than actually takes place after we arrive at the edge of Ocelot Pond and release the captives of the previous night. We cast our lights around the edge of the pond until the beam of Sasha's headlamp falls on what appears to be a very thick frog, and she reaches down to pick it up. This thick frog is actually two frogs, the smaller male riding on top of a female, his front legs clasping her around her abdomen. She has swum out to him because she is heavy with eggs, and he clings to her waiting for her to release those eggs. We do not pluck up any singletons unattached to a mate because their sex would have to be determined and, in the case of a female, her state of readiness to mate would be unknown. As I consider the coupled túngaras caught in the headlamp beam, it occurs to me that this mating is the only social incident either frog will likely experience. As Ryan Taylor–the Salisbury State University scientist, not to be confused with his mentor Mike Ryan–points out to me, all we know about the túngaras' life–or the lives of most frogs, for that matter–is what we have observed at the mating pond. We don't know what takes place in the leaf litter away from the pond. As far as we know, túngara society is the simplest kind. Each frog lives alone, striving on its own for food and safety until sex pulls a male frog and a female frog into physical contact. This sex-only social arrangement is a kind of primitive proto-society that, like the more complicated societies of mammals and birds, underwrites the animal's survival. Whine-chuck, the frog's voice, is what draws the two together to create this temporary society. The male's two-part call is one-way communication, like a bumper sticker. The female doesn't call back and, in fact, doesn't vocalize at all. She responds by silently taking action, and she follows the calls that she likes to locate the male.

Hunkered down in the shallow water at the edge of the pond, the male uses his trunk muscles to squeeze a pressurized stream of air over his larynx, at the same time filling the two vocal sacs aligned under each side of his jaw. In addition to the penetrating, outer-space zing this produces, the vocal sacs themselves are remarkable as themselves. They inflate until each one is larger than the frog's head and the frog appears to have huge water wings to keep him afloat. If there is any starlight or moonlight in the night sky, they reflect this, ballooning with luminosity. But the inflation of the vocal sacs does not directly cause the sound the túngara makes. The vocal sacs work the same way as the bag on a set of bagpipes. Like the bagpipe bellows under the piper's elbow, they are a reservoir for air that will be pushed out with the next squeeze of the frog's trunk muscles and the next whine.

The sound the male túngara produces with these athletics, like the ultrasonic pulse of one of Griffin's bats or Sheila's voice, is simple physical pressure. At the most elementary level, sound is a series of pressure waves, atmospheric pressure waves. Marine acoustics expert Peter Scheifele, whose work on beluga whales and dolphins I visit later, loves to point out that everything in the world, animate and inanimate, resonates with these waves: you, me, the plate on the kitchen counter, the kitchen counter. Each thing in the world has its own resonant frequency.

Frequency, one of the fundamental physical characteristics of sound, is the speed at which the atmospheric pressure waves are repeated, and this speed is conditioned by the medium through which the waves are transmitted. In a dense medium, sound travels five times as fast as it does in air. Frequency is what determines pitch, and it is measured in the number of wave cycles per second or hertz (Hz) or kilohertz (kHz), units named for the late nineteenth-century physicist Heinrich Hertz. The greater the frequency, the higher the pitch. Just to help you orient yourself, the note A given by the oboe, which is the pitch an orchestra tunes to, is 440 Hz. Because almost all objects vibrate in multiple frequencies at the same time, frequency or pitch rarely exists in isolation. It is accompanied by harmonics, which are oscillations in multiples of the frequency. This gives each sound a unique character, or timbre, especially the sounds of animal voices, our voices, and musical instruments.

A second defining characteristic of any sound is intensity, which we perceive as loudness. The amount of energy that carries the pressure waves along determines loudness. While frequency is calibrated in hertz, intensity is measured by watts. The intensity of my dog's alarm bark is far greater than the intensity of a spring peeper's call. In addition, there is the variable of attenuation–what happens to sound as it travels. The degradation of sound over distance affects its perception by not only intended listeners but also eavesdroppers, other animals that happen to be in the neighborhood. This is a factor not only in the vocalizing of birds, which communicate through the air, but also in the calls of whales and elephants, whose calls are transmitted through water and the earth.

