Evolution of Voice in Species

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Evolution of Voice in Species

Nothing in Biology Makes Sense Except in the Light of Evolution (Dobzhansky, 1973)

Introduction

The concept of evolution, which is now basic to life sciences, has provided new and in some ways revolutionary answers to questions asked for centuries. The two most important of these are: "why we are here, what is the purpose of human existence?" and "what is the nature of the world of life that surrounds us?" Evolution tells us that we are here because of a long series of past events that do not differ in kind from the events and processes that produced the millions of different organisms that surround us. The most important processes are: (1) interaction between organism and their environment that are highly diverse both historically and geographically, (2) the continuity of heredity and cultural tradition, and (3) the occasional disturbance of these regularities by chance.

The diversity of living world is apparent not only in the large number of species, but also in their heterogeneity. Organisms are extremely diverse in size, way of life, and habitat, as well as in structure and form. Yet, despite their prodigious diversity, organisms share much in common. Oxygen, hydrogen and carbon are common chemical elements in all organisms; together they account for about 98.5 percent by weight of any living being. Four kinds of macromolecules - proteins, carbohydrates, lipids and nucleic acids - are the basic molecular constituents of all living processes. The genetic information of all organisms, from bacteria to man is encoded in the double-helical

structure of DNA. The processes of transcription and translation and the genetic code are essentially uniform through all life.

Some, not all organisms share certain similarities. These similarities can be used to classify, i.e., to characterize, some groups of organisms and distinguish them from others. Centuries ago biologists noted that living things can be arranged in hierarchic fashion, that some organisms (and group of organisms) resemble each other more than they resemble other organisms (or groups). The basic process responsible for the hierarchy of similarities among living things is of course evolution - some organisms resemble each other more than others because they are more closely related by lines of descent.

Morphological similarities among organisms were probably always recognized by humans. Aristotle (384-322 B.C.) classified organisms on the basis of similarities. The modern theory of evolution, originating from Darwin (1859), provides a causal explanation of the similarities among living beings. Organisms evolve by a process of descent with modification. Changes, and therefore differences, gradually accumulate over the generations. The more recent the last common ancestor of a group of organisms, the less their differentiation; similarities of form and function reflects phylogentic propinquity. For this reason, phylogenetic affinities can be inferred on the basis of relative similarity.

The notion of restrictions or constraints on evolution has been with us since Darwin (1859). Although most researchers agree on their importance, detailed analysis and quantification of the role of evolutionary constraints has proved an elusive goal (Smith et al, 1985; Carroll 1997), and many different classifications of constraints have been proposed. Phylogenetic constraints result from developmental and historical factors. They stem from the gradualistic principles that underlie the generation of variation in evolution: recombination and mutation can only explore that small portion of adaptive space that is adjacent to a particular species' current position.

Signals/communicating ways are generally defined according to the physico-chemical nature of the stimulus or the sensory properties of the organ which act as detector-receptors. They are chemical (smell), visual (sight), electrical (galvanic sensibility), tactile, kinaesthetic (vibratory sense) and acoustical (hearing).

Voice is the conversion of airflow into acoustic energy (that is, longitudinal pressure waves in the audible frequency range). Typically, this airflow emanates from the lungs. Tetrapod (four-legged animals) lungs are filled during normal respiration by various means, including diaphragmatic contraction in mammals, buccal pumping in some reptiles and amphibians, intercostal contraction in birds, and even a piston-like retraction of the liver in crocodilians (Liem, 1985). Due to the lung elastic recoil resulting from alveolar elasticity and surface tension, optionally combined with muscular compression from intercostal or abdominal muscles, this air can be pressurized, resulting in a flow outward through the glottis. It is this airflow that typically provides the energy

for vocalization, either directly or indirectly by filling air sacs. The diversity of systems for moving air in and out of the lungs is of less relevance in understanding vocal diversity than diversity in the vertebrate voice source. Broad comparative treatments of diversity and function in the vertebrate respiratory system can be found in Gans, (1970); Liem, (1985); Perry, (1989); Lasiewski, (1972) for birds.

Only few fishes (teleosts) produce sound via expulsion of gas from the swim bladder in a manner homologous with vocalization in tetrapods.

Although most tetrapod vocalizations are apparently generated on expiration, inspiration also plays an important role in vocalization in some anurans (Amphibians), mammals and birds. In anuran advertisement calls, for example, air typically flows outwards from the lungs into a distensible submandibular air sac, which can inflate in some cases to the size of the animal itself (Dudley & Rand, 1991). It is this outward flow that fuels vocal cord vibration and vocalization. The air captured in the sac is then returned, via deflation, to the lungs, where it can then fuel another vocalization (Gans, 1973). This conservation of air serves at least two functions. First, it enables anurans to vocalize at higher rates and for longer than would otherwise be possible (due to the inefficiency of lung inflation in this group; Rand & Dudley, 1993). The relevance of call duration to both energy expenditure and to female choice has been documented in anurans (Klump & Gerhardt 1987; Welch, Semlitsch, & Gerahrdt,1998), and provides a good example of a non-arbitrary signal parameter. Second, the inflated air sac may serve as an impedance-matching device, more efficiently transferring acoustic energy to the

environment (Watkins, Baylor & Bowen, 1970). A similar mechanism may operate in non-human primates with distensible air sacs (Gautier, 1971).

Non-human primates such as chimpanzees *(Pan Troglodytes* and *P. paniscus)* produce vocalizations, such as low hoots and pant hoots, which have both inspiratory and expiratory components (Marler, 1969; Marler & Tenaza, 1977; de Waal, 1988). In birds, which have an extremely complex and efficient respiratory system, the respiratory dynamics underlying vocalization appear equally complex. Many song birds appear to produce shallow rapid respiratory cycles termed "mini-breaths", which allow extended periods of unbroken song and suggest a level of respiratory/vocal coordination far superior to that seen in other tetrapods (Hartley & Suthers, 1989).

In terrestrial vertebrates, vocalizations are initially generated by a structure, which converts airflow from the lungs (or air sacs) into acoustic energy. This structure is known as the acoustic source, or voice source, and its anatomical location varies among tetrapods. In amphibians, reptiles and mammals, the source is typically the *larynx.* In birds, an evolutionary novel structure called the *syrinx* serves as the voice source. In both cases, the source contains mobile elastic structures which act as mechanical vibrators, and can reduce or stop the passage of air though the source by constricting its lumen. In the larynx, these vibrators are the vocal folds, and in the syrinx, the identity of the vibrators was long thought to be the medial tympaniform membranes (Miskimen, 1951; Greenewalt, 1968). However, recent direct visualization via endoscopy suggests that the vibratory structures are the syringeal labia in passerines (Goller & Larsen 1997b)

and the lateral tympaniform membranes in pigeons (Goller & Larsen 1997a). Although the medial tympaniform membranes may play some acoustic role, their complete ablation does not prevent nearly normal vocalization (Larsen & Goller 1999). In both the larynx and syrinx, energy created by the passage of air though the constriction between the vibrators acts to set them into motion. When the vibrators collide, (or approach close enough to modulate air flow) they generate acoustic energy. The main acoustic difference between the larynx and syrinx is their location: the larynx is located at the top of the trachea, while the syrinx is located at its base. Although birds also possess a larynx, there is little evidence that the avian larynx is used as a sound-producing source (White, 1968). Figure 1 sows the different anatomical sound sources in amphibians, birds, and mammals. Appendix I gives a comparative anatomy and performance of vocal organ in vertebrates.
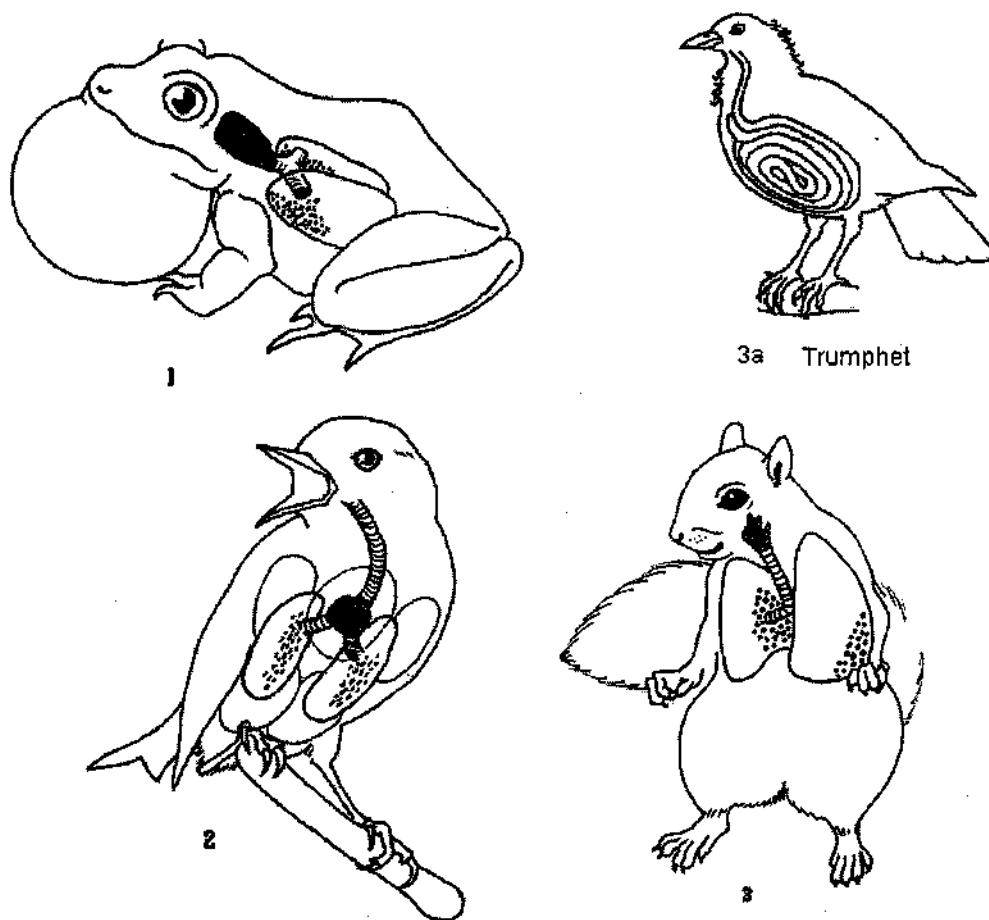
Figure 1: Representative tetrapods showing (in gray) the different anatomical sound sources in each group (schematic). 1. Anuran amphibians use a larynx with vocal folds to produce sound, & often vocalize into an inflatable vocal sac. 2. Birds (a passerine is shown here) have an evolutionarily novel structure, the syrinx, which is located at the base of the trachea. 3a. Tracheal elongation in Trumpet Manu code *Manucodia keraudrenii* 3. Mammals (a rodent is shown) use a larynx & vocal folds as the sound source.

