ANIMAL VOCAL COMMUNICATION: A NEW APPROACH

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resulted in the best parts of the book attributable to him. Jane Smith corrected the many problems of detail in the text, and smoothed and clarified many convoluted passages during the process of copy editing.

Prologue

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 tropical-living birds, even though the hawk struck in the State of Maryland, USA. The widowed male continued to sing and otherwise defend his permanent year-round territory using a repertoire of 42 song types. He sang one type 5 to 120 times before switching to another. During the two months after he became independent from his parents, his song-learning phase, he had learned 85% of his song types from neighboring males; he learned the remaining 15% while dispersing 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. The male approached it with plumage fluffed, quickly sang three song types without the usual pause between them, then attacked. The intruder gave high-pitched *pi-zeet* calls, an appeasement or friendly call between mates or siblings. It then gave high *pee pee pee* calls as the resident male continued to attack, producing short growls during each attack flight. Between attacks, the resident male also uttered harsh, low *chirrs* between attacks. The intruder fled silently. At 10:30 a.m. a second intruder was detected. This time the intruder responded to the resident's attack by fluffing and simultaneously calling a chattering *thirrrrrrrrr*. Next, the new bird gave the chattering call during the resident's song rather than after it. Now the male fluffed and hopped stiffly around the intruder like a miniature strutting turkey, uttering high-pitched *tsuck* calls. The intruding female uttered *pi-zeeets* when the male approached, and chattered when he sang or might attack her. A pair bond had formed seven months before they nested in the spring.

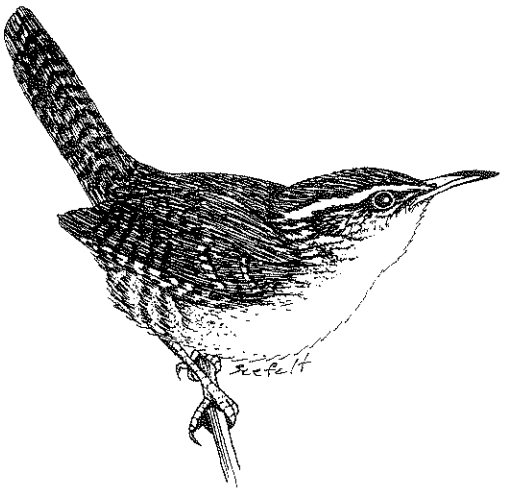

Fig. P.1. A Carolina wren. Males and females have identical plumage.

The pair foraged within earshot of one another throughout the daytime hours. Only the male sang and only the female produced *dit-dits* and chatters, whereas both *pi-zeeted*, *chirred*, *rasped*, growled when attacking intruding wrens, and *chirted*. *Chirts* were variable in timing and in their component frequencies and were used when a hawk perched near or when a pair member was moving a long distance. Mostly the female used *chirt* sequences when a hawk remained nearby; the male foraged for food while the female kept up the surveillance. If the hawk moved, even slightly, the female's *chirts* shifted to a higher pitch than before the movement. Then, the alerted male stopped foraging. *Chirts* were combined with *pi-zeets* when one of the mates approached the other from a long distance, and they were combined with *rasps* or *chirrs* when chasing an intruder. Snakes elicited *rasps*, whereas most predators elicited *chirt* sequences.

After two more years had passed, the male was killed by a feral house-cat. Within two hours, wren pairs on either side had moved onto the territory and had chased the female away.

Anna and her mother

Anna, an energetic eleven-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 heere.' 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.

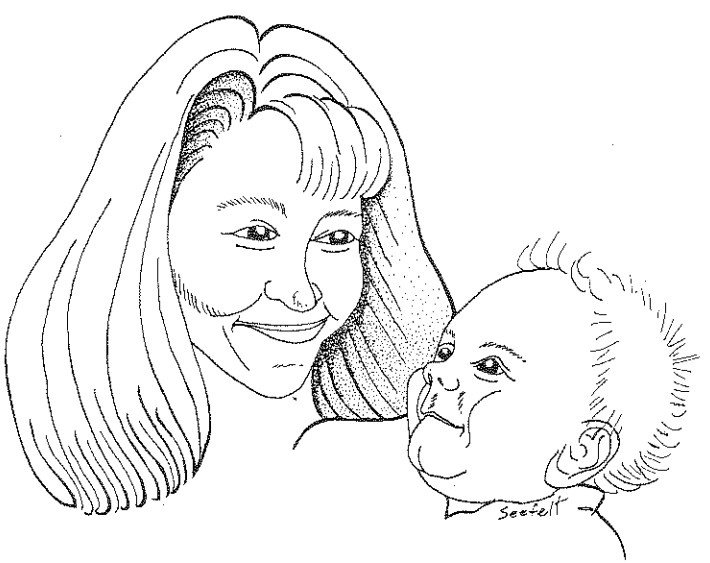

Fig. P.2. Anna and her mother.