If you are listening to any of these animals, the sound of its voice is a quantifiable physical event until it collides with your inner ear. Then it becomes a perceptual event. As soon as the tiny hairs in your cochlea begin to translate this sound into impulses of the auditory nerves and these travel the neural pathways of the central auditory system, you become aware of the sound. What begins as a simple pressure wave ends up as a cognitive construct.

Acoustics is the study of the interplay between these two kinds of events, physical and perceptual, and like acousticians, the behavioral ecologists and cognitive psychologists who have shared their investigations with me have to work both the physical and perceptual sides of the street. If you want to reveal what is going on between the túngaras when the male calls and why that is going on, you have to learn how the sound travels between the frogs, what happens when it collides with the female's ears, and how its impulses are translated into voltage that fires her auditory brain.

The frogs listening to the call near the pond, including those of their own kind, have ears located behind their eyes. It is a much-simplified version of our own ear–a flattened eardrum or tympanic membrane exposed at the skin surface and, instead of a cochlea with hair cells to transmit sound waves through nerve cells to the brain, two fleshy papillae, one for low frequencies and one for high frequencies. These papillae are the reason that frogs attend to calls from only their own species. They are "tuned" to a particular range of frequencies, making a túngara more acutely sensitive to the sounds of another túngara than to the sounds of other frequencies made by a different kind of frog.

The female túngara is built to be fussy about the frequencies and their duration within the male's advertisement. While the male's whine is enough to attract a female, the sonic sweep of the whine combined with the lower staccato chuck is five times more effective. Going even further, the female justly rewards additional repetitions of the chuck.

"One of my graduate students, Karin Akre, took a video," Mike tells me, "that shows that if the female has kind of settled on a particular male and she's swimming out toward him but doesn't get that second chuck, she makes him give it to her. She passes him, and as she passes him, she gives him a little shove." I have to watch the few seconds of video quite closely to be able to catch the brisk but barely perceptible bump. This little body slam usually works, and the male gives out with a second chuck. She must have more than one chuck, but so long as the male's whine is followed by at least two chucks coming after the whine with exactly the right timing in exactly the right rhythm, she requires no excitement beyond that.

This tuning to particular frequencies, intervals, and rhythms exists in many other animals. It is especially evident among birds, but it is also important to us in terms of how we hear conversation and music. We recognize a question by its rise in inflection, change in pitch, from the basic tone of conversation. When the question is repeated, we are alerted to its importance. If it is repeated again, it gains real urgency. Likewise, a musical note gains power with repetition–Antonio Carlos Jobim's "One Note Samba" is a telling example of this–and we take particular pleasure from melodic phrases that hover in certain intervals around the fundamental tone in the scale. Any departures from these anticipated tonal distances are often what we find most cogent and descriptive in a tune. Likewise also, as the female túngara waits for her eggs to ripen, she is listening for something telling. What it takes for her to hear something telling and then go to the male is readiness. The female won't tune into the space-age calls until her eggs are ripe enough, and to swim out to him she must be truly ready, urgently ready, because there is no teasing with courting frogs, no opportunity for foreplay.

For his part, the male needs to be stingy with the good stuff because he has to invest a lot in his calls. Each big sound he squeezes out of him costs a lot of energy–he can produce only so many whines and chucks during calling hours–and calling can cost him his life. Each successive call in a series has a higher probability of costing him his life. The same sounds that are so tempting for the female are equally alluring to predators, and, as Amanda points out about the diminutive túngaras, "everybody eats the froggies"–snakes and birds and, especially, fringe-lipped bats, the so-called frog-eating bats (this mundane-sounding name actually expresses the amazement of the noted bat authority Merlin Tuttle when he discovered on Barro Colorado a bat with a frog in its mouth). There is evidence that the bat targets the frog not by its usual echolocation but by the frog's calls. What all this means for the male túngara is that giving voice can wear you out, get you a mate, or get you dead.