The quantitative details of laryngeal vibration are still an area of active investigation, even for humans. Investigations of non-human larynges usually stem from the difficulty of obtaining or working with human cadaveric larynges rather than from an interest in comparative physiology (Brown & Cannitto 1995; Mergell, Fitch & Herzel, 1999 are exceptions). Nonetheless, over the years the larynges of a wide variety of

mammalian species have been investigated, and all available data are consistent with the *hypothesis that the vibratory mechanics of the larynx are fundamentally similar among all mammals including humans.* Nonhuman mammals whose larynges have been experimentally studied include baboons, sheep, dogs, horses, cattle, and Syke's monkeys (Slavit, Lipton & McCaffrey, 1990; Bless, Inagi, Khidr & Ford, 1998; Hirano, 1991; Brown & Cannitto, 1995). In all cases, the vocal folds act as vibrators, and the myoelastic-aerodynamic theory applies. Although current evidence suggests that similar considerations apply to the avian syrinx, it is only very recently that in situ vibrations of the syrinx have been directly observed (Larsen & Goller, 1999), and the basic mechanisms underlying avian sound production are still the subject of active investigation. Since the vocal folds are solid masses of tissue, while the syringeal membranes are relatively thin and light, it is quite likely that the details of their vibratory pattern will differ in some ways. Nonetheless, current data for all tetrapods is consistent with the idea that the voice source involves movement of a set of vibrators (vocal folds or syringeal membranes), which modulate airflow and thus generate acoustic energy.

Often the oscillation of the vibrators is periodic, with their opening and closing occurring regularly. The time it takes for one open/close cycle is the period, and the rate at which these cycles occur is the fundamental frequency (abbreviated F0). A fundamental insight of the myoelastic aerodynamic theory is the realization that this rate of opening and closing is determined passively, by the setting of muscle tensions, effective mass of the vibrators, and lung pressure. It is unnecessary for any muscles in the vocal folds to twitch, or the motor neurons to fire, at the fundamental frequency. Indeed

for the sounds of many vertebrates this would be impossible, since the fundamental frequencies are much higher than the maximum rate of muscular tetany or even neural firing. Only relatively low vibration rates can typically be generated by rapid muscle twitching in tetrapods (e.g. 25 Hz purring in cats, Remmers & Gautier 1972). The neurally passive feature of the larynx or syrinx is best demonstrated by the fact that a larynx or syrinx can be removed from the body and deprived of all nervous input, and still be induced to produce sound by blowing air through the approximated vocal folds or syringeal membranes (Rüppell, 1933; Schmidt, 1965).

The acoustic energy generated at the source must pass through the remainder of the respiratory tract before it can emanate out into the environment. In birds, this portion of the respiratory system is termed the suprasyringeal vocal tract, while in other terrestrial vertebrates it is the supra-laryngeal vocal tract. Although the entire vocal production system, including lungs, source and supra-laryngeal respiratory passages, is sometimes termed the vocal tract, it is convenient when discussing tetrapod vocal acoustics to restrict use of the term "vocal tract" to the supra-syringeal or supra-laryngeal air passages and their associated articulators, as the term "vocal production system" refers to the entire system. As a broad generalization, there is much more diversity in vocal tract morphology than in the voice source: a large anatomical literature records a huge variety of air sacs, diverticula, elongated snouts or trachea or other resonating structures among vertebrates. However, most of these studies are old and many are in German language, and these morphological features have received little attention from modern bioacousticians. Furthermore, the functional importance of these features has received

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almost no study, despite the fact that such variation may play a significant role in shaping the communication system of different species. The column of air contained in the vocal tract, like any column of air, has elasticity and mass, and thus will vibrate preferentially at certain frequencies termed normal modes or "resonances". As the sound energy generated by the source passes through this air column, it may set one or more of these modes into vibration. The presence of the vocal tract will thus enhance the transmission of these frequencies while damping or attenuating others; it acts as a spectral filter on the source signal. In speech science, these filtering frequencies are termed "formants", from the Latin formare "to shape", because they sculpt the vocal signal on its way from the source out to the environment. This term is preferable to the term "vocal tract resonances" both due to its brevity and because it highlights the independence of source and filter, which is indicated by most available work on the subject. Thus the most basic acoustic model of the vocal production system has two components: the sound-generating source (syrinx, larynx, etc.) and the filter (the air column contained by vocal tract). The function of the filter varies among species. In both humans and other species, formants can also be internally referential, providing cues to identity, body size, age, or gender (Rendall, 1996; Fitch, 1997; Riede & Fitch, 1999; Fitch & Giedd, 1999). A different use of the vocal tract filter is to suppress certain frequencies, typically to enhance the salience of some particular source components (e.g. the second harmonic). This is the case in some birds (Nowicki 1987) and bats (Hartley & Suthers 1988). In all cases, it is extremely important to recognize that formants are an independent acoustic entity from the source (the fundamental frequency and its harmonics), in terms of production, acoustic analysis, and perception.

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For anuran amphibians the role of supra-laryngeal filtering is more difficult to assess, at least in part because of the pervasive use of the term "dominant frequency". In anuran bioacoustics, dominant frequency refers to the highest amplitude frequency in the spectrum of a call, without regard to whether this is the fundamental, one of its harmonics, a noise- or impulse-excited formant, or a carrier frequency with amplitude-modulation sidebands. While this term is convenient for acoustic analyses, it obscures the important differences between such acoustic features, both in terms of understanding vocal production and possibly in perception as well. For example, many anuran vocalizations possess features that superficially resemble formants, with a high amplitude peak at one of the higher harmonics of a series. However, the data of Rand & Dudley (1993) suggest that, at least for the four species they examined, this peak does not represent a formant frequency, since the location of the highest-amplitude spectral peak did not change in a helium/oxygen atmosphere. Such spectral peaks could be caused by low-frequency amplitude modulation (e.g. by the arytenoids) of a higher carrier frequency (e.g. from the vocal cords), as suggested by Ryan (1985) and Schneider (1988). Alternatively, they could result from an interaction between a generalized descending spectral envelope (i.e. the -6 db/octave amplitude drop-off characteristic of most vocal sources) and impedance characteristics of the frog's body (where low frequencies are radiated poorly due to small body sizes). The point here is that the abundant and excellent work in anuran bioacoustics could be more easily integrated into the rest of bioacoustics (including work on humans, other mammals, and birds) if explicit production-related terminology were adopted (e.g. separating formants from fundamental frequency or harmonics), rather than relying on the catch-all acoustic term "dominant

frequency". Increased precision of acoustic description will enable researchers interested in the anatomy and physiology of sound production to more easily pin down the mechanisms relevant in perception and communication, and thus in the evolution of mate choice or speciation, in this important group of vertebrates. Another term that is confusing because it is used ambiguously is "pitch". Pitch is defined as "that attribute of auditory sensation in terms of which sounds may be ordered on a musical scale". Pitch is a subjective quality, defined in human terms that cannot be measured directly. It is, strictly speaking, inappropriate to use the term in animal bioacoustics. However, the term is convenient and its usage widespread, making it unlikely to vanish from the technical literature. Thus, it is critical that bioacousticians use the term consistently and precisely. For most periodic sounds perceived pitch corresponds to the physical variable fundamental frequency (or its inverse, waveform period). Exceptions include periodic sounds that lack energy at the fundamental, so called "missing fundamental" stimuli. A sound with energy only at 200, 300, and 400 Hz will often have a perceived pitch corresponding to a sine wave at 100 Hz, despite the lack of physical energy at this frequency, due to perceptual processes that "restore" the missing fundamental. Although such phenomena may be relevant in calls produced by birds or bats, where the fundamental is suppressed (Nowicki & Marler, 1988; Hartley & Suthers, 1988), in general there is a close correspondence between "pitch" and fundamental frequency.

The vibratory frequencies of source and filter appear to be independent in vertebrates. There is little evidence for anything but weak coupling either in the human voice or in other vertebrates that have been studied thus far. Thus, to a first

approximation, the frequencies produced by the vocal source (typically a fundamental and its harmonics) are independent of the filtering frequencies of the vocal tract (Miller 1934, Sutherland & McChesney 1965, Pye 1967, Greenewalt 1968, Capranica & Moffat 1983, Nowicki 1987, Hartley & Suthers 1988, Rand & Dudley 1993, Westneat, Long, Hoese & Nowicki 1993, Brittan-Powell, Dooling, Larsen & Heaton 1997).

