Animal Communication: What Do Animals Say?

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We have long wondered what functions and meanings animal vocalizations have for animals and how these are related to our own unique speech. Since Darwin (1872), biologists have described vocalizations with the view that, once many repertoires are studied, the process of comparing animals' sounds will lead to an understanding of how communication evolves. Since the 1950s the descriptions of sounds have utilized the sound spectrograph, a machine that produces a two-dimensional picture of sound (figs. 1 and 2). Armed with the sound spectrograph and reliable battery-operated tape recorders, researchers could objectively describe sounds rather than rely on verbal descriptions alone. However, the "meaning" of a vocalization was not deduced by describing the sound: responses to the sounds by listeners within their particular context (e.g., their internal physiological state and environmental cues) were used to understand the meaning of a sound (Smith 1977). Thus, the physical description of sounds was seen as only a first step in our understanding of how animals use them.

My own work focused on possible relationships between the physical structure of vocalizations and their functions in communicating (Morton 1975, 1977, 1982). Like others, I defined function by observing how listeners responded to the vocalizations, but my interest centered on the functional benefits these responses produced for the caller. It soon became obvious that animal sounds are not arbitrary like our speech sounds. Different human languages use different sounds for the same thing; for example, we say "go away" in English and "vah́ yah sey"in Spanish. But, every bird or mammal that attempts to make another individual move away from it uses a low-pitched, usually harsh sound — a growl. If the listener does not move away, the growler is likely to attack: this tells us that the growler is aggressive. If animal sounds were arbitrary like our speech, surely somewhere in the animal kingdom we would find some other sound used by highly aggressive animals, but we do not.

Why would evolution favor the use of a growl to promote a useful benefit to an aggressive animal? Perhaps a return to speech will give us a clue. You can say "go away" many different ways, but if you are really serious about it you will say it with a lowered pitch and even try to get the last word lower on the last syllable. In other words, you "growl" too! Apart from what the words "go away" literally mean, your intonation adds meaning to the listener and, you hope, to the benefit you will get (that he *will* go away). The reason that evolution has favored the growl seems to be based on a physical relationship between the low sound frequency and the size of the sound-producing object: the larger the object, the lower its resonant frequency, the longer the wavelength of sound it produces, and the lower the perceived sound. A large "bass" drum produces a lower sound than a small snare drum, for ex-