The hooded warbler

A male hooded warbler occupied his nonbreeding territory in the Yucatan Peninsula, Mexico, from 20 September until 15 April. He used metallic-sounding *chink* calls to defend this territory, calling about once each two seconds, but uttered harsh growling sounds before chasing the (rare) intruder who did not leave his territory. Calling and foraging for food took place near and on the ground. On 15 April, he began his return trip to his breeding territory in northwestern Pennsylvania, arriving there on 10 May. Here, he not only *chipped*, but sang one song over and over from positions high in the trees of his forested territory – a loud, clear, ringing, tonal, *weeta weeta weeTEEoo*, sung at a regular cadence of 5–8/min, faster if another male sang nearby. Other males had returned as well but no females. Some he distinguished as returning oldtimers such as himself, 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 to beat newcomers.

A female entered his territory on 18 May, three days after her arrival on the breeding grounds, and began nest building on 19 May. She uttered only *chink* calls, and stayed low while foraging, just as she had on her winter territory, in Belize. As soon as she began nest building, the male stopped repeating the same song and 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. He had changed from repeating a single song type, unique to him, to a mixed repertoire shared with neighboring males. Some songs used in 'mixed' singing were only found in this local population, indicating 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, laying eggs, 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. The male was apparently unaware of this for he fed all the nestlings at the same rate as the female fed them. 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

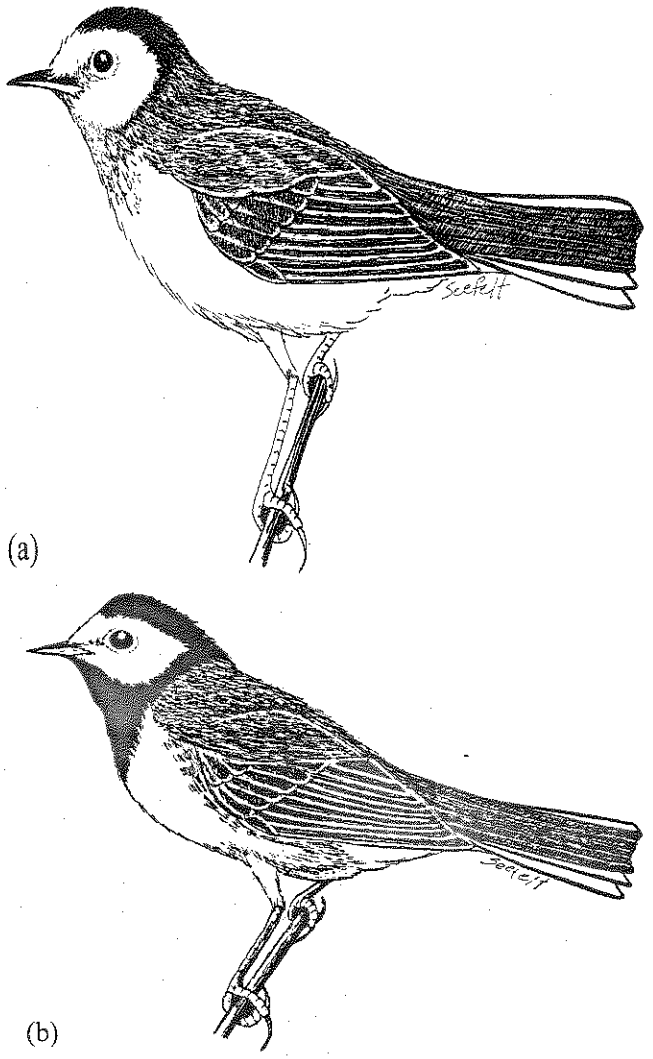

Fig. P.3. Female (a) and male (b) hooded warblers differ in plumage and only males sing; otherwise, they share the same vocalizations.

the high-pitched *chinks* and returned to foraging. The fledglings uttered high-pitched *chippity-chups*, particularly when a parent was nearby. But the male tended to feed two young and the female the other two young. After a few days, the male took on most of the feeding duties while the female began to build a second nest which would receive a new set of eggs within a week.