Although all of the vocal production systems considered here work in roughly the same fashion, and are governed by the same physical principles, there is an impressive diversity of form in the vertebrate vocal tract. An important distinction between the syrinx and the larynx is that the typical syrinx contains two independent sets of vibrating membranes, one in each bronchus, which are also under independent nervous control (via left and right branches of the twelfth cranial nerve, the hypoglossal). Based on this anatomy, Greenewalt (1968) proposed the "two voice" theory, which holds that the two sides of the syrinx in many birds are independent, allowing two independent fundamental frequencies to be produced by one bird. Greenewalt based his theory upon observation of spectrograms, but more direct evidence was provided by Nottebohm (1971), -who sectioned the right or left hypoglossal nerves in several songbird species. He found that disabling the right side had little effect on canary or chaffinch song, while sectioning the left nerve produced dramatic effects, with most syllables disappearing entirely from the song. Thus these birds are lateralized for song production, with one side being dominant. Such asymmetries have also been discovered in other species, but in some species such as zebra finches the asymmetry is reversed (Williams, Crane, Hale, Esposito & Nottebohm 1992). Conclusive evidence for the two-voice theory was provided by Suthers (1990)

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elegant experiments with mimic thrushes, which produce elaborate songs including imitations of other species songs. By implanting pressure and flow sensors in living birds, Suthers was able to definitively observe the two voice sources creating independent portions of the awake, singing bird's final song.

Although full use of a two-voice system appears limited to birds by virtue of the anatomy of the syrinx, it should be noted that the two vocal folds of the mammalian larynx can also vibrate independently in certain cases. Normally, the vocal folds collide with every vibratory cycle, which forces them into the same frequency and phase. However, mammals appear to lack the fully independent anatomy and nervous control, which would allow each vocal fold to generate rapidly varying and independent pitches as in many birds. Thus, true two-voice phonation appears to be limited to the class Aves.

The primary function of the tetrapod larynx, both functionally and in terms of its history, is as a valve controlling access to and protecting the respiratory tree. Full of sensitive mucosa, the larynx will quickly shut and exclude any foreign bodies that near it. In mammals, the larynx also can engage into the nasopharyngeal opening, forming a sealed respiratory passage from nostrils to the lungs. Still, during swallowing of large solid food items, and at all times in humans, food must pass over the opening of the glottis during swallowing before entering the digestive tract. This situation, as noted by Darwin, means that the "gatekeeper" role of the larynx is ever present. Its role as a sound-producing organ must always coexist with this gate keeping role.

In contrast, the avian syrinx appears to serve only one function: sound production. In birds, the larynx is devoted to the gate keeping role exclusively, while the syrinx is free to create sound. This freedom is at least partly responsible for the considerable variability of the syrinx as an organ (Wunderlich, 1886; Warner, 1972a, b), which can have from zero to nine pairs of muscles and is variously located tracheally, bronchially or tracheo-bronchially. Raikow (1986) observed a correlation between syringeal complexity and the number of species in various taxa of passerine birds, and suggested that morphological changes in syringeal form might facilitate reproductive isolation and thus speciation. In contrast, the mammalian larynx is always made up of the same basic cartilages and muscles, and although the shapes and sizes of these may vary somewhat, the larynx is overall quite a conservative organ. In anurans, the situation appears to be intermediate: there is considerable variability in laryngeal structure, though still minor compared to that seen in the syrinx.

Why adapt an evolutionary perspective? Researchers interested in the mechanisms underlying vocal production and/or auditory perception might argue that the ultimate evolutionary force structuring a communication system offer little insight into the proximate morphological and neuronal mechanisms that underlie acoustic behaviour. One reason that an evolutionary viewpoint is valuable is that many aspects of animal morphology and behaviour may appear non-optimal from an engineering perspective, but can be understood as an optimal solution to a problem, given a certain phylogenetic starting point and well defined development, physical or mechanistic constraints (Fitch & Hauser, 2002). An evolutionary perspective also encourages an exploration on

interspecies similarities and differences, providing a comparative framework. *In this context, an effort has been made to trace the evolution of voice in animals from terrestrial vertebrates based on the fundamental frequency of their voice/calls and also to make a database of voice of animals which can be used by interested researchers to explain the evolution of speech and language and species-specific processes involved in human communication.*

Review of literature

Over a hundred years ago, Charles Darwin provided the essential elements of the evolutionary framework. Darwin's 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, behaviour and so on. (2) Some of these variations are heritable; in other words, some of the distinctive characteristics of individuals can be passed on to their young, so that off springs tend to resemble their parents more than they do other members of the species. (3) Even though adults produce many number of offspring, population don't consistently grow in proportion to the number of offspring produced. This implies that most offspring must die without reproducing. (If most individuals did not die before reproducing, then populations of even slowly reproducing species such as humans would increase exponentially and occupy all available space on earth; obviously, such population growth is rare, and cannot be sustained for long). (4) Because of their special inherited attributes some types of individuals are likely to cope more effectively

than others with problems arising from such sources as predators, competitors, and disease. These individuals will tend to leave more descendants than other members of the species with different and less successful inherited traits. Across consecutive generations, the greater reproductive success of the more successful individual will lead to their becoming the most common type within the population.

Many of the Darwin's idea are still central in modern understanding of behaviour. Some of the special inherited attributes are tendencies to behave in particular ways; these have consequences that lead to greater reproductive success, and thus to increase in the numbers of individuals who behave that way in subsequent generations. Such consequences are now called the functions of behaving in those ways. From the perspective of natural selection, it is easy to understand, for example; how the tendency to emit calls when a predator comes on the scene might have been favoured (such behaviour is common during predatory encounter). Such calling might help one's own offspring by inducing them to take refuge before the predator becomes a threat, thereby facilitating the offspring's survival and subsequent reproduction. If these calls do not incidentally assist the young of others and if the tendency to call is heritable, then those who call will have more surviving, reproducing off springs and become the dominant forms in the population. In this case, the function of calling is to warn vulnerable off springs (Sherman, 1977).

In 1871, Darwin identified what he considered to be a different kind of selection, and a distinct category of functions of behaviour, in his book 'The Descent of Man, and

communicative utility of visual signals was doubtlessly facilitated by the availability of still photography and drawings as means of describing their structure.

It was one thing to describe a signal and identify its current functions, but a different matter to identify its evolutionary origins. Darwin's answer, in 'The Expression of Emotions in Man and Animals' (Darwin, 1872), was that many signals originated as results of other processes, and not because of their utility in communication. The vocalizations of air breathing vertebrates, for example, may have originated as a by product of the violent muscular contractions of the respiratory system that come with strong excitement, resulting in 'purposeless sounds' (Darwin, 1871).

Although Darwin felt that most emotional expressions originated for reasons other than communication, he was clearly aware of the importance of those expressions in communication (Darwin, 1872). Thus actions originating for one reason can subsequently acquire commutative functions. (Some of Darwin's idea about how non communicable actions became signals is not accepted today; he believed that habitual use of expressions could induce heritable variations that are result in the habits transmission to offspring).

A more modern and also quite Darwinian explanation of this process is as follows (Ploog, 1992; Andersson, 1994): In ancestral aquatic vertebrates (fishes), the larynx (which ultimately became the vocal apparatus) was essentially a valve in the floor of the pharynx (the muscular tube connecting the mouth with the oesophagus). While the individual was underwater, this valve served to cap the swim bladder (which was the

evolutionary precursor to the lungs). At the water surface, the valve opened, allowing air to be forced in to the swim bladder, which provided buoyancy. During the evolutionary transition from aquatic to terrestrial life, the swim bladder acquired respiratory function. Associated with this change in function of the swim bladder was an elaboration of the larynx; this included the evolution of fibers to pull larynx to open, and subsequently the addition of cartilage, both changes allowing more air to be pulled in to the lungs. This elaboration of the larynx for its respiratory function created a structure that tended to produce sound, for example, when air is abruptly inhaled when the individual is startled. Due to some effect of such incidental sounds on co-specifics, the sound producer may have been more successful in its social interactions and therefore more reproductively successful; as a result, the tendency to produce such sounds during social interactions would spread through natural or sexual selection. In this way, sounds produced as by products of respiration may subsequently become signals as a consequence of selection arising from their social effects. Females might respond positively to such expressive males for several reasons; for example, the loudness or persistence of sounds might be used as a cue to assess a potential mate's stamina, thereby making it possible for the female to choose the best sire for its offspring. Under these conditions emotional expressions could become more widespread with each successive generation because they enhanced the male's reproductive success by increasing his attractiveness to females.

Once a signal originates within a species, it may change, remain the same over time, or disappear (Moynihan, 1970). Furthermore, the signal may remain the same or

change in new species that arise from old. When a signal of a given species is examined today, how does one decide whether this is a new form or one inherited from an ancestral species? Clearly, a dilemma is that such questions deal with changes that are too slow for humans to study directly. So, we create indirect methods, based on the study of the effects of those slow changes. Darwin's answer was to seek the same signal in other species; the more wide spread the signal, the more likely it is that it was inherited from ancestral species rather than a new creation (Mayr, 1988). Darwin's argument about the evolutionary origins of signals was supported with extensive documentation of the similarities in ways of expressing emotions among many species of animals, including humans. Such comparison among species has became a powerful method for identifying the behavioural 'raw material' from which signals may have been derived and the nature of the evolutionary changes that have occurred (Tinbergen, 1952).

About 1950, auditory signals began to replace visual ones as the most commonly studied form of communication. This rapid expansion of bioacoustic studies was due almost entirely to the ease with which sounds could be recorded, analyzed and used as playback 'models' (Owing & Morton, 1998). None of the technological advances was developed specifically for the study of animal auditory communication. Nevertheless, the implications for this field were remarkable. Now, computers can be used to store and playback sounds, and even to modify or synthesis them. Playing back vocalizations to animals was first performed in 1891 on monkeys in zoos using the graphophone (Garner, 1892). The use of technology developed for human electronic and communication and

entertainment continues to provide new device for acoustic studies (Baptista & Gaunt, 1994).

These technical developments began to alleviate the limitations that hampered Darwin's insight into vocal signals. Especially important was the invention of the sound spectrograph, a device for objectively describing the structure of sounds. First applied to animal vocalization during the 1950s, the spectrograph set the relationship between the form and function of vocalizations. Marler (1955) was among the first biologists to break this new scientific ground.