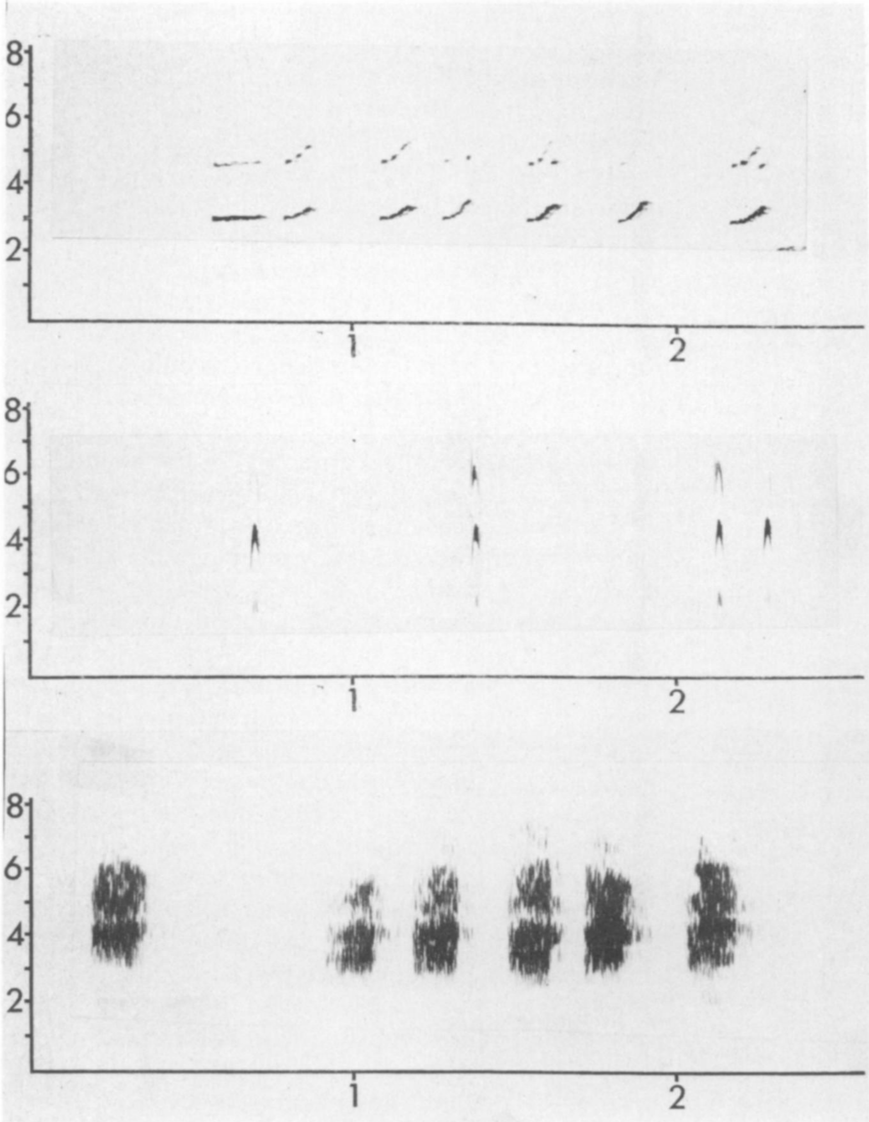

FIGURE 1. Sound spectrograms of Carolina Wren sounds. Time in Sec. is depicted along the horizontal axis, sound frequency kHz along the vertical axis. The three sounds are given by frightened birds (Top, rising and tonal spectrogram); alerted birds (Middle, the "bark"); and aggressive birds (lower, harsh, rasping sound).

ample. Perhaps evolution favors the growl in aggressive animals because a low sound makes the growler seem larger to a rival and more threatening.

This idea is difficult to test using birds or mammals because they stop growing at sexual maturity and are all about the same size. (Of course, males and females may differ in size but selection rarely favors a male growling at a female and vice versa.) But in the more primitive vertebrates, frogs and toads, for example, growth continues after sexual maturation and breeding males may differ in size as they compete for females.

This size difference is just what frogs and toads communicate; the deeper the sound, the larger the animal. Davies and Halliday (1978) determined that European toads, *Bufo bufo*, have deeper croaks the larger they become. They further showed that the sight of a large toad will not intimidate a smaller rival as well as the sound alone, played through a speaker. Other studies have shown that female frogs also choose the largest males based on their call pitch (Ryan 1980, Wells 1977). Alligators and crocodiles probably use sound to depict size in the same manner as toads and frogs, but this is understandably much more difficult to study!

It is fair to conclude that size is symbolized by sound in these ever-growing animals. Furthermore, cheating is impossible because (hypothetically) a small frog that develops a large resonating throat pouch disproportionate to its body size still must fight with conspecifics. "Truth in advertising" is maintained by these physical contests. It is my idea that this size/sound symbolism represents the ancestral condition of vocal communication.