There are thousands of the little frogs just in Gamboa and more than enough risk to go around. But as I walk around the hamlet I see evidence of the male's rewards for risk taking. In the gutters, drains, low spots where the leaf-cutter ants cross the lawns–any place where water collects–I notice the foamy white dollops of túngara egg masses. They look exactly like a couple of tablespoons of whipped egg white. These are what all the frog noise is about. When the whines and chucks finally draw the female close enough to him–or at least close enough to knock one more chuck out of him–he clambers aboard his bigger half and clasps her around her torso. She doesn't release her eggs right away, and it's not known exactly how this embrace eventually encourages the female to release her eggs. But later the same night they produce that frothy white mass that encapsulates the next generation of whines and chucks. This is the same kind of stuff that accumulates at the edges of the pond on our farm, and the locals have a euphemism for it, *frog spit.*

When we take the evening's catch back to Mike Ryan's lab in Gamboa, the females are in a state of readiness. In most cases, they have already made their choices and the males cling to their backs. Readiness equals estrogen, Mike says, and his colleague Kathleen Lynch has established the rough outlines of the estrogen curve the female túngara rides every six weeks or so. Her hormonal peak demands an answer, and we watch the females in the lab to see how they respond to the answers they hear.

Mike has permanent quarters in the big central building everybody calls One-Eighty-Three, which serves as office space, dormitory, and communications headquarters for all the researchers in Gamboa. Here a couple generations of the Ryan team have spent thousands of nocturnal hours watching female frogs to determine the details of exactly what sounds will turn a female on and push her from readiness to decisive action.

His lab occupies two rooms, neither of them large. The smaller room is almost completely occupied by a sound chamber that looks like a giant white freezer box with a door in the side. This chamber is an exact replica of the one in Mike's lab at the University of Texas, where he tests captive-bred túngaras. Inside, nothing resembles the pond. The walls, ceiling, and floor are white plastic. When the door closes behind you there is near-total darkness and something that approaches true silence. I find the sensory deprivation a little dizzying and unnerving, but the female frog doesn't. According to Mike, frogs have very keen night vision but, interestingly enough, not particularly acute hearing.

As Amanda and the research assistants set up the sound chamber for the female túngara's first experiment, Mike describes the responses the experiment will elicit. "You know," he tells me, "there is a pretty good article on what's going on here–'Don't the Girls Get Prettier at Closing Time,' 1979." When I succeed in locating it, I find a country-western take on a topic in psychology: how time and urgency affect decision making. The article quotes songwriter David Allen Coe to assert that "there's more to country music than 'mama, or trains or trucks or prison or gettin' drunk,' " and it analyzes the responses of more than a hundred bar-goers, both male and female, in three different watering holes to prove Mickey Gilley's sung testimony that "the girls get prettier at closing time." Apparently it's not just the girls who get better looking. During three different time periods throughout a single evening, the researchers asked their respondents to rate the appearance of members of the opposite sex in the same establishment. When they crunched the responses through some statistical analyses, this revealed that, as closing time approached, people of the opposite sex did in fact look more appealing to the subjects. This was true for both the males and the females who responded. Although noting that the research design made no provision for accounting for the effects of booze on perceptions, the authors declared that Mickey Gilley's hypothesis was confirmed: narrowing the window of opportunity forces decisions that might not have been made without a time limit.[1] For the túngaras, closing time exists only for the females. For each of them, it comes about every six weeks, when she rides the crest of her estrogen wave. At this point she must choose a male or else the energy and physical resources she has invested in her eggs will go to waste. Mike's laboratory research is designed around this closing-time urgency.

The sound chamber is where the female frogs will listen to the jukebox until closing time. Mike is the only songwriter whose tunes are available on the jukebox, and although he is too modest to claim this, he has to know a lot about sound and a lot about physiology to write these tunes. The jukebox is a state-of-the-art software program on the computer outside the chamber, which drives the speakers inside the chamber. It is a highly sophisticated system with which Mike can tweak the frequency of the space-age whine or slice or add in a fraction of a second to a chuck, and although it has more bells and whistles than most of the systems I saw, these bells and whistles are designed with strict tolerances and fidelity equal to the best systems used for birdsong.

I stay outside the sound chamber with Jenny and Sasha and Amanda, who is Mike's straw boss in the lab. Amanda is a small, thin person with very long, very blond hair and very blue eyes. She is extremely well organized and in full command of the computers, custom software, and sound equipment. A brisk, efficient manager, she worked her way through a belated undergraduate degree at the University of Texas as a bartender in a "gentlemen's club" and tells me that dealing with drunks honed her management skills. While Sasha and Jenny defer to Amanda, all three of them have to be on their toes to keep the experiment running.