Consistent with the ethological (behavioural) view that animal signals were stereotyped, sound spectrographs were initially used to provide an objective description of a 'typical' example of each type of call in a species' repertoire. Nevertheless, this descriptive tool made it possible to detect within-type structural variation in calls not conspicuous to the human auditory system. Once detected, this variation could be explored to determined whether it reflected 'errors' in call production or whether variation within the same call type made a difference in communication. Beer (1973; 1975) pioneered in such work, discovering evidence that adult laughing gulls varied the structure of their long-calls depending on whether their fledging chicks or other adults were the targets of these vocalizations. The availability of playback methods made it possible to verify experimentally that different variants of calls make a communicative difference. Indeed, it was the use of playbacks that led Beer to his discovery of the structural variation in long-calls.

The recognition of functional variation in vocal structure also fed growth in appreciation of the complexity of animal communication. Animal vocal repertoires were generally believed to be quite limited (Moynihan, 1970).

Animal vocal repertoires are extremely rich, but in contrast to human verbal behaviour they are generated almost exclusively by laryngeal modulations and only to a minimal degree by supralaryngeal activity (i.e., articulation). A phylogentic development can also be seen in the cerebral organization of vocal behaviour. In amphibians, reptiles an I lower mammals, the dorsal mid brain - pons transitional zone seems to be the only art a responsible for the production of vocal utterance. This area probably serves in integrating vocal fold movements, expiration, intra- and extra- oral muscle activity in to species-specific vocal patterns; its destruction results in mutism. In higher mammals, including primates, this area does not lose its original function but is brought under the control of the cortex around the anterior sulcus cingulli (supplementary motor area and anterior cingulated gyrus). The latter seems to play an essential role in the initiation of vocal utterance in situations which do not have a rigid stimulus-response characteristic, i.e. in voluntary vocal behaviour. The highest level of voice production finally is rep -esented by the cortical face area, the destruction of which is without consequence to the innate vocal behaviour of animals but produces dysarthria in man (Jurgens & Ploog, 1976).

Available research on terrestrial vertebrate vocal production is unevenly distributed: the best-researched groups are oscine birds (Nowicki & Marler, 1988; Gaunt

& Nowicki, 1998), anurans (Schneider, 1988) and among mammals, echolocating bats (Suthers & Fattu, 1973; Suthers 1988) and humans (Fant, 1960; Lieberman & Blumstein, 1988; Titze, 1994). Much less is known about reptile vocal production (Gans & Maderson, 1973), and little or nothing is known about vocal production in most non-passerine birds and most mammalian orders. Significant unresolved questions remain about production in virtually all vertebrate groups, other than for humans. Even in our own species, vocalizations other than speech and singing are little studied. However, because research in speech science also has provided the basic concepts and analysis tools for the rest of bioacoustics, the data from human vocal production can be used to discuss call production in other vertebrates (Greenewalt, 1968; Lieberman, 1968; Hartley & Suthers, 1988).

All terrestrial vertebrates possess a vocal tract, which can be predicted from basic physics to have a substantial acoustic effect on production of many call types. In both birds and mammals, the evidence for formant frequencies is abundant, based on even a cursory examination of spectrograms. Despite this, there has been little attention to formants, or research on the anatomy, physiology or acoustics of the non-human vocal tract, compared to research on the larynx or syrinx. In humans, the vocal tract plays a far more critical role in speech than does the larynx, and thus we have a detailed understanding of the anatomy and physiology of the human vocal tract and accurate quantitative models of its acoustics at rest and in movement. Thus, compared to our knowledge of the human vocal tract, research on animal vocal tract acoustics and dynamics is in its infancy, and information on comparative anatomy of the vocal tract is

scattered throughout works focusing on digestion or respiration. Even the most basic questions have been addressed for only a few species. However, despite a long pause in publications since the late sixties (Lieberman, 1968; Greenewalt, 1968; Lieberman, Klatt & Wilson, 1969), there appears to be a growing realization of the importance of the vocal tract in sound production in birds and mammals, especially in the last decade (Suthers & Fattu, 1973; Andrew, 1976; Nowicki, 1987; Suthers & Hector, 1988; Suthers, Hartley & Wenstrup, 1988; Hartley & Suthers, 1988; Owren, 1990; Suthers, 1994; Owren & Bernacki, 1988; 1998, Hausberger, Black & Richard, 1991; Hauser, 1992; Hauser, Evans & Marler, 1993; Westneat et al, 1993; Hauser & Schon-Ybarra, 1994; Fitch & Hauser, 1995; Owren, Swyfarth & Cheney, 1997; Fitch, 1994, 1997, 1999, 2000a, b, Rendall, 1996; Riede & Fitch, 1999). Figures 2-9 show sections of larynx of birds and mammals.

Ventral view   Frontal view
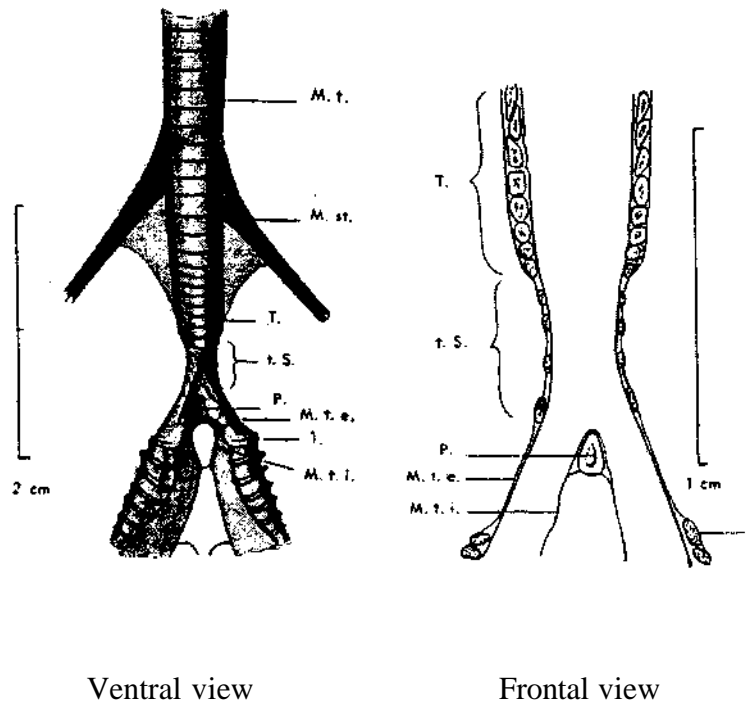
Figure 2: Ventral and frontal views of syrynx of Gallus gallus domesticus (Cock).

M.t. Muse, tracheolateralis   P. Pessulus
M.st. Musc.sternotrachealis   M.t.e. Membrana tympaniformis externa
T. Ossified lower tracheal ring (drum)   M.t.i. Membrana tympaniformis interna
T.S. Syrinx membrane, tracheal portion   I. First bronchial ring
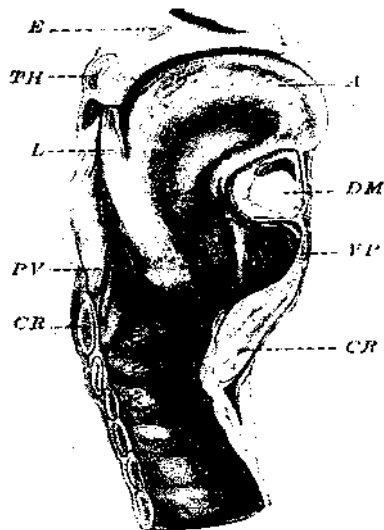
A: Arytenoids
CR: Cricoid
DM: Dorso-medial process
E: Epiglottis
L: Elastic bundle
PV: Processus vocalis
VP: Posterior intralaryngeal sac
Th: Thyroid

Figure 3: Phonatory glottis formed between the upper arytenoids edges in *Otaria jubata* (Seal).

Figure 4: Sagittal section of the larynx with short fold as "precussor" of a vocal cord *Atherura macroura* (a Porcupine).
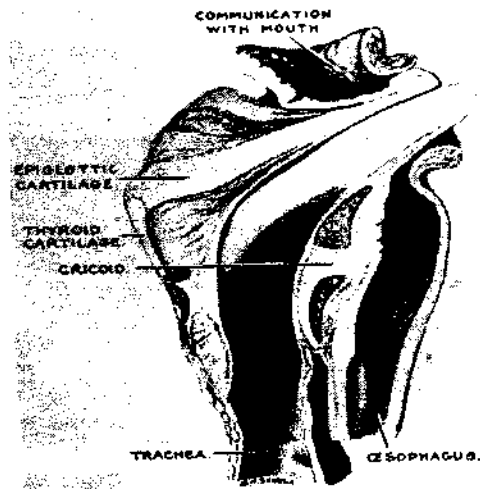
Figure 5: Sagittal section of larynx in Dolphin.

