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Excerpt
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Introduction

The Túngara Frog

The male Túngara frog floated in the small pond on the floor of a clearing in a Panamanian rain forest. Although he was diminutive by absolute standards (between 3 and 5 cm long from snout to rear end), he was nevertheless one of the largest of the many males in the pond. He inflated his throat sack to a startling size, approximating that of his head and body combined, and began to produce surprisingly loud calls – *whiine; whiine; whiine.* Responding to this sound, other males in the pond began to call similarly, which in turn stimulated our male to produce more complex vocalization – *whiine, chuck-chuck, whiine, chuck-chuck.* Soon these frogs were living up to their reputation as one of the most vocal of frog species; the moist tropical air was filled with the clamor of their *whiine, chuck-chucks.*

A fringe-lipped bat was hunting on the wing nearby, and heard these vocalizations. Taking advantage of the fact that the *chuck* portions of the calls are especially easy to locate, the bat pinpointed a calling frog, swooped and caught it. Silence immediately descended upon the pond, but was short lived; a few males soon resumed calling and the chorus once again spread throughout the pond, but this time no *chucks* were added as the chorus grew – *whiine; whiine; whiine.* A female entered the water, swimming among the calling males and stopping periodically within 10–20 cm of a male, listening to his calls. She moved on without interacting, wriggling free from one male who attempted to clasp her sexually, and finally pausing near two males who began to add *chucks* to their calls – *whiine, chuck; whiine, chuck.* She oriented initially toward the smaller of these two males, then toward the lower pitched *chuck* sounds of our large male. Moving quickly to the larger male she accepted his sexual clasp.

The female swam to the pond shore, carrying our now-silent mounted male with her, and left the pond, possibly to escape the danger from predation generated by the conspicuousness of the continuing vocal chorus. After midnight, when chorusing had ceased, the female re-entered the pond, still carrying her mate. For about an hour she released eggs near the pond's edge and our male took each batch with his hind legs, fertilized them and created a foam nest for them by whipping their outer cover into a "meringue." When the nest was complete, the female swam from underneath our male, who lingered for a minute, apparently fatigued by egg-beating, before disappearing into the darkness.