On the computer screen we can see video surveillance of the chamber floor. It looks like a basketball court under extremely dim light. At each end, located inside a rectangle resembling the free-throw area, there is a speaker, and in the center of the floor a circle like the one for tip-offs. The games here are always night games. They start around 10 P.M. and run until 3 A.M. or so.

Jenny separates a pair of frogs, disentangling the female from the male's embrace, sets her down in the center circle, and gently claps a plastic funnel over her. The cord attached to the funnel runs up through the chamber ceiling to allow Jenny to raise the funnel from outside the chamber.

With the female túngara hunkered down under the funnel in the center circle, the game inside the chamber begins with an interlude of frog song. First the female frog is treated to a single whine repeated from both speakers, then to a whine-chuck played by a single speaker at the opposite end of the chamber. Thirty seconds of silence. Then Jenny pulls the cord to lift the funnel and release the female. She is on her own and loaded with eggs. This is a test of preference and memory. Will she be able to keep the two calls in mind throughout the period of silence? And which speaker with which call will she choose?

Play commences. The female has five minutes to leave the center circle and a total of fifteen minutes to indicate her choice by hopping into the free-throw zone around the speaker with the most enticing sound. Because Mike has already established that the females prefer calls that include the chuck, this game is a test of memory. The female that can listen to the introduction of the chuck and retain that sound impression throughout the distractions of the less appealing unadorned whine calls, throughout the silence, and hop up to the speaker responsible for the more delicious whine-chuck scores one point for memory and cognition.

The three women outside the chamber work intently. The experiment requires concentration and coordination and quiet. We don't talk much, and when we do, no one speaks at a normal volume because even this built-to-spec sound chamber can't preserve pristine silence, which, although the frogs don't have particularly acute hearing, is required to preserve the integrity of the experiment. Jenny manages the frog contestants and the stopwatch, Sasha controls the sounds played back and records results on a data sheet, and Amanda, who has a number of seasons' experience, spots the two of them and advises.

On the computer screen the image of the court is very large and the player, the female, is tiny, the size of a bread crumb. The frog calls are playing at either end of the court, but nothing happens. The female is apparently unmoved. She remains hunched down in the center circle. Jenny consults the stopwatch. We keep our eyes on the screen. No go.

Amanda shrugs and says in a whisper, "Well? This froggie may foul out."

But she doesn't. Just moments before the stopwatch blinks up to five minutes, the female makes a quick, slippery move out of the center circle. She appears to be on her way to the speaker on the right-hand side of the court. But maybe not. She pauses and turns back into a lifeless bread crumb. The digits flash by on the stopwatch. She now has only about four minutes to make her choice.

Amanda is not sympathetic. "She is the kind you'd like to squish," she says under her breath.

In the end, this female túngara fouls out. She exceeds the fifteen-minute time limit without making a choice. The bar closes, and she goes home alone.

The next contestant is more decisive. After an initial minute or two of deliberation in the center circle, she makes a long, smooth bound out of the circle in the direction of the right-hand speaker but far to one side of the court. After a pause she begins to approach the speaker in an arc. Her arc is punctuated by a series of delays–for deliberation, reconsideration, whatever.

"This is characteristic," Amanda says softly about the approach. "It's a kind of dance."

In her final hop, the female enters the free-throw rectangle and parks herself sideways in front of the speaker. She scores!

There is a general sigh of satisfaction, and Jenny enters the chamber, her back filling the video image on the screen, to scoop up the frog and place her back under the funnel.

Each female is presented with four variations of the same test and has fifteen minutes to complete each one. Taking into account occasional retests, it's not unusual for each frog to spend more than an hour as a contestant. Amanda tells me Mike's goal for the summer is two thousand frogs, and I wonder, What is it about two thousand female frogs, sounds from two speakers, and the decisions the frogs make that has anything to do with the sounds that Sheila Jordan makes–or, for that matter, the sounds that you and I hear and make? Is it just that the frog song buzzes into their frog ears and resonates through the auditory brain?