Birds and mammals use a much wider variety of sounds than primitive vertebrates, ranging from low growls to high squeaks. An individual might produce all of these in one interaction with a conspecific. Surely it is not simply indicating its size like frogs and toads. However, like the evolution of inner ears from primi-

FIGURE 2. A 13-day old Carolina Wren (*Thryothorus ludovicianus*), whose sounds are depicted in fig. 1.

tive gill arches, selection has shaped something new from a pre-existing entity. From the primitive size/sound symbolism, communication in birds and mammals now involves motivation. They indicate their moods through the use of vocal sounds when communicating with conspecifics at near distances (Morton 1977). This is not to say that animals feel angry when they growl, for we have no idea whether our feelings are the same as the motivation in animals. But by observing what happens when an animal growls (or squeals), we can use words such as ''aggressive'' or ''fearful'' to describe whether it will probably attack or flee when it growls or squeals. If you read down the list in each column of table 1 you will attain an empirical lesson in the general use of ''growls'' and ''squeals'' by birds and mammals and see how these are tied to aggression and fear, respectively.

The relation between sound structure and motivation can be more completely described as a sort of code. Animals do not always either growl or squeal; they usually have a variety of sounds that fit along a two-dimensional continuum. (One dimension is sound frequency (pitch), the other is the band width. A wide band sound (many frequencies simultaneously) sounds noisy or harsh; a narrow band sound is tonal or whistle-like). For this reason, I call the growl and squeal endpoints and describe the whole code in fig. 3. Since the syrinx (in birds) and the larynx (in mammals) are capable of producing a wide variety of sounds, only a few are diagrammed in figure 3. The important point is to look for the two dimensions of frequency, indicated by the height of the ''sound'' above the baseline of its box, and tonality, indicated by the width of the sound. These two dimensions tend to vary together such that an aggressive animal uses both low-pitched and wideband sounds. This code is illustrated with a real animal, the Carolina Wren, *Thryothorus ludovicianus*, in figure 1 (cf. fig. 2). The

TABLE 1. Mammalian Sounds Used in Hostile or "Friendly," Appeasing Contexts

Species (family)	*Hostile*	*Friendly or appeasing*
Virginia Opossum, *Didelphis marsupialis* (Didelphidae)	Growl	Screech
Tasmanian Devil, *Sarcophilus harrisii* (Dasyuridae)	Growl	Whine
Wombat, *Vombatus lasiorhinus* (Phascolomidae)	Deep growl	quer-quer-quer
Guinea Pig, *Cavia porcellus*(Caviidae)	Grunt, snort	Squeak, *wheet*
Mara, *Dolichotis patagonum* (Caviidae)	Low grunts	Inflected *wheet*
Curo curo, *Spalacopus cyanus* (Octodontidae)	Growl	Short squeaks
Degu, *Octodon degus* (Octodontidae)	Growl	Inflected squeak
Spiny rat, *Proechimys semispinosus* (Echimyidae)	Growl	Twitter, whimper
Agouti, *Dasyprocta punctata* (Dasyproctidae)	Growl, grunt	Squeak, *creak-squeak*
Pocket Mouse, *Heteromys* (2 sp.) (Heteromyidae)	Low scratchy growl	Whining squeal
Pocket Mouse, *Liomys pictus* (Heteromyidae)	Low scratchy growl	Whining squeal
Desert Pocket Mouse, *Perognathus* (4 sp.) (Heteromyidae)	Low scratchy growl	Whining squeal
Kangaroo Rat, *Microdipodops pallidus* (Heteromyidae)	Low scratchy growl	Whining squeal
Kangaroo Rat, *Dipodomys* (6 sp.) (Heteromyidae)	Low scratchy growl	Whining squeal
Lemming, *Dicrostonyx groenlandicus* (Cricetidae)	Snarl, grind	Whine, peeps, squeals
Uinta Ground Squirrel, *Citellus armatus* (Sciuridae)	Growl	Squeal
Maned Wolf, *Chrysocyon brachyurus* (Canidae)	Growl	Whine
Bush Dog, *Speothos venaticus* (Canidae)	Buzzing growl	Squeal
Coati *Nasua narica* (Procyonidae)	Growl	Squeal
Large Spotted Genet, *Genetta tigrina* (Viverridae)	Growl-hiss	Whine or groan
African Elephant, *Loxodonta africana* (Elephantidae)	Roaring, rumbling sounds	High frequency sounds
Indian Rhinoceros, *Rhinoceros unicornis* (Rhinocerotidae)	Roaring, rumbling	Whistling
Pig, *Sus scrofa* (Suidae)	Growl	Squeal
Llama *Lama guanacoe* (Camelidae)	Growl	Bleat (long distance only ?)
Muntjac *Muntiacus muntjac* (Cervidae)	Not given	Squeak
Squirrel Monkey, *Saimiri sciureus* (Cebidae)	Shriek calls, err	Peep calls, trills
Spider Monkey, *Ateles geoffroyi* (Cebidae)	Growl, roar, cough	Tee tee, chirps, twitter, squeak
Rhesus Monkey, *Macaca mulatta* (Cercopithecidae)	Roar, growl	Screech, clear calls, squak, nasal grunting, whine, long growl