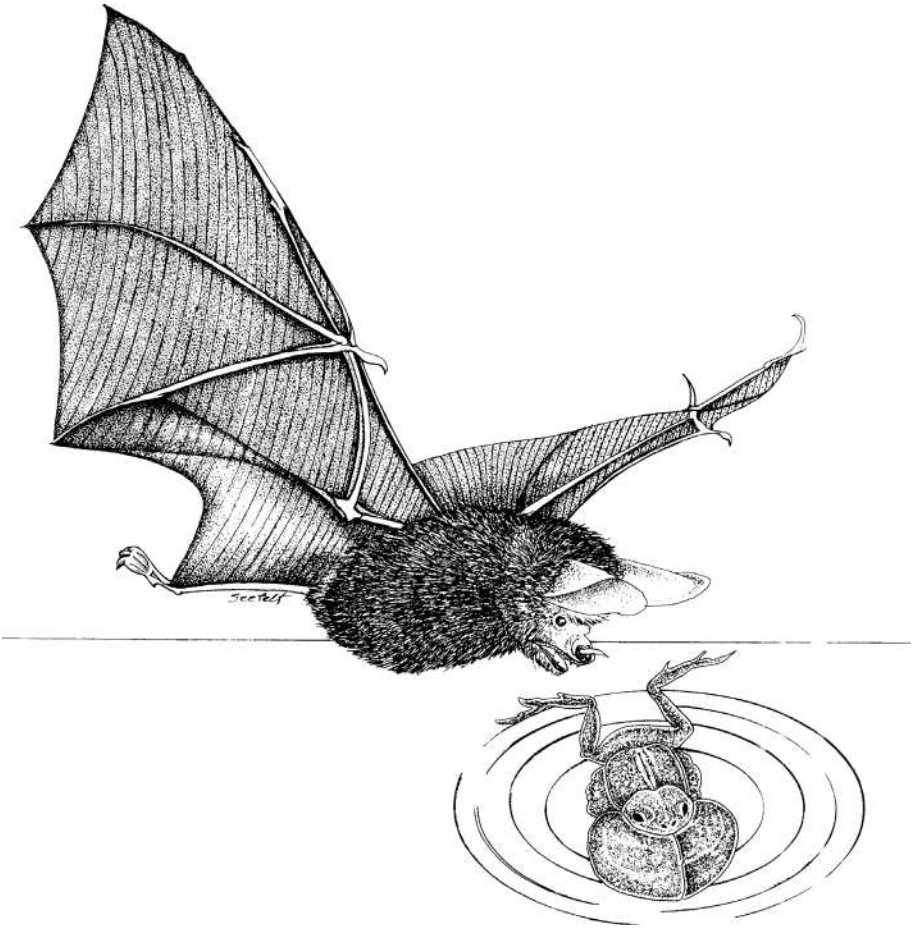

Fig. 0.1 A fringe-lipped bat about to catch a Túngara frog.

The Carolina Wren

A male Carolina wren was widowed in the flash of a sharp-shinned hawk's attack. It was late September, but singing and pairbonding are possible throughout the year for this wren, as is the case with its tropical-living relatives, even though the hawk struck in the State of Maryland, USA. The widowed male continued to sing and defend his permanent year-round territory using a repertoire of forty-two song types. He did not flaunt his repertoire but, instead, sang one of his songs from 5 to 120 times before switching to another. During the two months after he left his parents' care, the song learning portion of his life, he learned 85 percent of his songs from males surrounding his new territory, neighbors, but learned 15 percent while dispersing from his birthplace or from males more distant from his territory and not found in his neighbors' repertoires.

At 9:00 a.m. a stranger wren was detected. Our male approached it with plumage fluffed, quickly sang three song types without the usual pause between them, and then attacked the new bird. The new bird gave high-pitched *pi-zeet* calls, an appeasement or friendly call between mates and siblings. It then gave high *pee pee pee* calls as the resident male continued to attack, producing short growls during each flying attack. Between attacks, the resident male also uttered harsh, low *chirrs*. The intruder fled silently.

At 10:30 a.m. a second intruder was detected. Unlike the first one, this intruder responded to the resident male's attack by fluffing up and calling a chattering *thirrrrrrrrrrrr*. Next, the new bird gave this chattering call during the resident male's song rather than after it. Now, the resident male stopped attacks and, fluffed with its tail upright, hopped around the intruder like a miniature strutting turkey while uttering high-pitched *tsoock* calls. The intruding bird, a female, uttered *pi-zeets* whenever the male approached, and chattered when he sang or might attack. A pair bond had formed seven months before they nested in the spring.

The pair foraged within earshot of one another throughout the daytime. Only the male sang and only the female produced *dit-dits* and chattered, whereas both pairmembers *pi-zeeted, chirred*, *rasped*, growled, and *chirted*. The prolonged series in which chirts were delivered varied greatly in their timing and pitch and were used when a hawk perched overhead or when a pair member moved a relatively great distance. It was primarily the female who *chirted* while watching a hawk; the male foraged for food while the female kept up the surveillance. If the hawk moved, even slightly, the *chirts*