In the nocturnal universes of the sound chamber and Ocelot Pond there are two evolutionary forces at work, both of which were recognized and defined by Darwin: natural selection and sexual selection. Although Darwin is more readily associated with his ideas about natural selection and survival, he was also the first to observe the systematic process that is the "struggle between individuals of one sex, generally the males, for possession of the other sex."[2] As he saw it, sexual selection was a secondary process that played out either through direct combat among males vying for a female or through mate choice, a prerogative usually exercised by females. "The males," he said, ". . . do not obtain possession of females, independently of choice on the part of the latter." But, probably because the idea of combat made the struggling males and the trophy female a more individually dramatic scenario, the notion of males vying for a female became the underlying assumption in research about mating by scientists who were, not coincidentally, predominantly male.

This stereotyped assumption about sexual selection prevailed, and Darwin's proposals about sexual selection in general and mate choice in particular went largely untended until the 1970s. Biologists, now including more women, began to turn their attention to the process of sexual selection, mating, and reproductive "success." In the 1980s this trend progressed, and behavioral ecologists, including Mike Ryan, began to focus more intently on the roles of the female and female biology in mate choice.

With the frogs, mating takes place in darkness and in pandemonium that involves not just a couple of male frogs and a female but multitudes of males and females of many species. The males of each species have a distinctive call, and their calls are a force for order. Consider frog courtship at Ocelot Pond without benefit of vocal communication. Nighttime mayhem: combat among males of all the frog species calling in the chorus, struggles between males and unwilling females, indiscriminate matings producing offspring that mock the protections of speciation. By enabling species recognition, standing in for combat, and separating the ready and willing from the unprepared, frog calls and their reception enforce social order. They constitute an evolved process supporting the evolution process itself. Short-lived animals like frogs and mice serve as models for human biology. We know a lot about how the mating process works in túngara frogs, about what hormonal and neurological transactions drive the call-and-response that pulls male and female túngaras together, and that should tell us something about the nature of our own vocalizing and sexual responses.

Female readiness and receptivity are critical elements of human matings, and Mike's investigations of túngara desire have brought him recognition as an authority on sexual attraction even outside the realm of ecology. He served on the dissertation committee of a psychology student who was studying receptivity and behavior of women. In order to look at how readiness influenced how women try to make themselves look during the various phases of their menstrual cycle, the psychologist handed out a play-money budget to each of her woman subjects and monitored their Internet purchasing decisions. Her rather unsurprising finding was that women become increasingly interested in revealing, come-hither clothing when their hormonal readiness begins to peak.

At one of his public lectures the year before, Mike met a film director who was working on a romantic comedy in which the plot was juiced by pheromones, and one of the characters was a biologist who was an expert on pheromones. A Cameron Diaz-like star would play the part of the woman attracted by the pheromones. Would Mike read the script and correct matters of scientific fact? His response was characteristic, open-minded, and imaginative, even about this commercial romance. He read the script, and afterward, acting on spritely inspiration, he went back to the story and suggested a telling change in the ending: The charismatic male lead pursuing Cameron Diaz didn't get her. The biologist did. The director liked the change and suggested that, if the film ever made it into production, perhaps Mike should play the biologist.

Without ever turning his attention away from his little frog, Mike Ryan has asked deeper and deeper questions about túngara voice and sexual attraction: What is it about the whine-chuck and its frequencies that draws the females down through the leaf litter to the edge of the pond? How does the female pick out the male túngara's call from the other noisy calls in the rest of the chorus? When she hears an irresistible call, does she remember where the sound came from? If the males sing in competition with one another, how do they know when to chime in and what sound will be winning? Is the sound of the whine-chuck the only cue that compels the female to the male or some combination of signals? Is there any cognition involved in the female's choice, or is it unconsidered, just a response to a stimulus? How do these female decisions affect the ways in which the males evolve?

These questions have a legacy older than Mike's field, which is now known as behavioral ecology. Darwin recognized that behavior and evolution were inextricably interconnected. But like his ideas about sexual selection, his writings on the connections between behavior and evolution were largely ignored until the years just after World War II. In the meantime, there were any number of biologists who were becoming interested in animal behavior in and of itself and in ways of observing animal behavior without imposing ideas about human behavior on the animals. Like all scientists, they wrestled with subjectivity to reveal objective, factual information. This trend rolled out on two tracks: field studies undertaken in the United States and the United Kingdom and those launched in Continental Europe.