Figure 6: Sagittal section of larynx in Equs caballus (Horse).
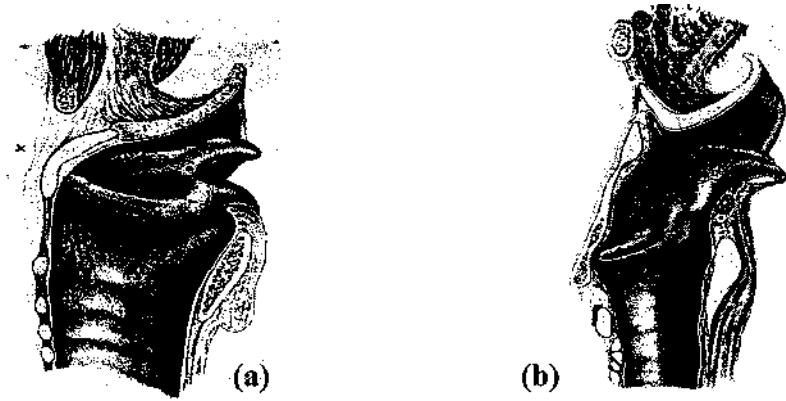
Figure 7: Sagittal section of larynx in dog (a) and swine (b).
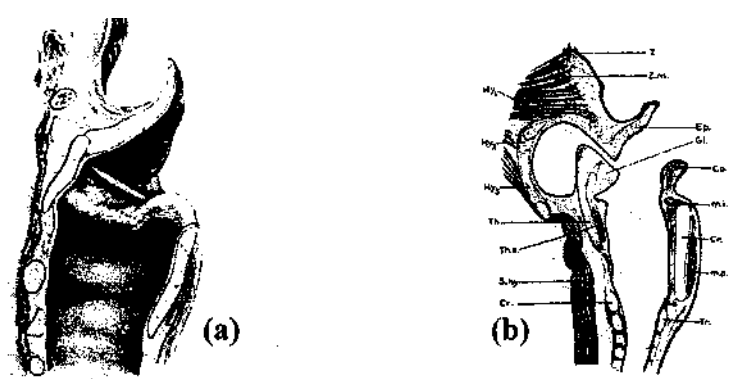
Figure 8: Sagittal section of larynx in cat (a) and Guenon (b)

Co. Commissura interarytenoidea

Gl. Glands

m.i. Musc, interarytenoideus

m.p. Musc, cricoarytenoideus posticus

Th.a. Musc, thyreoarytenoideus

Z. Tongue, mucous membrane

Z.m. Tongue, muscle

Hy. 1 Os. hyoideum

Hy. 2 Os. hyoideum, concavity

Hy. 3 Os. hyoideum, inferior hook

Ep. Epiglottis

Th. Thyroid

Cr. Cricoid

Method

Material: Voice/calls of the animals (amphibians, birds and mammals) were recorded from the field in forest areas, Zoo and other places. As it is difficult to find all the animals in an area the recordings of the calls animals were also taken from other sources like internet, CD's, cassettes   etc. For the present study, calls/sounds of 26 amphibian species, 116 bird species, and 103 mammals' sounds samples were collected. However, these sound samples do not reflect any specific vocalizations. Tables 1 to 3 show the taxonomic classification of amphibians, birds, and mammals and figure 10 shows the taxonomical classification of vertebrates.

Sl. No.	Family	Genus	Species	Common name
1.	Leptodactylidae	Eleutherodactylus	Marnockii	Cliff chirping frog
2.	Microhylidae	Hypopachus	Variolosus	Sheep frog
3.	Microhylidae	Gastrophryne	Olivacea	Great plains narrow mouth frog
4.	Hylidae	Pseudacris	Clarkii	Spotted chorus frog
5.			Streckeri	Streckers chorus frog
6.			Triseriata	Striped chorus frog
7.		Hyla	Arenicolor	Canyon tree frog
8.			Versicolor	Northern gray tree frog
9.		Pseudacris	Crucifer	Spring peeper frog
10.		Similisca	Bandinii	Mexican tree frog
11.	Ranidae	Rana	Catesbeiana	Bull frog
12.			Areolata	Crawfish frog
13.			Sphenocephala	Southern leopard frog
14.			Berlandieri	Rio grande leopard frog
15.			Blairi	Plains leopard frog
16.			Clamitans	Green frog
17.	Bufonidae	Bufo	Speciosus	Texas toad
18.			Woodhousii	Wood houses toad
19.			Coqnatus	Great plains toad
20.			Debilis	Green toad
21.			Valliceps	Gulf coast toad
22.			Americanus	American toad
23.	Pelobatidae	Scaphiopus	Couchii	Couchs spade foot (toad)
24.	Rhinophrynidae	Rhinophrynus	Dorsalis	Mexican burrowing toad
25.	Megophryidae	Leptobrachium	Abbotti	Eastern spade foot (toad)
26.	Scaphiopodidae	Spea	Multiplicata	New mexico spade foot (toad)

Table 1: Taxonomic classification of amphibians (Phylum: Chordata, Class: Vertebrata, Sub Class: Amphibia, Order: Anura).

Sl.No.	Order	Family	Genus	Species	Common name
1.	Apterygiformes	Aptergidae	Apteryx	Australis	Kiwi
2.	Podicipeiformes	Pocipedidae	Podiceps	Cristatus	Great-crested grebe
3.	Sphenisciformes	Spheniscidae	Aptenodytes	Forsteri	Emperor Penguin
4.	Procellariiformes	Procellariidae	Fulmarus	Glacialis	Northern Fulmar
5.			Puffinus	Puffinus	Manx Shearwater
6.		Pelecanidae	Pelecanus	Onocrotalus	White Pelican
7.		Phaethonthidae	Phaethon	Aethereus	Red-billed Tropic Bird
8.		Sulidae	Sula	Bassana	Northern Gannet
9.		Phalacrocoracidae	Phalacrocorax	Carbo	Great cormorant
10.	Ciconiiformes	Ardeidae	Ardeola	Ibis	Cattle egret
11.			Cochlearius	Cochlearius	Boat-billed Heron
12.			Ardea	Cinerea	Grey Heron
13.		Ciconiidae	Leptoptilos	Crumeniferus	Marabou Stork
14.			Ciconia	Ciconia	White Stork
15.		Threskionithidae	Platalea	Leucorodia	Spoon Bill
16.	Anseriformes	Anatidae	Tadorna	Tadoma	Common Shelduck
17.			Anas	Platyrhynehos	Mallard duck
18.			Somateria	Mollissima	Common Eider
19.			Branta	Canodensis	Canada Goose
20.			Anser	Anser	Gray lag Goose
21.			Mergus	Merganser	Goosander merganser
22.			Cygnus	Cygnus	Whooper Swan
23.		Anhimidae	Chauna	Torquato	Southern Crested Screamer
24.	Falconiformes	Saittariidae	Sagittarius	Serpentarius	Secretary bird
25.		Falconidae	Falco	Peregrinus	Peregrine falcon
26.				Sparverius	American Kestrel
27.				Tinnunculus	European Kestrel
28.		Accipitridae	Buteo	Buteo	Buzzard
29.			Haliaeetus	Leucocephalus	Bald Eagle
30.				Vocifer	Fish Eagle
31.			Accipiter	Gentilis	Northern Goshawk
32.		Pandionidae	Pandion	Haliaeetus	Osprey
33.	Galliformes	Phasianidae	Alectoris	Rufa	Red-legged Partridge
34.			Pava	Cristatus	Peacock
35.			Phasianus	Colchicus	Pheasant
36.			Colinus	Virginianus	Bobwhite Quail
37.		Tetraonidae	Tetra	Urogallus	Capercaillie
38.			Lyrurus	Tetrix	Black Grouse
39.			Centrocercus	Urophasianus	Sage Grouse
40.			Lagopus	Mutus	Ptarmigon
41.	Gruiformes	Gruidae	Grus	Leucogeranus	Siberian white crane
42.		Rallidae	Fulicaatra	Atra	Coot
43.			Gallinula	Chloropus	Moorhen

Sl.No.	Order	Family	Genus	Species	Common name
44.	Charadriiformes	Charadriidae	Vanellus	Vanellus	Lapwing
45.		Scolopacidae	Calidris	Alpina	Dunlin
46.			Gallinago	Gallinago	Snipe
47.			Scolopax	Rusticola	Wood Cock
48.		Recurvirostridae	Recurvirostra	Avosetta	Avocet
49.			Himantopus	Himantopus	Black-winged Stilt
50.		Haematopodidae	Haematopus	Ostralegus	Oystercatcher
51.		Laridae	Larus	Ridibundus	Black-headed Gull
52.					Herring Gull
53.			Sterna	Paradisaea	Arctic Tern
54.		Alcidae	Fratercula	Arctica	Atlantic Puffin
55.			Alca	Torda	Razor Bill
56.	Columbiformes	Columbidae	Columba	Livia	Rock Pigeon
57.				Palumbus	Wood Pigeon
58.	Psittaciformes	Psittacidae	Melopsittacus	Undulatus	Budgerigar
59.			Kakatoe	Galerita	Sulfur-crested cockatoo
60.			Psittacus	Erithacus	Gray parrot
61.	Cuculiformes	Cuculidae	Cuculus	Canorus	Cuckoo
62.			Geococcyx	Californianus	Road Runner
63.	Strigiformes	Strigidae	Bubo	Bubo	Eurasian Eagle Owl
64.			Athene	Noctua	Great Horned Owl
65.					Little Owl
66.			Asio	Otus	Long-eared owl
67.		Tytonidae	Tyto	Alba	Barn Owl
68.	Caprimulgiformes	Caprimulgidae	Caprimulgus	Europeans	Nightjar
69.		Steatronithidae	Steatornis	Caripensis	Oil Bird
70.	Apodiformes	Apodidae	Apus	Apus	Swift
71.	Trogoniformes	Trogonidae	Pharomachrus	Mocinno	Quetzal
72.	Coraciiformes	Alcedinidae	Alcedo	Atthis	Eurasian Kingfisher
73.			Ceryle	Rudis	Lesser Pied Kingfisher
74.			Dacelo	Gigas	Kookaburra
75.		Meropidae	Merops	Apiaster	Bee-eater
76.		Upupidae	Upupa	Epops	Hoopoe
77.	Piciformes	Picidae	Colapter	Auratus	Northern Flicker
78.			Dryocopus	Martius	Black Woodpecker
79.				Major	Great Spotted Woodpecker
80.			Picus	Viridis	Green Woodpecker
81.			Jynx	Torquilla	Wryneck
82.	Passeriformes	Furnariidae	Furnarius	Rufus	Rufous Ovenbird
83.		Hirundinidae	Delichon	Urbica	House Martin
84.			Hirundo	Rustica	Swallow
85.		Alaudidae	Alauda	Arvensis	Skylark
86.		Motacillidae	Anthus	Spinoletta	Rock Pipit
87.			Motacilla	Alba	Pied Wagtail
88.		Laniidae	Lanius	Exubitor	Great gray Shrike
89.		Bombycillidae	Bombycillia	Garrulous	Wax Wing
90.		Cinclidae	Cinclus	Cinclus	Dipper
91.		Mimidae	Dumetella	Carolinensis	Gray cat bird
92.			Mimus	Polyglottos	Norhtem Mocking bird
93.		Paridae	Parus	Major	Great Tit
94.			Aegithalos	Caudatus	Long-tailed Tit
95.			Parus	Caeruleus	Blue Tit