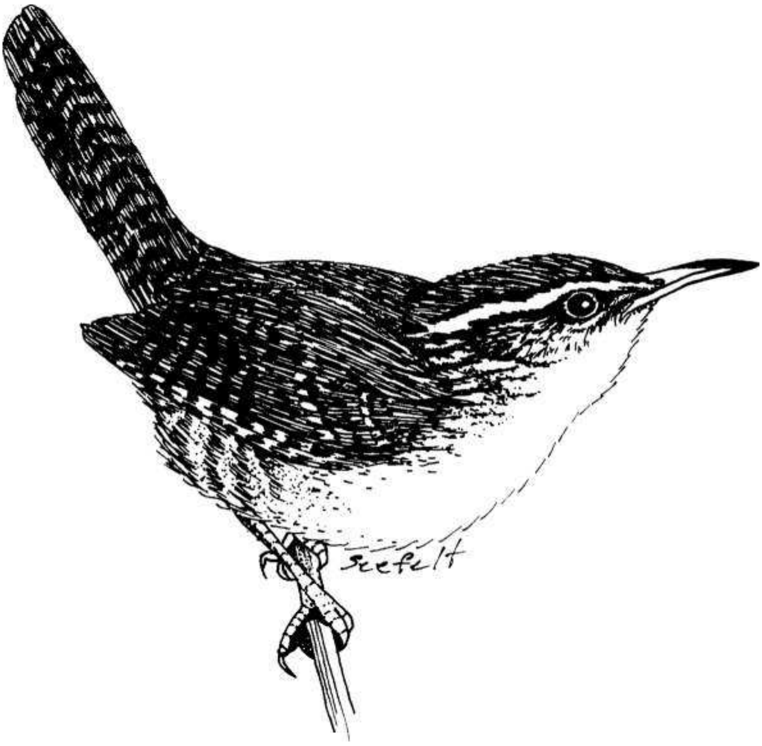

Fig. 0.2 A Carolina wren. Males and females have identical plumage.

shifted to a higher pitch and the alerted male stopped foraging. Chirts were sometimes combined with other call notes. For example, *chirts* were combined with *pi-zeets* when one of the mates approached the other from a long distance or were combined with *rasps* or *chirrs* when birds chased an intruder. Snakes elicited rasps, whereas to most predators the wrens produced *chirt* bouts.

After two more years had passed, the male was killed by a feral housecat. Within two hours, wren pairs with adjacent territories had moved onto the territory and had chased the female away.

The Hooded Warbler

A male hooded warbler occupied his nonbreeding territory in the Yucatan Peninsula, Mexico, from 20 September until 15 April. About every two seconds he produced a metallic-sounding *Chink!* call as he foraged for insects near the ground, flashing his white outer tail feathers to flush them. The calls usually sent prospecting birds, male or female, fleeing, but if one did intrude, our male met it with harsh growling sounds and a chase. On 15 April, he began his return migration to his breeding territory in northwestern Pennsylvania, arriving there on 5 May. Here, he not only called *chink* but, now from far above the ground in the forest, he sang a single type of song, unique to him, that sounded like *weeta weeta weeTEEo* – loud, clear, and ringing through the woodland territory, sung at a regular cadence of 5–8/min, faster if another male sang nearby. Other males had returned as well but no females yet. Some were returning old-timers such as him, whereas some were new. These newcomers he responded to vigorously. If they sang near his boundary, he flew to it and displayed his black throat and drooped his wings. Rarely was fighting needed.

A female entered his territory on 18 May, three days after her arrival on the breeding grounds, and began nest building the next day 1/2 meter up in a small bush. She uttered only *chink* calls, and stayed near the ground while foraging, just as she had on her winter territory, in Nicaragua. Remarkably, as soon as the female began nest building, the male stopped repeating only his single unique song and now mixed five other songs into his repertoire, singing at a faster rate, 10–12/min, especially when other males were nearby, often matching their song types during countersinging matches. Some songs used in “mixed” singing were only found in this local population, showing that the males had learned them after arriving here. Few of the males and none of the females had been raised here.

During the time she was nest building, egg laying, and incubating them, the female called *chink* repeatedly whenever she was away from the nest. Of the four young hatched in their nest, two were fathered by a neighboring male.