In the 1920s the German theoretical biologist Baron Jakob von Uexküll began to develop a set of ideas that put the animal and its perceptions front and center without prejudging them. He proposed the idea that every animal perceives the world through its own particular sensory apparatus, and he called this world *umwelt.* Your umwelt is composed of the sights, sounds, smells, and other sensations available to you through your physiology. The túngara umwelt is the leaf litter, the pond, and the puddle as experienced by the frog. Your *innenwelt*, and that of the frog, is the interior processing of those perceptions. Uexküll, who resisted Darwin's account of evolution, simply ignored the question of how the behaviors he was trying to systematize would affect a species in the long run or influence the emergence of new species. Yet the distinction he made between our perceptions and those of animals remains important today.[3]

In Austria in the early 1930s, the freshly minted PhD Konrad Lorenz was making detailed observations of home-raised jackdaws, which are members of the crow family, ducks, and geese on his family estate while he waited for a university appointment. Like von Uexküll, Lorenz was interested in scientifically separating our understanding of animals from our thinking about humans, but he subscribed wholeheartedly to the theory of evolution and understood there must be some connection between the process of evolution and behavior. Lorenz was very opinionated, confident that his years of firsthand observations of animals gave him superior insight, and he had a tendency to disparage much of the behavior research going on in Europe at the time. There were notable exceptions. The first was von Uexküll's work, whose attempts at systematization and ideas about umwelt and innenwelt Lorenz respected, and although von Uexküll was a generation older, he returned this respect and even drew on Lorenz's jackdaw experiments for his own writing.

Another exception was the work of Niko Tinbergen, a young professor at the University of Leiden. Tinbergen had been engaged in field studies of herring gulls in the Netherlands, and he and Lorenz began to correspond and then to visit to discuss their ideas about what made animals tick. One summer Tinbergen moved with his family to Lorenz's estate in Altenberg, and over the next few years the friends drew other scientists into the study of what was soon to be called ethology. This term was appropriated. Originally, it designated the study of human nature, but soon this definition was swamped by the term's new association with animal behavior. Eventually, in 1973, the two friends, along with Karl von Frisch, would jointly receive the Nobel Prize for Physiology or Medicine for their work in "ethology." Before this, however, World War II broke into their work on animal behavior and nearly devastated their friendship. Although Lorenz was struggling for academic recognition and found it financially difficult to maintain his estate, his upper-class origins made him sympathetic to Nazi ideas about racial purity and superiority. He published articles promoting the superiority of the "pure, wild" over the "domesticated," and like many other Austrians, he welcomed the Germans' bloodless takeover of Austria. He received a long-awaited appointment to a chair at the University of Königsberg.

As Lorenz jockeyed for standing in Germany, Tinbergen's work was thrown into disarray. The Nazis invaded the Netherlands in 1940, and two years later, Niko Tinbergen was imprisoned in an internment camp for two years. By pulling strings in Germany, Lorenz was able to secure an offer of release for his friend. Tinbergen refused.

Then in 1944, Lorenz, who had been called up by the Germans to serve as a physician, was captured by the Russians and imprisoned for almost four years. After the war, Tinbergen, discouraged by the difficulties of research and the morale in his own war-torn country, moved to England to take a position at Oxford, where he continued the efforts he had begun before the war to build an international community of ethologists.

For several years, relations between Tinbergen, who had trouble tolerating the fact that Lorenz had been "more or less nazi," and Lorenz were tetchy. But Tinbergen was keenly interested in reconstructing the group of ethologists that had begun to form before the war and tentatively began a reconciliation with Lorenz, who, worried that Tinbergen might harbor lingering resentments, responded cautiously. Documenting their interactions is a remarkable photograph, taken at a 1952 conference, of the two friends out hiking in the midst of their colleagues, as if Europe and their friendship hadn't been torn apart by the war. In later years there would be clashes between the two, but these were over scientific issues.

As the field of ethology was rebuilding from years of war and coalescing as an international endeavor, Lorenz and Tinbergen were much preoccupied with "releasers" of behavioral energy and the natural systems that expressed these. Lorenz envisioned that the forces that shaped animal behavior worked something like water in a hydraulic system, exerting pressure until they were released as animal activities. He continued to refine these ideas and to publish books for popular audiences that propagated the ideas emerging in ethology.