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 sac 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 a 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*.

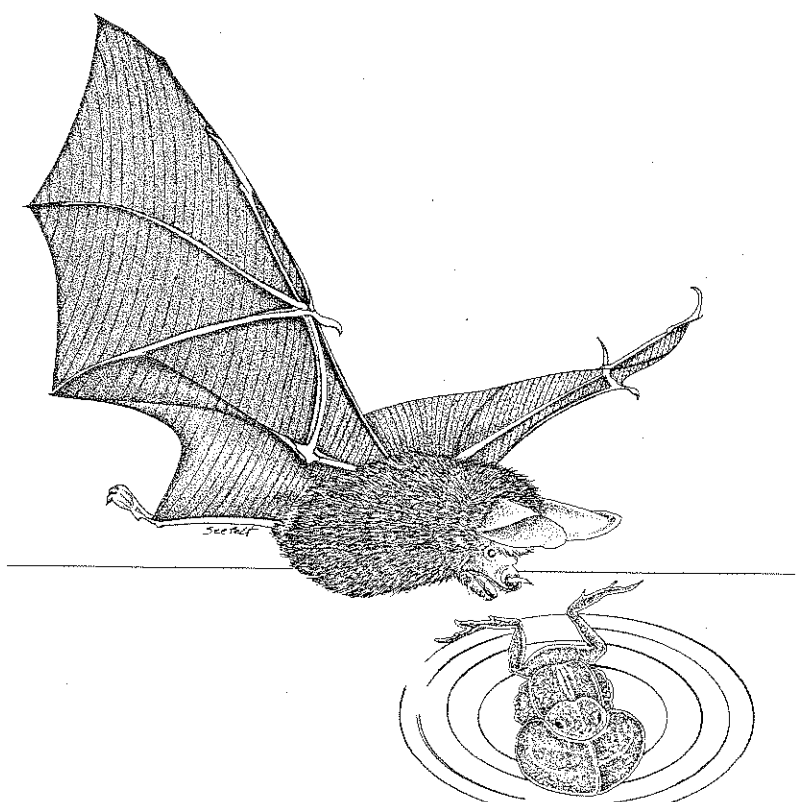

Fig. P.4. A fringe-lipped bat about to catch a Túngara frog.

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 covering 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.

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 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