Sl.No.	Order	Family	Genus	Species	Common name
96.	Passeriforms	Sittidae	Sitta	Europaea	Nuthatch
97.		Emberizidae	Plectrophenax	Nivalis	Snow bunting
98.			Emberiza	Citrinella	Yellow Hammer
99.		Ictiridae	Agelaius	Phoenicus	Redwinged black bird
100.			Sturnella	Magna	Eastern Medowlark
101.		Turdidae	Turdus	Merula	Black bird
102.			Saxicola	Torquata	Stone Chat
103.			Monticola	Solitarius	Blue Rock Thrush
104.			Erithacus	Rubecula	European Robin
105.		Fringillidae	Pyrrhula	Purrhula	Bullfinch
106.			Carduelis	Carduelis	Eurasian gold finch
107.		Ploceidae	Passer	Domesticus	House Sparrow
108.		Sturnidae	Buphagus	Africanus	Yellow-billed Oxpecker
109.			Sturnus	Vulgaris	Starling
110.			Gracula	Religiosa	**Hill Myna**
111.		Oriolidae	Oriolus	Oriolus	Golden Oriole
112.		Thraupidae	Piranga	Rubra	Summer Tanager
113.		Corvidae	Pyrrhocorax	Graculus	Yellow-billed chough
114.			Corvus	Canorus	Carrion crow
115.			Garrulus	Glandarius	Eurasian Jay
116.			Corvus	Corax	Common Raven

Table 2: Taxonomic classification of birds (Phylum:Chordata, Class: Vertebrata, Sub Class: Aves).

Sl. No.	Order	Family	Genus	Species	Common name
1.	Marsupialia	Dasyuridae	Sarcophilus	Harrisii	Tasmanian Devil
2.		Phascolarctidae	Phascolarctos	Cinereus	Koala
3.	Chiroptera	Pteropodidae	Pteropus	Livingstoni	Flying Fox
4.		Noctilionidae	Moctilio	Leporinus	Fisherman Bat
5.		Vespertilionidae	Pipistrellus	Pipistrellus	Pipistrelle Bat
6.	Primates	Lemuridae	Eulemur	Macaco	Black Lemur
7.			Lemur	Catta	Ring Tailed Lemur
8.		Indriidae	Indri	Indri	Indri
9.		Cebidae	Cebus	Albifrons	Capuchin Monkey
10.			Aotus	Trivirgatus	Owl Monkey
11.			Ateles	Geoffroyi	Spider Monkey
12.		Callitrichidae	Leontrapithecus	Rosalis	Golden-lion Tamarin
13.		Cercopthecidae	Theropithecus	Gelada	Gelada Baboon
14.			Mandrillus	Sphinx	Mandrill
15.			Nasalis	Larvatus	Proboscis Monkey
16.			Cercopithecus	Aethiops	Vervet Monkey
17.			Macaca	Mulatta	Rhesus Macaque
18.		Hylobatidae	Hylobates	Lar	Lar Gibbon
19.		Pongidae	Gorilla	Gorilla	Gorilla
20.			Pan	Troglodytes	Chimpanzee
21.			Pongo	Pygmaeus	Orangutan
22.	Xenarthra	Dasypodidae	Dasypus	Novemcinctus	Nine banded Armadilla
23.	Lagomorpha	Ochotonidae	Ochotona	Princeps	Pika
24.		Leporidae	Oryctolagus	Cuniculus	Old world Rabbit
25.	Rodentia	Sciuridae	Sciurus	Vulgaris	Eurasian Red Squirrel
26.				Carolinensis	Gray Squirrel
27.			Tamiasciurus	Hudsonicus	American Red Squirrel
28.			Tamias	Striatus	Eastern American chip monk
29.		Castoridae	Castor	Canadensis	Beaver
30.		Gliridae	Glis	Glis	Edible Dormouse
31.		Hystricidae	Hystrix	Africaeaustralis	Crested Porcupine
32.		Hydrochaeridae	Hydrochaeris	Hydrochaeris	Capybara
33.		Dasiproctidae	Dasyprocta	Leporina	Agouti
34.		Capromyidae	Myocastor	Coypus	Coypu
35.	Cetacea	Monodontidae	Delphinapjerus	Leucas	Beluga Whale
36.		Delphinidae	Tursiops	Trumcatus	Amazon Dolphin
37.					Bottle Nosed Dolphin
38.			Orcinus	Orca	Orca (Killer Whale)
39.		Balaenoteridae	Megaptera	Novaeangliae	Humpback Whale
40.	Carnivora	Canidae	Canis	Familiaris	Dingo
41.			Lycaon	Pictus	African Hunting Dog
42.			Alopex	Lagopus	Arctic Fox
43.			Otocyon	Megolotis	Bat-eared Fox
44.			Fennecus	Zeeda	Fennec Fox
45.			Vulpes	Vulpes	Red Fox
46.			Canis	Lupus	Wolf
47.		Ursidae	Aliuropoda	Melanoleuca	Giant Panda
48.			Ursus	Americanus	American Black Bear
49.				Maritimus	Polar Bear

Sl. No.	Order	Family	Genus	Species	Common name
50.	Carnivora	Procyonidae	Ailurus	Fulgens	Red Panda
51.			Nasua	Nasua	Coati
52.		Mustelidae	Galictis	Vittata	Grison
53.			Meles	Meles	Old world Badger
54.			Lutra	Lutra	Eurasian otter
55.			Pteronura	Brasiliensis	Giant Otter
56.			Mustela	Erminea	Stoat
57.					Bobcat
58.		Viverridae	Suricatta	Suricatta	Meerkat
59.			Arctictis	Binturong	Binturong
60.		Hyaenidae	Crocuta	Crocuta	Spotted Hyena
61.		Felidae	Felis	Concolor	Coyote
62.				Pardalis	Ocelot
63.				Servai	Servai
64.				Silvestris	Wild Cat
65.			Neofelis	Nebulosa	Clouded Leopard
66.			Acinonyx	Jubatus	Cheetah
67.			Panthera	Leo	Lion
68.				Pardus	Leopard
69.				Tigris	Tiger
70.	Pinnipedia	Otariidae	Zalophus	Californianus	Californian Sea lion
71.		Phocidae	Phoca	Groenlandica	Harp Seal
72.			Mirounoga	Leonina	Southern Elephant Seal
73.		Odobenidae	Odobenus	Rosmarus	Walrus
74.	Proboscidea	Elephantidae	Loxodonta	Africana	African Elephant
75.			Elephas	Maximus	Indian Elephant
76.	Hyracoidae	Procaviidae	Procavia	Capensis	Rock hyrax
77.	Sirenia	Trichechidae	Trichecus	Manatus	Manatee
78.	Perissodactyla	Equidae	Equs	Przewalskii	Wild Horse
79.				Burchelli	Zebra
80.		Tapiridae	Tapirus	Indicus	Malayasian Tapir
81.		Rhinocerotidae	Diceros	Bicornis	Black Rhinoceros
82.	Artiodactyla	Suidae	Sus	Scrofa	European Wild Boar
83.			Phacochoerus	Aethiopicus	Warthog
84.		Hippopotamidae	Hippopotamus	Amphibius	Hippopotamus
85.		Camelidae	Camelus	Bactrianus	Bactrian Camel
86.				Dromedarius	Dromedary Camel
87.			Lama	Glama	Llama
88.			Vicugna	Vicugna	Vicuna
89.		Cervidae	Capreolus	Capreolus	Roe Deer
90.			Rangifer	Tarandus	Caribou
91.			Dama	Dama	Fallow Deer
92.			Muntiacus	Muntjak	Barking Deer/Indian Muntjac
93.			Cervus	Elephus	Red Deer
94.			Axis	Axis	Spotted Deer
95.			Odocoileus	Virginianus	White Tailed Deer

Sl. No.	Order	Family	Genus	Species	Common name
96	Artiodactyla	Bovidae	Madogna	kirki	Dik dik
97			Gazella	thomsoni	Thomson's Gazelle
98			Syrcerus	coffer	African Buffalo
99			Tragelaphus	scriptus	Bushbuck
100.			Saiga	tatarica	Saiga
101.			Antidorcas	marsupialis	Springbok
102.			Connochaetes	taurinus	Wild beast
103.					American Bison

Table 3: Taxonomic classification of mammals (Phylum: Chordata, Class: Vertebrata, Sub Class: Mammalia).
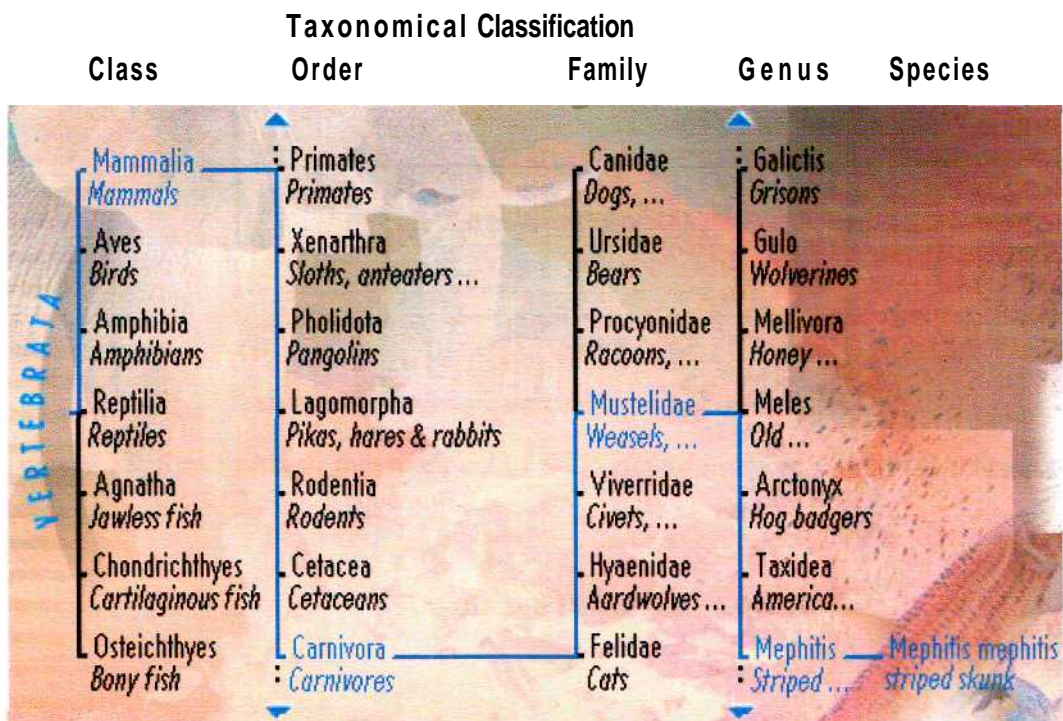
Figure 10: Taxonomical classification of vertebrates.