Lorenz, who is generally credited with being the father of ethology, considered himself a psychologist, and he held appointments in departments of psychology. While Tinbergen's early academic positions were in departments of psychology, he considered himself a biologist who happened to study psychology. Like von Uexküll and Lorenz, Tinbergen stressed that in order to understand how animals behave, you need to recognize that animals experience the world in ways that are different from the ways we do. But he went beyond this fundamental of ethology to bring significant advances in rigor and theoretical sophistication to the new branch of science. Focusing on enforcing systematic order on scientific notions about the reciprocal causes of behavior and evolutionary effects, he wanted to unravel the Gordian knot of biology, psychology, and inheritance that each animal represents. He spent years in a detailed consideration of instinct and sought to reduce scientific understanding of it to its essential, objective terms. He was trying to steer clear of soft, emotive terms and to replace these with statements of objective, observable fact. It is due in large part to his influence that animal behaviorists by and large no longer use verbs like *think, feel, intend* or nouns like *consciousness* or *mind.* Animals behave. That is what they do.

Eventually Tinbergen boiled down the process of understanding behavior to four essential but interrelated questions that when answered could explain any behavior: What is the physiological cause of the behavior? How does the behavior help the animal survive? How has the behavior evolved? And last, How does the behavior develop within the individual animal? These were the issues that set the research agenda for ethology, linked the study of animal behavior to ecology and evolutionary biology, and prepared the ground for the transformation of ethology to what is now known as behavioral ecology. This is a large and still-growing field in which biologists like Mike Ryan examine the things that animals do, the ways they act, under the lens whose primary designer was Niko Tinbergen. The concepts propounded today by Richard Dawkins and other biological theorists who see the gene as the primal force in and explanation for all biological life flow directly from Tinbergen's determination to reduce any account of animal behavior to irreducible fundamentals.[4]

Accordingly, if you are a behavioral ecologist, what is going on at Ocelot Pond is communication, which is the sending and receiving of signals, pure and simple. It is not frog language, and it does not *mean* anything. It is stimulus and response. While I am in Gamboa I am aware that this thinking is dominant, but because of my training as a music student and my work as a writer, I return often to Donald Griffin and his ideas about animal consciousness. Griffin, while keeping up his work on bat sound for quite a while, went on to explore the animal minds that perceive sound signals and to produce books that questioned the premise that only humans have consciousness and experience thinking. I love these books because, like Kipling's animal stories, they try to enter the minds of many different animals, from insects to apes. There is no way to read Griffin on animal cognition without becoming acutely aware of the processes of your own thought. This is probably why the signaler-signal-receiver model strikes me as being about as cold-blooded as the túngaras themselves. But Griffin is not in ascendancy in Gamboa, and the highly objective models spawned by Tinbergen are. Whatever communication takes place between two organisms takes place in *signals,* and eventually I will discover just how useful this idea is.

Mike takes this objectivity a step further, finding that even *signal* is burdened by too many assumptions. In behavioral ecology, you frequently come across the notion that *signals* convey *information,* but while I am in Gamboa Mike and two equally senior colleagues have in press a commentary that, after criticizing the use of *language* for animals on the basis of subjectivity, strips *signal* of even an association with information. In this article they point out that animal behaviorists have found *information* a convenient grip and use it quite loosely, and they call for tighter definition that drills down to what exactly information is.[5]

Mike has parsed the sounds of the male túngara's signals in minute segments to specify the female's choosiness within precise tolerances, and now team member Ryan Taylor is trying to put the male call itself into perspective by asking if sound is the only thing at work in the female's decisions. Is it only the frog's voice that draws the female across the dark pond to the male?

In an apartment at One-Eighty-Three two floors up from Mike's lab, Ryan Taylor is at work trying to figure out what role, if any, the flash of luminosity from the fully blown-up vocal sacs plays in the female's decision. When I visit the apartment, Ryan is keeping it dark, and the heat and humidity up here are crushing. Occupying the combination living and dining room is a tent of black plastic in which play will take place without the benefit of soundproofing or video monitoring. To watch, Ryan will just poke his head under a flap in the plastic tent.