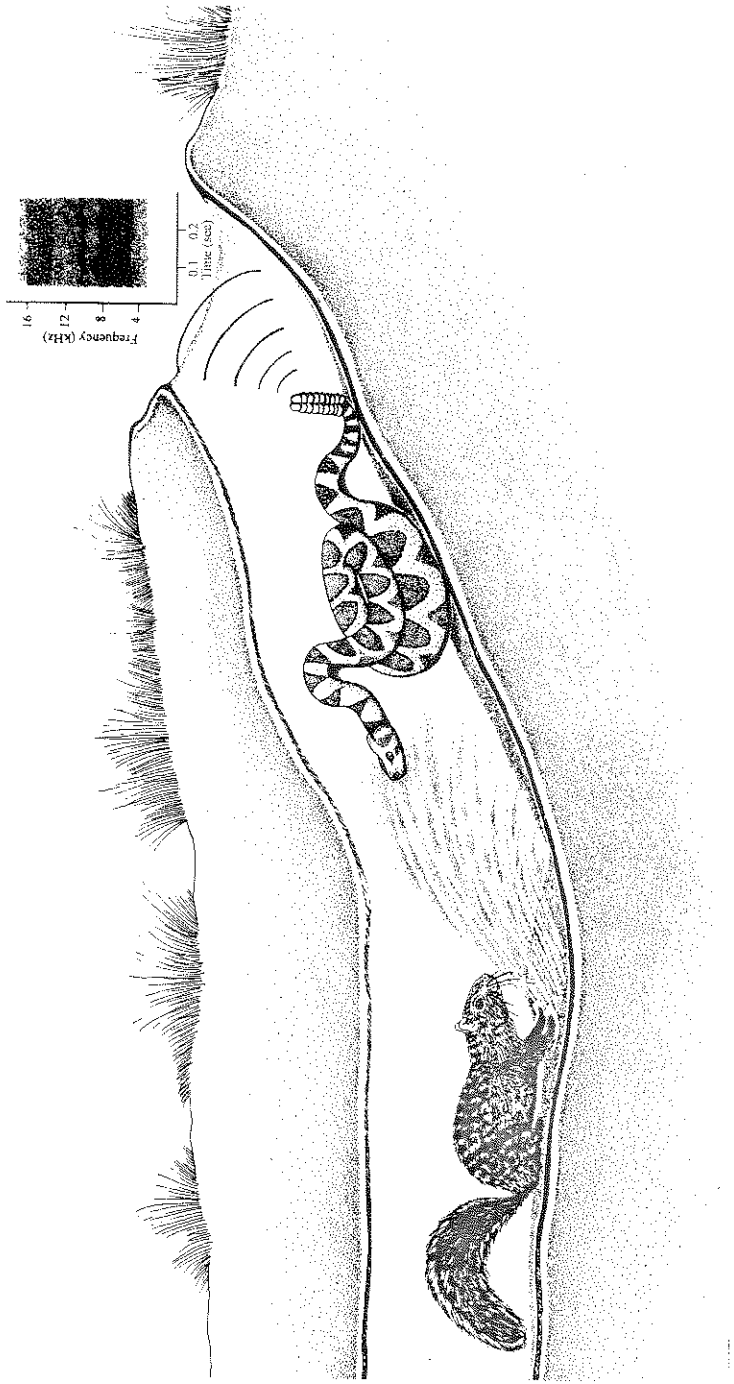

Fig. P.5. A California ground squirrel, defending her pups, assesses a rattlesnake by causing it to rattle.

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 system 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 of her pups had been transferred to their new nest site.

The wren, the warbler, Anna's mother, the Túngara frog, and the ground squirrel often vocalized only during an important but rare event such as a fight, but at other times called almost constantly. Nevertheless, it is possible in most cases to identify discrete sounds (the individual *whine* calls of Túngara frogs, for example) that reflect vocal communication. The discrete nature of most vocalizations gives communication the appearance of a discrete event, a call and a response, rather than an ongoing process. However, it will be argued that such discrete vocalizations reflect an underlying process of regulating the vocalizer's circumstances. An analogy to feeding illustrates our point. Animals must eat, a discrete event, but this is in service of maintaining their energy balance. Effectively regulating one's energy balance and social circumstances is, in turn, a prerequisite for success in other processes, such as competing for mates and territories, and ultimately in reproducing.

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 has often been favored by natural selection because it substitutes for behavior that is even more energetically

costly, such as attacking. In addition, fighting is more likely than communicting to result in injury or attract predators, important costs in addition to those on the energetic balance sheet. This idea is developed further in Chapter 3.

Signaling is similar to eating in another fundamental way: they both reflect exploitation of a resource. Eating capitalizes upon the nutrients available in other organisms; signaling exploits the process of assessment by other animals. Indeed, this provides a more general reason for the prevalence of communication; the fact that animals constantly assess their environments (in order to make adaptive behavioral decisions) makes it possible for individuals to use signals to manage their circumstances. A simple evolutionary example, initially formulated by Charles Darwin, illustrates this point (see also Andrew, 1972; Krebs & Dawkins, 1984). Why do dog-like mammals intimidate rivals not only by biting them, but also by exposing their canine teeth in a threat signal? Retracting the lips from the teeth is a necessary preparation for biting (so that the lips are not bitten). For this reason, retraction of the lips can be used as a cue to assess when biting is likely to occur. The use of this assessment cue creates a regulatory opportunity: a wolf can deal with rivals by using the 'cheaper' threat display instead of the more costly act of biting.