Method: The recorded voice/sounds were stored on to the computer at a sampling frequency of 16 k Hz. The highest and lowest fundamental frequencies (FO), and presence and absence of FO were extracted using PRATT Software. In the absence of FO, frequency of noise concentration was extracted from spectra as obtained on COOLEDIT software. Narrow band spectrograms were also obtained to countercheck

presence of voicing. Figures 11 and 12 illustrate measurement of LFO, HFO, and frequency of noise concentration.
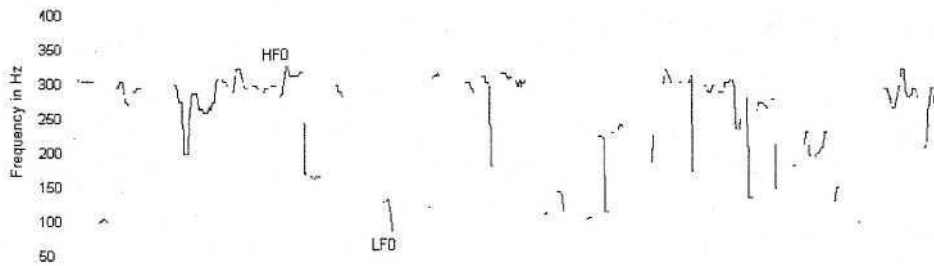
Figure 11: Illustration of measurement of LFO, and HFO in secretary bird.
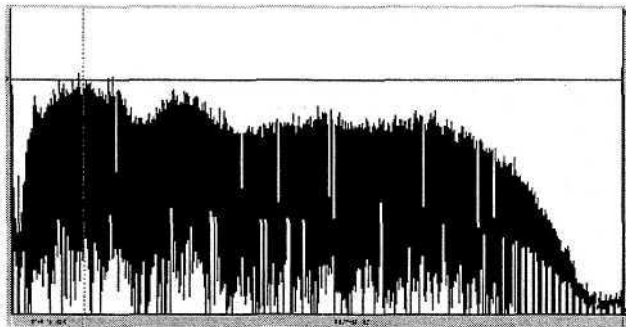
Figure 12: Illustration of measurement of frequency of noise concentration (cursor at the first peak frequency).

Results and Discussion

The results indicated that not all animals had vocalizations. The fundamental frequency varied widely. Among amphibians studied, spotted chorus frog and Great Plains narrow mouth frog did not have vocalizations. The lowest frequency (LFO) of vocalization in other frogs ranged from 86 Hz to 2556 Hz and the highest frequency (HFO) ranged from 90 Hz to 2949 Hz. Bull frog had the lowest LFO and HFO, and spring peeper frog had the highest LFO, and striped chorus frog had the highest HFO. The range of frequencies was highest in Mexican tree frog.

Among toads, couches spade foot toad had the lowest LFO and HFO and great plain toad had the highest LFO and HFO. The range of frequencies was lowest in green toad and highest in couches spade foot toad. Frequency of noise concentration in spotted chorus frog was lower than that in great plain narrow mouth frog. Also, range of FO was lower in frogs compared to that in toads. Table 4 shows LFO, HFO, frequency range, and frequency of noise concentration in amphibians. Figure 13 illustrates narrowband spectrograms of vocalizations of some amphibians.

SI. NO.	Family	Species	LFO	HF0	R	Frequency of noise		
1,	Leptodactylidae	Cliff chirping frog	1741	2224	483			
2.	Microhylidae	Sheep frog	134	546	412			
3.	Microhylidae	Great plains narrowmouth frog				222	1771	3754
4.	Hylidae	Spotted chorus frog				92	1543	3124
5.		Streckers chorus frog	2291	2423	132			
6.		Striped chorus frog	1655	2949	1294			
7.		Canyan tree frog	179	183	4			
8.		Northern gray tree frog	1123	1256	133			
9.		Spring peeper frog	2556	2797	241			
10.		Mexican tree frog	101	2617	2516			
11.	Ranidae	Bull frog	86	90	4			
12.		Crawfish frog	796	1592	796			
13.		Southern leopard frog	401	959	558			
14.		Rio grande leopard frog	367	371	4			
15.		Plains leopard frog	616	662	46			
16.		Green frog	187	207	20			
Average			765	1180	415			
17.	Bufonidae	Texas toad	1763	2159	396			
18.		Wood houses toad	1048	1559	511			
19.		Great plains toad	2016	2629	613			
20.		Green toad	1606	1653	47			
21.		Gulf coast toad	1064	1379	315			
22.		American toad	1490	1968	478			
23.	Pelobatidae	Couches spade foot (toad)	120	1535	1415			
24.	Rhinophrynidae	Mexican burrowing toad	188	315	127			
25.	Megopjiryidae	Eastern spade foot (toad)	155	1427	1272			
26.	Scaphiopodidae	New Mexico spade foot (toad)	1247	1469	222			
Average			1070	1609	540			

Table 4: Lowest FO (LFO), highest FO (KFO), range of FO (R), and frequency of noise concentration in amphibians.

Bull frog
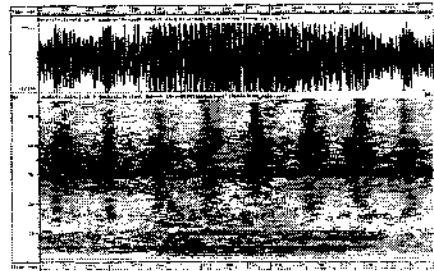
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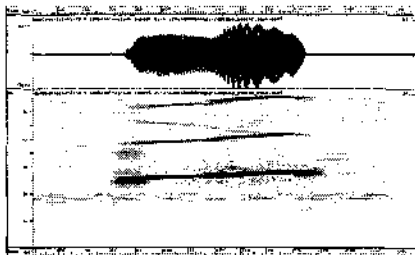
Spring peeper frog
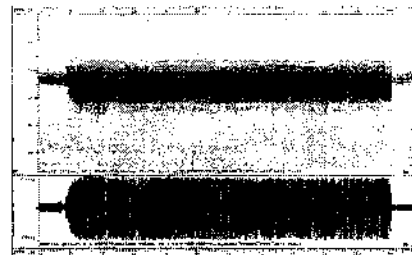
Great plain narrow mouth
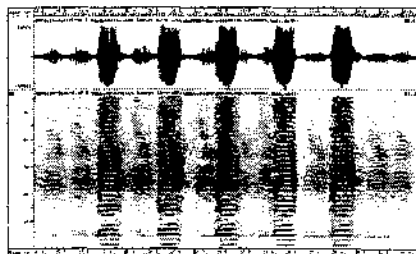
Mexican frog
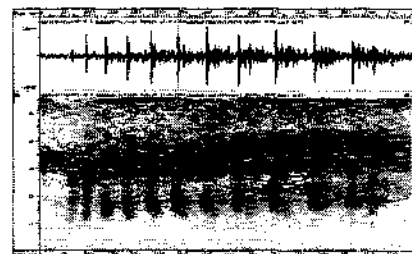
Striped chorus frog

Figure 13: Narrow band spectrograms of vocalization of some amphibians.

Among birds studies, oil bird, cattle egret, Eurasian Jay, and long-tailed tit did not have vocalizations. Black headed guill and white pelican had the lowest LFO, and yellow hammer had the highest LFO. White pelican had the lowest HFO, and skylark, pied wagtail and European robin had the highest HFO. The range of FO was zero in little owl, lowest in white pelican, and highest in capercaillie. Table 5 shows the LFO,

HFO, range of FO, and frequency of noise concentration in birds. Figure 14 shows the photographs of birds along with narrow band spectrograms of bird calls.