When the nestlings were 7 days old, a chipmunk approached the nest. The female used more rapidly uttered *chink* calls with a higher pitch than normal. As the chipmunk climbed toward the nest, the male flew at it and the female produced very high-pitched, rapid *chinks*. Not yet capable of flight, the nestlings fluttered out of the nest, dispersing in all directions. After the chipmunk left, the parents stopped the high-pitched *chinks* and returned to foraging. The fledglings uttered high-pitched *chippit-chup* calls, particularly when a parent was nearby. After a few days, the male took on most of the feeding duties while the female began to build a second nest that would receive a new set of eggs within a week.

The California Ground Squirrel and the Rattlesnake

The female California ground squirrel was huddled in her underground nest with her five-week-old pups when she detected the faint sound of something moving through the dry-leaf litter near the mouth of her burrow. This was no rustling sound like a walking

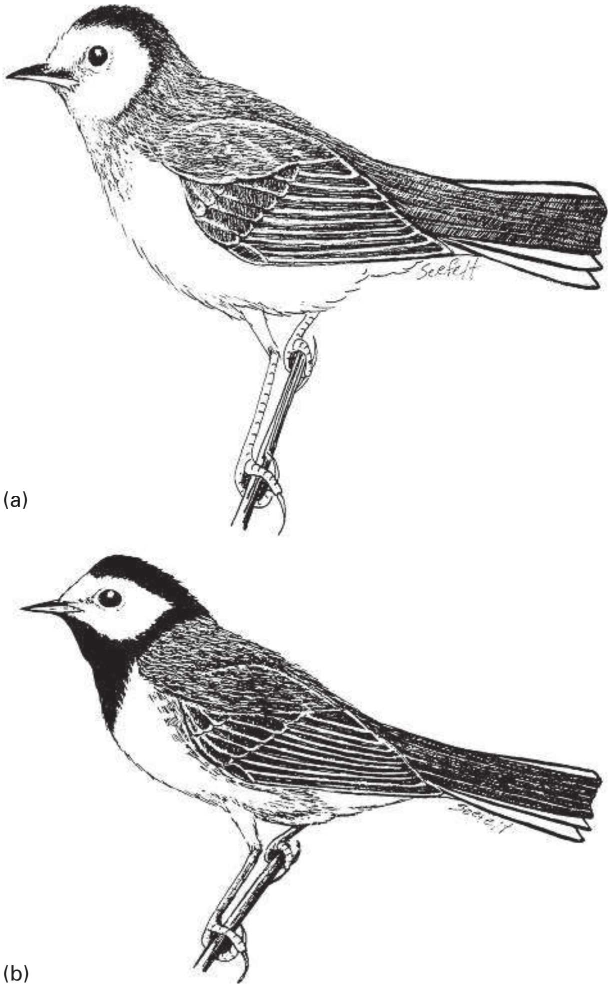

Fig. 0.3 Female (a) and male (b) hooded warblers differ in plumage and only males sing; otherwise, they share the same vocalizations.

animal; it was the continuous *ssshh* of something sliding. Leaving her pups, she moved cautiously toward the entrance, unable to see in the burrow's darkness, but sniffing and listening intently. As she progressed, the odor of the intruder became more apparent. Rattlesnake!

The squirrel's pace slowed as she strained to pick up more precise cues. Where exactly was the snake? Was it small, or large enough to be hunting her pups, and to pose a serious threat of injury to herself? Was it cold and sluggish from the cool spring morning, or had it warmed itself to an action temperature in the sun? Gathering a mound of dirt in front of her, she kicked it ahead of her, paused to listen, stepped forward, and sprayed a second load of earth into the darkness. This second fusillade struck the snake full in the face, causing it to rattle as it withdrew its forequarters into a ready-to-strike defensive posture. The mother backed off quickly at the distinctively dangerous sound of a large, warm rattlesnake, stumbling over one of her pups who had followed her to the scene.