Communication is a two-way process. The behavior of each communicant is both cause and effect of the other's behavior. Each exchange is difficult to understand in isolation. It is also difficult to consider communication in isolation from other behavior. Communication is better understood in terms of the *regulatory* problems each participant faces: each tries to regulate the behavior of the other. Natural selection should favor mechanisms that are effective in minimizing the difference between preferred and actual states of the other's behavior. An animal can regulate the behavior of another animal either through direct physical manipulation or by communicating. Communicating with *vocalizations* is just one means of regulating social circumstances. Concurrent changes in posture, locomotion, and body orientation might, in a male California ground squirrel, for example, function together to keep another male away from an estrous female (Owings & Hennessy, 1984).

This all-inclusive view of communication differs in a fundamental way from earlier ones. Students in a graduate seminar on animal communication were asked to give a short definition of animal communication. Eighty-five percent defined communication as the 'transfer of information from one animal to another.' The remaining students stated something

like 'when one animal's signal influences the behavior of another.' The more popular definition, information transfer, arises from application of a concept in wide use, the 'information concept.' The root meaning of communication is 'sharing,' suggesting that some transfer takes place, as in the information often said to be exchanged during speech. The information concept has proven very useful in making sense of animal communication (Smith, 1977), but we will argue that it has become too central, deflecting our attention from the more fundamental idea of regulation.

The concept of sharing during communication is also problematic. Smith (1977) used the term sharing in part to emphasize that information transmitted to someone else is not lost by the sender; thus, it is shared, not given away. But, the additional implication, of mutualism or cooperation, was also part of this approach, as it was for many other researchers in communication at that time (Dawkins & Krebs, 1978). The assumption that cooperation lies at the root of all communication is now recognized to be inconsistent with a basic tenet of the logic of natural selection: that conflict is just as likely as cooperation. For example, courtship and pairbonding in animals were viewed as a form of cooperation to reproduce (Trivers, 1972). Now, it is recognized that there are conflicting interests between mates and, of course, mates do not reproduce 'for the good of their species' (Williams, 1966). We now think of reproduction in terms of mixed reproductive strategies, with males and females often copulating with nonmates. Communication has changed too. The view that communication is selected to maintain orderly interactions and social structures is likewise an outdated concept. As a field of evolutionary biology, communication research must be guided by the logic of natural selection.

One way that this guidance can be made explicit is to use 'communication' as a general term for the subject, but to use 'management' to describe the part of the process that includes the production of a vocal signal. Selection favors those able to use signals to manage the behavior of others in their own interests. Other individuals perceive the signal, and respond or not to the signal in *their* best interest. Signaling and perceiving serve self-interest. The term 'perceiving' is used here, rather than the more common 'receiving,' to emphasize the active role of this process in communication. Perceiving individuals achieve their importance as a force in communication and its evolution through their 'active assessment' of signals.

The warbler, wren, mother, frog, and squirrel illustrate diverse forms of vocal communication. How do we discover general explanations for the form of the signals, the responses of perceiving individuals? Why would natural selection favor such interactions and why do they take the form they take? These questions and others are summarized in Chapter 5, after the conceptual and practical tools have been provided to understand them. Our goal is to provide both a way to think objectively about vocal communication and a way to perform research to answer the specific questions that generate your interest in communication.

1

Overview of ideas

What concepts have been used to explain the sorts of behavior described in the prologue? The purpose of this chapter is to review the variety of those ideas. The overview is historical in part, but is also organized around Nikolaas Tinbergen's four-part classification of questions that can be posed about behavior – about the evolutionary history and functions of behavior (ultimate questions), and about the immediate regulation and development of behavior (proximate questions).

This chapter does not distinguish between the ideas that do and do not form a part of a modern synthesis. Our synthesis is presented in Chapter 2, and is developed from only a portion of the concepts discussed here. The goal in Chapter 2 is to identify that subset of old and new concepts with the greatest capacity to provide an understanding of communicative behavior.

1.1 An evolutionary approach: ultimate questions

1.1.1 Natural selection and the functions of behavior

Well over a hundred years ago, Charles Darwin provided the essential elements of the evolutionary framework in which this book is cast. His principle of evolution through natural selection is very powerful, but also so elegantly simple that it can be summarized by just four points (Alcock, 1989). (1) There is variation among the individuals within a species, in body form, physiology, behavior, and so on. (2) Some of this variation is heritable; in other words, some of the distinctive characteristics of individuals can be passed on to their young, so that offspring tend to resemble their parents more than they do other members of the species. (3) Even though adults produce many offspring, populations do not consistently grow in proportion to the number of offspring produced. This