Avian Sounds Used in Hostile or "Friendly," Appeasing Contexts

Species (family)	*Hostile*	*Friendly or appeasing*
White Pelican, *Pelicanus erythrorhyncus* (Pelicanidae)	Harsh nasal growls*	Not given
Mallard, *Anas Platyrhynchos* (Anatidae)	Loud harsh *gaeck* (♀)	Soft whimper: *kn* and *quais* (♀)
Sparrow Hawk, *Falco sparverius* (Falconidae)	Harsh *chitter*	Whine
Bobwhite, *Calinus virginianus* (Phasianidae)	Loud, rasping "caterwauling"	*Tseep; squee*
Ring-necked Pheasant, *Phasianus colchicus* (Phasianidae)	Hoarse *krrrrah*	Squeak (♀)
Solitary Sandpiper, *Tringa solitaria* (Scolopacidae)	Harsh, metallic sound	Rising shrill whistle
Stilt Sandpiper, *Micropalama himantopus* (Scolopacidae)	*Trrrr*	*Toi, weet*
Cassin Auklet, *Ptychoramphus aleutica* (Alcidae)	Growled *krrr krrr*	Kreek
Orange-chinned Parakeet, *Brotogeris jugularis* (Psittacidae)	*rrrrr*	Low intensity "chirp"
Burrowing Owl, *Speotyto cunicularia* (Strigidae)	*rasp*	*eep*
Red-headed Woodpecker, *Melanerpes erythrocephalus* (Picidae)	Chatter, rasp	Not given
Harlequin Antbird, *Rhegmatorhina berlepschi* (Formicariidae)	Growling *chauhh*	*chee*
Chestnut-backed Antbird, *Myrmeciza exsul* (Formicariidae)	Snarling nasal *chiangh*	Musical chirps: *cheup*
Eastern Kingbird, *Tyrannus tyrannus* (Tyrannidae)	Harsh *zeer*	High-pitched *tee*
Barn Swallow, *Hirundo rustica* (Hirundinidae)	Deep harsh stutter	Whine call
Purple Martin, *Progne subis* (Hirundinidae)	*zwrack*	*sweet*
Mexican Jay, *Aphelocoma ultramarina* (Corvidae)	Not given	Variable *weet*
Scrub Jay, *A. coerulescens* (Corvidae)	Harsh rattle	*whew, scree*
Dwarf Jay, *A. nana* (Corvidae)	Harsh rasp	*shreeup*
Common Crow, *Corvus brachyrhynchos* (Corvidae)	Growl	Soft and plaintive
Carolina Chickadee, *Parus carolinensis* (Paridae)	Click-rasp	Lisping tee, soft dee, high see
Blue-gray Gnatcatcher, *Polioptila caerulea* (Sylviidae)	*peeω*	*speee*
American Redstart, *Setophaga ruticilla* (Parulidae)	Snarl	*zeeep*, high-pitched *titi*
Yellow-headed Blackbird, *Xanthocephalus xanthocephalus* (Icteridae)	Harsh, nasal *rahh-rahh*	*pree pree pree*
Crimson-backed tanager, *Rhamphocelus dimidiatus* (Thraupidae)	Rasping harsh hoarse notes	*Sseeeeeeeet*
Brown Towhee, *Pipilo fuscus* (Fringillidae)	Snarling throaty notes	*Seeep*, squeal duet
Common Redpoll, *Acanthis flammea* (Fringillidae)	Harsh *cheh cheh cheh*	*sweeeee*
African Village Weaverbird, *Ploceus cucullatus* (Ploceidae)	Harsh growl	look!see!; high squeal