Chattering loudly, the mother returned to deal with the snake as the sound of her call sent the pup back to its nest. While she continued to vocalize repetitively, she began to construct a substantial plug of earth between herself and the snake, pausing intermittently to pack it tightly by pounding it with her head. Once the rattlesnake's access to her pups was eliminated, she stopped calling, relaxed perceptibly, and re-entered the nest. Picking up a pup in her mouth, she left her burrow via another exit and traveled to the burrow of an adult male some 25 meters away, depositing her youngster there. As she shuttled back and forth between old and new nest sites, she showed evidence of continued concern about snakes, pausing intermittently to wave her fluffed tail from side to side in a distinctive visual signal. She did not rest until all six pups had been transferred to their new nest site.

Anna and her Mother

Anna, an energetic 11-month-old infant, had been placed in her new, spring-suspended "bouncy chair" for the first time, and was just mastering the skill of bouncing in it. Her mother, who was speaking briskly in her steady, low-pitched voice to a visiting neighbor, smiled as the bouncing began, slowed the pace of her words, and switched to a high-pitched, lilting tone of voice. "WELL! Aren't YOU the smart one? HOW'D you learn to do that so FAST?" Anna paused, locking eyes with her mother, and both broke into delighted smiles as Anna kicked herself into even higher bounces, and her mother encouraged her, "THAT'S my SMART girl; she's no slug like her MAMA was!" When her mother resumed speaking to her neighbor, switching immediately back to her "adult" voice, Anna quickly tired of bouncing, and struggled to stand in her chair. These efforts had yielded success by the time her mother noticed; once again mother radically changed her manner of speaking, emitting a single, sharp, low-pitched "NO!!" But, mother's prohibition was too late: Anna toppled from her chair, producing a loud thump with her head as she landed on the (mercifully carpeted) floor. Frightened and a bit hurt, Anna began to cry as her mother rushed to pick her up. As she sat in a rocking chair to begin to comfort Anna, mother adopted yet another distinctive pattern of speaking, gently shushing her crying baby, and speaking quietly with long, smooth, low and falling pitch contours, "Ssshhhh: thaaat's okaay; maaama's here." As Anna became quiet, her mother continued to rock and cuddle her and resumed her conversation with the neighbor, once again making the striking transition to the choppy, rapid-fire, monotonic pattern of speaking used when addressing other adults.

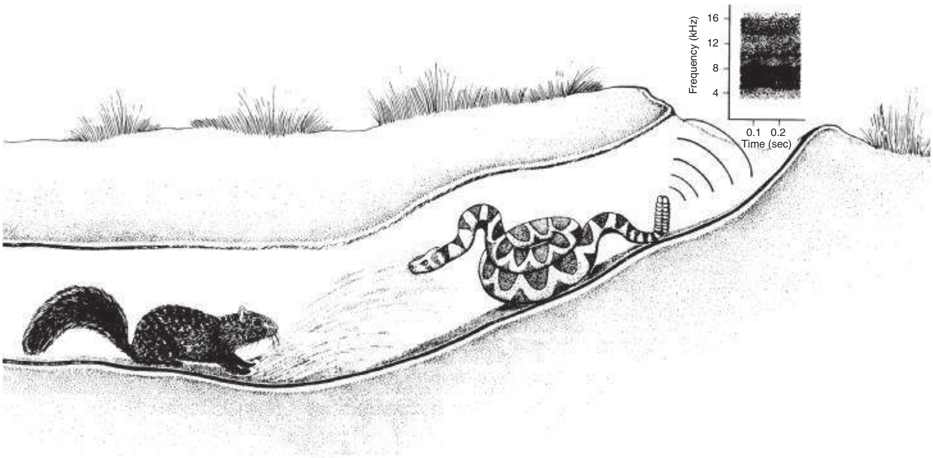

Fig. 0.4 A California ground squirrel, defending her pups, assesses a rattlesnake by causing it to rattle.

Fig. 0.5 Anna and her mother.