What he needs in order to test for the effects of the inflated vocal sacs on the female frog is not just a fresh batch of female frogs every night but also a male frog whose vocal sacs he can control. Enter Robo-Frog, who after morphing into successively more sophisticated versions is now officially Faux Frog. As the progression of his nomenclature suggests, Ryan, who was raised in Louisiana, has a twinkle in his eye, a little southern amusement about what is ridiculous or ironic. Good thing he has this, because he has had to go to some pretty funny lengths to get a facsimile of the male túngara that the females can believe in. Ryan began with a wire skeleton with a balloon attached on either side of the head, an air compressor, and rubber tubing to send air into the balloons. The only reliable thing about the balloons was that they would break. He moved on.

Using the same system for inflation, Ryan next tried faux vocal sacs made of condoms tied to the frog frame with dental floss. He braved the long looks at the checkout counter and bought condoms by the gross and skeins of tooth twine. The condoms performed only slightly better than the balloons. But after a while, there was a happy accident one night in which something else broke, the frog skeleton. In order not to lose results from the females still waiting to be tested that night, he replaced the broken frame with a clothespin to secure the faux vocal sacs in front of the speaker. This caused Taylor to discover an essential fact: so long as the imitation vocal sacs inflated credibly, the female túngaras were undeterred by the lack of a frog body.

In the meantime, however, to eliminate questions about the importance of the image of the male's body in the female's choices, an engineer working on other biology research projects in New York City and a graduate student in Mike's department who was a talented artist had set to work to build a more accurate representation of a túngara. Faux Frog is plastic, and he is perfect: his size, his hunkered-down ready-to-bound posture, his lifelike warts. His blue-green skin is only slightly bluer-green than túngaras recruited from the ponds and puddles around Gamboa. Along with this new and more beautiful body, Faux Frog has more reliable faux sacs–an inflation device that allows for calibration of the timing between the faux sacs' inflation and the faux calls. This is a urinary catheter with the bulb segmented into two "sacs."

"The female," Ryan says, "has to make the best of a bad job," and he explains that the female túngara has to make her decision amid the din of the chorus of as many as eleven different kinds of frogs, the distraction of many túngara males, and the physical urgencies of her estrogen ramping up and her eggs getting heavier. His description reminds me of a childbirth instructor who said that when the moment to push came, the urgency would be undefeatable. "It's like being in a line in Filene's Basement. You have found a pair of shoes that you really love, and you need to pay for them. You can't get out of line because there are fifteen people in line behind you, and suddenly you have an attack of diarrhea." When I tell him about this he nods, and then he says with a characteristic twinkle in his eye, "There's a pretty good article that might help you with all this–'Don't the Girls Get Prettier at Closing Time.' Did Mike mention that one to you?"

Turns out that in Panama the country-western bar metaphor is controlling. It is a fun, simple explanation of the pressures enforcing the túngaras' mating decisions. But it doesn't address the details of how many chucks of what duration it takes for the male to reel in a female or of the involvement of visual corroboration of the call, and it certainly doesn't begin to say anything about how the frogs develop their calls or the way túngara calls will influence the evolution of the frog or vice versa. I begin to ponder what these myriad details imply about the voices of larger, bigger-brained animals and about our own vocalizing.

"I thought this was going to be simple," I confess to Mike as we are driving back out to Ocelot Pond on my last night of frog catching. The túngara may be a simple little animal with a one-way communication system that is about as interactive as a bumper sticker, and its call may be a couple of simple sounds. But simplicity stops right there. Mike's research over the years has made it evident that the apparently simple scenario of the male's two-part call summoning a female for insemination and the female's approach is actually an elaborately wrought transaction involving the endocrine system, larynx and tympanic membrane, nerves, and brain.

"The frogs?" He smiles. "Not so much simple as scientifically accessible. That's what I usually say, *scientifically accessible*–and," he adds as if this will make everything clear, "you know about Tinbergen, right? The four questions?"

I do–Immediate cause of behavior? Survival effects? Evolution? Development in an individual?– and I can see how the experiments, the hormones, the perception, reflect Tinbergen's systematic views on behavior. "Still, it's pretty complicated."

"Yeah. But not so complicated if you consider some of the other animals," he says. "I mean, some of the mammals–and then there are the birds." He pauses, and after a little while he says, "Yeah, then there are the birds. . . ."

But it is too soon to go there just yet. Mike has set me on a path of hormones and signals and social life, and this will lead me to a park in England.