* Verbal or onomatopoetic (italics) renditions of sounds quoted from source author's descriptions.

chevron-shaped sound in the center is similar to the central block sound of figure 2; it is what I call the "bark." The chevron shape fits the code: a sound intermediate to the high and low pitch endpoints should rise *and* fall, not tend toward either one.

A familiar example will illustrate the code. Your pet dog is sleeping on the front porch. As you approach, Fido wakes up and begins barking. The bark means that Fido has perceived something of interest to him but the stimulus is too far away for him to make a "decision." Should he attack or be friendly? When you get closer, or yell his name, he changes from barking to whines, sleeks his fur, and wags his tail at a low angle. On the other hand, if the mailman had elicited the barks, Fido might begin to growl as he approached. It is clear from Fido's actions what moods he exhibited through his vocalizations.

What was not known until many studies of wild animals were completed was that Fido's sounds and moods are not very different from other mammals' and birds' (table 1). While a bird's "chirp" might not sound like a dog's "bark," the sound spectrograph shows their similar chevron shape and observations show their similar contexts. Not all species may have vocal repertoires encompassing the full range of the code. Others may show extensive grading in vocal structures or combinations of barks and other types of sounds. All these species differences reflect the myriad sources of natural selection that can affect vocal communication. Animals may be social or solitary, densely packed or widely spaced apart, depending on ecological factors. Vocal communication in animals is a result of many factors and cannot be studied in isolation, as though animal communication was a branch of human linguistics, if we are to understand its evolution. Animals, of course, do not "say" anything, but express moods through vocalizations when it is adaptive for them to do so. One of the major goals of animal communication studies is to experimentally verify why it is adaptive for an individual animal to give a particular type of vocalization in a particular context. We are better able to do this when we realize that the physical structure of animal sounds reflects motivation and that this relationship has had a long evolutionary history. The tie of sound structures to size indication is not restricted to vocalizations alone. When a dog growls it also makes itself visually larger by erecting its fur; when it whines, it sleeks its fur and hunches down to look smaller.

If size symbolism through sound has such a long evolutionary history, it would not be surprising if human speech, as complex and arbitrary as it is, contained elements similar to our animal ancestors. The changes in the pitch of our voices as we grow from childhood to adulthood and the difference between men and women at puberty reflects the size indication