The Túngara frog, the wren, the warbler, the ground squirrel, and Anna's mother illustrate how acoustic signals have served important functions since animals first climbed ashore. Phylogenetically related increases in cognitive ability and social intricacy went hand in hand with increased signal complexity, but some aspects of signals are conservative. For example, some aspects of Anna's mother's speech originated in vocalizations of the first terrestrial animals. While we cannot discover fossil evidence, we can surmise how vocal communication evolved from basically indicating size to revealing motivation by studying how physical components of signals are related to both. We discuss these in Chapter 3. The discrete nature of most vocalizations gives communication the appearance of a discrete event, a call and a response, rather than an ongoing process. But communication, like evolution, is an ongoing process, a means by which an animal attempts to regulate the behavior of others to its benefit over time.

In living animals, communication and eating are analogous processes. An animal eating a meal is a discrete event like a single bird song, but eating serves to maintain its energy balance over a longer period of time. Eating and vocalizing differ in an important way: eating acquires energy, whereas signaling by any modality – sound, sight, touch, electrical, or chemical – costs energy. So why is signaling so common? One answer to this question is that signaling substitutes for, or replaces, behavior that is energetically costly and dangerous, such as fighting. In addition, signaling can reduce the energy cost of defending a territory or advertising for mates. Think of how much energy a wren saves by singing from one spot versus patrolling around its large territory to find a mate. Attracting a mate vocally, and thereby saving energy, is probably a very old use of signaling. Even the earliest land animals, as represented by the Túngara frog, illustrate signaling used in this way. This idea is developed further in Chapter 3.

Signaling is similar to eating in another fundamental way: they both reflect exploitation of a resource. The resource for an animal eating is the nutrients available in other organisms; but for signaling, the resource being exploited is the process of signal assessment by other animals. Indeed, one key to understanding animal communication is to realize that assessment *is* a resource that can be exploited. A simple example, originally expressed by Charles Darwin, illustrates this point. Why do dog-like mammals intimidate rivals by exposing their canine teeth in a threat signal? In order to bite, the lips must be retracted so that the lips are not bitten, so retraction of the lips alone is assessed that biting is likely to occur. If the assessor backs off, the signal has effectively replaced the more expensive act of biting, benefits the signaler by lowering its energy costs, and will be favored by natural selection in the long run. Lip retraction is often coupled with other signals in other modalities, such as a low-pitched growl, to encourage assessment that benefits the signaler.

Could it be that animal communication is not driven by signaling but, instead, by the assessors of signals? We are used to thinking in terms of signalers sending information but this, we feel, is not at all what animal communication entails. We may have been led astray by an information approach for the last 75 years. Assessment may be the main source of natural selection on signaling and best explains our example of lip retraction as a signal. It is not the signal itself but feedback from the assessment of the signal that favors its use. This assessment also, and importantly, affects the physical properties of the signal, its structure or form. We delve more deeply into this neglected topic in Chapters 2 and 3 and, indeed, this new approach forms the foundation for this book.

A major reason that research into animal communication has largely ignored assessment and the relation of signal form to signal function while favoring a search for “information” in signals may have originated with the view that biology does not have the tools to deal with the subject. An influential researcher, W. John Smith (1977, 1997), suggested this and advocated the science of linguistics be applied to animal communication. As Terrence Deacon pointed out in *The Symbolic Species* (1997), using human language as a basis to compare other species’ communication “as exceptions to a rule based on the one most exceptional and divergent case is a perverse analytical method.” We agree that reliance on human language concepts to understand animal communication is faulty. Human language concepts are so embedded in our thinking that they often sneak into otherwise competent research. A chief way to overcome this bias is to get rid of the term “information” (i.e. transmitted information) altogether when describing animal communication, reserving the term to describe how we, as humans, describe communicating animals to other humans, not to how other animals communicate with each other.

Here, we present a new approach to animal vocal communication that highlights the biological principles we feel underlie the evolution and usage of vocal communication. Hopefully, the perversity that Deacon saw in the field will be alleviated. But most importantly, we hope young researchers will be attracted to apply the logic described here to future research.