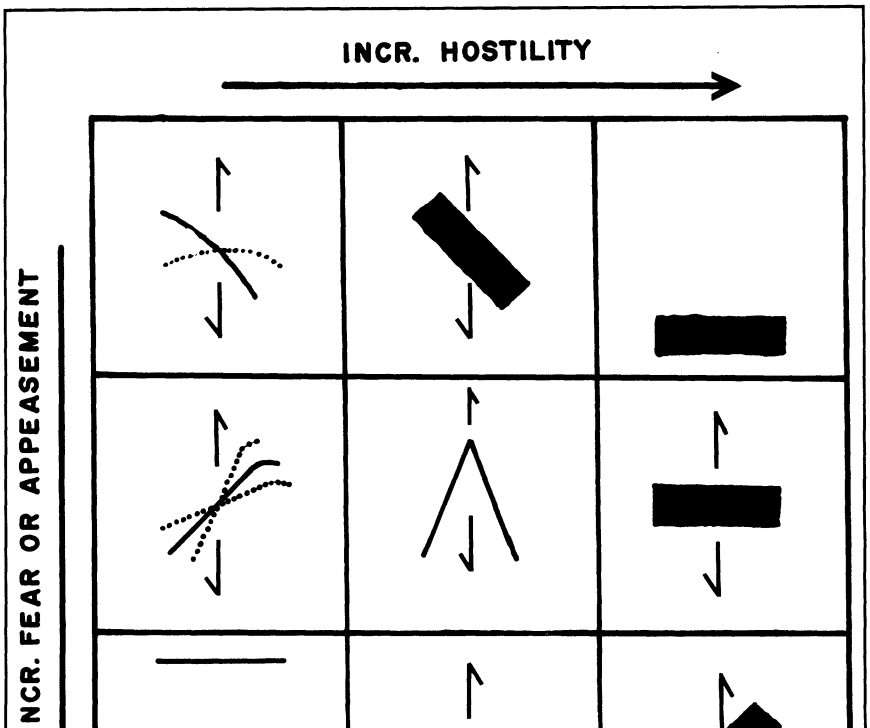

FIGURE 3. A diagrammatic representation of sound structures to illustrate the motivation-structural code. Each block shows a hypothetical sound spectrogram (vertical scale, frequency; horizontal scale, time) with thin lines depicting a tonal sound and thick lines, harsh or broad band sounds. The arrows mean that the frequency of the depicted sound may vary up or down, approaching either the low- or high-frequency endpoints at the upper right and lower left blocks, respectively.

In the upper left block, motivation is weakly tending toward fear if the thin line slopes upward (its frequency rises) or weakly toward aggression if the slope is downward. In the middle left block, closer to the fear endpoint, sounds rise variously upward, between the dashed lines, and are atonal. The three blocks on the aggressive (right) side of the diagram are all broadband but the frequency is rising in the "distress" call, where fear and aggression are interacting. The central block depicts a chevron since the motivation and its sound structure are not nearer one endpoint than the other (from Morton 1977).

code of animals. What is not so commonly appreciated is that a high or rising voice characterizes "showing friendly intentions, appeasing, submissiveness, showing uncertainty or lack of confidence" while a low or falling voice "shows assertiveness, aggression, dominance, certainty, and self-confidence" (Ohala and Morton unpublished data). Women news broadcasters seem to know this since they must lower their voice pitch to convince listeners that they have the certainty and self-confidence necessary to reach national networks. And listen to the voice of someone talking to a small baby: he raises his voice to a falsetto. After all, who would want to frighten the baby by "sounding big"? Asking a question, an appeal, is done with a sentence that contains a rising pitch. There are many examples and those just given are found in all or most languages — they are termed universals in human speech. Speech, like vocalizations used by animals close to one another, seems to have motivation reflected in pitch and bandwidth.

Animals have many vocalizations that do not function over short distances. These long distance calls are under many different selection pressures than those discussed above. Bird songs are broadcast through the environment, often to no individual conspecific in particular. Since rivals are not "face to face," little, if any, of the motivational code is favored by selection. Instead, acoustic properties that promote transmission of the song over great distances are under strong selection. In Panama, for example, I found that forest birds use whistle-like songs averaging about 2,200Hz in frequency. Sound transmission studies showed that these frequencies attenuated the least. Using artificial pure tones, I showed that frequencies from 1,500 to 2,500Hz carried the farthest before fading into the background noise of the forest (Morton 1975). Grassland birds often use songs with a wide frequency band and sing from elevated perches to overcome the high attenuation of sound in these temperature and wind speed stratified open areas. Temperature and wind speed gradients cause sound waves to deflect upwards, which is why you can hear voices farther across a cool lake than a hot baseball field.

It is important to differentiate long and short distance sounds in studying the evolution of animal communication. But in both cases, the physical structures of the vocalizations are under strong, if differing, sources of selection. The arbitrary, cultural nature of our speech sounds is a truly unique feature of speech even if we can identify some elements of animal communication in how we say our words.

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