Sl. No.	Common name	LFO	HFO	R	Frequency of noise		
1.	Kiwi	478	2306	1828			
2.	Great-crested grebe	849	1092	243			
3.	Emperor Penguin	128	2507	2379			
4.	Northern Fulmar	81	1552	1471			
5.	Manx Shearwater	88	1620	1532			
6.	White Pelican	50	70	20			
7.	Red-billed Tropic Bird	284	1420	1136			
8.	Northern Gannet	208	317	109			
9.	Great cormorant	51	653	602			
10.	Cattle egret				602	1205	2067
11.	Boat-billed Heron	173	2263	2090			
12.	Grey Heron	213	1575	1362			
13.	Marabou Stork	1835	2600	765			
14.	White Stork	592	1962	1370			
15.	Spoon Bill	308	697	389			
16.	Common Shelduck	81	996	915			
17.	Mallard duck	1773	2846	1073			
18.	Common Eider	98	1845	1747			
19.	Canada Goose	58	550	497			
20.	Gray lag Goose	206	1566	1330			
21.	Goosander merganser	1253	1397	144			
22.	Whooper Swan	97	1320	1223			
23.	Southern Crested Screamer	248	2893	2645			
24.	Secretary bird	52	318	266			
25.	Peregrine falcon	294	2665	2371			
26.	American Kestrel	1979	2401	422			
27.	European Kestrel	555	2137	1582			
28.	Buzzard	588	2797	2209			
29.	Bald Eagle	1208	2971	1763			
30.	Fish Eagle	648	1654	1006			
31.	Northern Goshawk	1145	1354	209			
32.	Osprey	159	2782	2623			
33.	Red-legged Partridge	1677	2294	617			
34.	Peacock	394	1428	1034			
35.	Pheasant	823	1177	354			

SI. No.	Common name	LFO	HF0	R	Frequency of noise		
36.	Bobwhite Quail	1520	2813	1293			
37.	Capercaillie	52	2985	**2933**			
38.	Black Grouse	395	620	225			
39.	Sage Grouse	216	910	694			
40.	Ptarmiqon	1860	2951	1091			
41.	Siberian white crane	74	1680	1606			
42.	Coot	638	2924	2286			
43.	Moorhen	988	1393	405			
44.	Lapwing	758	2849	2091			
45.	Dunlin	478	2985	2507			
46.	Snipe	261	334	73			
47.	Wood Cock	60	908	848			
48.	Avocet	790	2810	2020			
49.	Black-winged Stilt	648	2933	2285			
50.	Oystercatcher	2293	2975	682			
51.	Black-headed Gull	50	1986	1936			
52.	Herring Gull	443	1622	1179			
53.	Arctic Tern	456	2984	2528			
54.	Atlantic Puffin	55	977	922			
55.	Razor Bill	61	980	919			
56.	Rock Pigeon	66	357	291			
57.	Wood Pigeon	61	590	389			
58.	Budgerigar	1222	2947	1725			
59.	Sulfur-crested cockatoo	338	2262	1924			
60.	Gray parrot	1103	2895	1792			
61.	Cuckoo	409	1002	593			
62.	Road Runner	441	578	137			
63.	Eurasian Eagle Owl	304	410	106			
64.	Great Horned Owl	224	2853	2629			
65.	Little Owl	265	265	0			
66.	Long-eared owl	1934	2208	274			
67.	Barn Owl	703	2848	2145			
68.	Niqht Jar	1918	2187	269			
69.	Oil Bird				667	1582	3283
70.	Swift	1089	2995	1906			
71.	Quetzal	743	1297	554			
72.	Eurasian Kingfisher	1869	2996	1127			
73.	Lesser Pied Kingfisher	1768	2975	1207			
74.	Kookaburra	367	2088	1721			
75.	Bee-eater	1440	2372	932			
76.	Hoopoe	533	640	107			
77.	Northern Flicker	578	2986	2408			
78.	Black Woodpecker	361	2933	2572			
79.	Great Spotted Woodpecker	932	1122	190			
80.	Green Woodpecker	653	2097	1444			
81.	Wryneck	1456	2036	580			
82.	Rufous Ovenbird	1091	2984	1893			
83.	House Martin	1034	2982	1948			

| Sl. No.	Common name	LFO	HF0	R	Frequency of noise		
84.	Swallow	1328	2994	1666			
85.	Skylark	2567	**2999**	432			
86.	Rock Pipit	2598	2984	386			
87.	Pied Wagtail	869	**2999**	2130			
88.	Great pray Shrike	2336	2822	486			
89.	Wax Wing	1222	2996	1774			
90.	Dipper	618	2983	2365			
91.	Gray cat bird	967	2938	1971			
92.	Northern Mocking bird	1817	2774	957			
93.	Great Tit	1368	2950	1582			
94.	Long-tailed Tit				53	6998	11010
95.	Blue Tit				53	2982	11010
96.	Nuthatch	2747	2997	250			
97.	Snow bunting	1411	1529	118			
98.	Yellow Hammer	**2760**	2835	75			
99.	Red winged black bird	344	2851	2507			
100.	Eastern Meadowlark	1792	2831	1039			
101.	Black bird	570	2912	2342			
102.	Stone Chat	559	2972	2413			
103.	Blue Rock Thrush	1964	2977	1013			
104.	European Robin	1560	**2999**	1738			
105.	Bullfinch	2201	2949	748			
106.	Eurasian gold finch	1401	2987	1586			
107.	House Sparrow	1499	2993	1494			
108.	Yellow-billed Oxpecker	767	2998	2231			
109.	Starling	803	2951	2148			
110.	Hill Myna	1509	2412	903			
111.	Golden Oriole	731	2988	2257			
112.	Summer Tanager	423	2995	2572			
113.	Yellow-billed chough	1103	2144	1041			
114.	**Carrion crow**	282	1879	1597			
115.	**Eurasian Jay**				1884	2702	3639
116.	**Common Raven**	943	1246	303			

Table 5: Lowest FO (LFO), highest FO (KFO), range of FO (R), and frequency of noise concentration in birds.
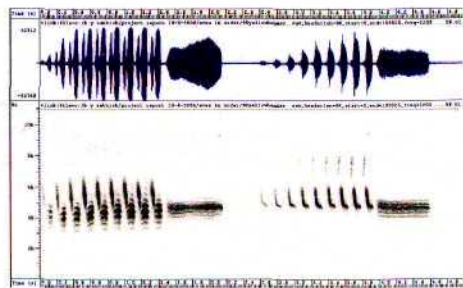
White pelican
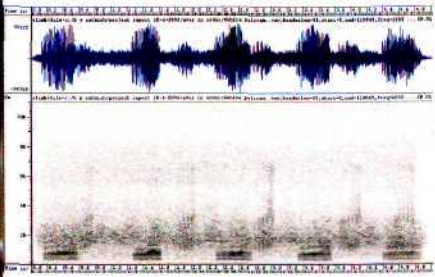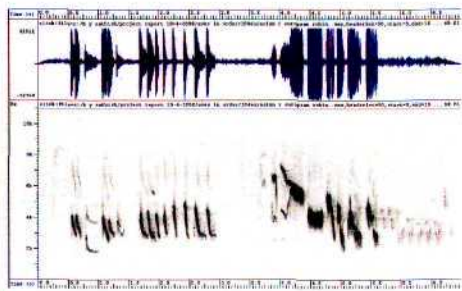
European Robin

Yellow Hammer

Figure 14: Photographs, and narrow band spectrograms of calls of some birds.

Several of the mammals did not have vocalization. Among the mammals studied, serval had the lowest LFO and Eurasian Otter had the highest LFO. American Bison had the lowest HFO and pika had the highest HFO. African buffalo had the lowest FO range and springbok had the highest FO range. Table 6 shows the LFO, HFO, range of FO, and frequency of noise concentration in mammals. Figure 15 shows photographs and narrow band spectrograms of vocalization of mammals.

Sl. No.	Common name	LFO	HFO	R	Frequency of noise		
1.	Tasmanian Devil	55	1620	1565			
2.	Koala	58	2982	2924			
3.	Flying Fox				7472		
4.	Fisherman Bat				785	7665	
5.	Pipistrelle Bat				3445		
6.	Black Lemur	42	2250	2208			
7.	Ring Tailed Lemur	124	2004	1880			
8.	Indri	63	869	806			
9.	Capuchin Monkey	698	1852	1154			
10.	Owl Monkey	239	322	83			
11.	Spider Monkey						
12.	Golden-lion Tamarin	1567	2982	1415			
13.	Gelada Baboon	778	2974	2196			
14.	Mandrill	41	772	731			
15.	Proboscis Monkey	619	2951	2332			
16.	Vervet Monkey	149	1975	1826			
17.	Rhesus Macaque	1466	2945	1479			
18.	Lar Gibbon	224	791	567			
19.	Gorilla	62	1963	'1901			
20.	Chimpanzee	249	1713	1464			
21.	Orangutan	237	2989	2752			
22.	Nine banded Armadilla	-	-	-			
23.	Pika	2398	296	598			
24.	Old world Rabbit	779	2044	1265			
25.	Eurasian Red Squirrel	440	1523	1083			
26.	Gray Squirrel	867	2386	1519			
27.	American Red Squirrel	2700	2979	279			
28.	Eastern American chip monk				53	1173	7149
29.	Beaver	116	498	382			
30.	Edible Dormouse	1056	2301	1245			
31.	Crested Porcupine				4885	7633	
32.	Capybara	1238	1494	256			
33.	Agouti	421	2774	2353			
34.	Coypu	315	582	267			
35.	Beluga Whale	41	2811	2770			
36.	Amazon Dolphin				376	1754	7665
37.	Bottle Nosed Dolphin	161	2974	2813			

Sl. No.	Common name	LF0	HF0	R	Frequency of noise		
38.	Orca (Killer Whale)				829	5103	8936
39.	Humpback Whale	567	2944	2377			
40.	Dingo	640	1002	362			
41.	African Hunting Dog	200	1218	1018			
42.	Arctic Fox	390	2750	2360			
43.	Bat-eared Fox	173	2432	2259			
44.	Fennec Fox	334	1603	1269			
45.	Red Fox	2229	2882	653			
46.	Wolf	41	846	805			
47.	Giant Panda	287	1560	1273			
48.	American Black Bear	470	2395	1925			
49.	Polar Bear	51	381	330			
50.	Red Panda	281	1990	1709			
51.	Coati				107	8204	9226
52.	Grison	1775	2641	866			
53.	Old world Badger	46	1008	962			
54.	Eurasian otter	3838	4668	830			
55.	Giant Otter				53	3574	7751
56.	Stoat	326	785	459			
57.	Bobcat						
58.	Meerkat	69	1104	1035			
59.	Binturong	164	2453	2289			
60.	Spotted Hyena	152	622	470			
61.	Coyote	139	1287	1148			
62.	Ocelot	79	2213	2134			
63.	Serval	11	258	247			
64.	Wild Cat	144	919	775			
65.	Clouded Leopard	53	2860	2807			
66.	Cheetah	203	622	419			
67.	Lion	46	2539	2493			
68.	Leopard	46	2906	2860			
69.	Tiger	48	178	130			
70.	Californian Sea lion	256	100	744			
71.	Harp Seal	113	2248	2135			
72.	Southern Elephant Seal	40	2922	2882			
73.	Walrus	47	232	185			
74.	African Elephant	193	489	293			
75.	Indian Elephant	44	747	703			
76.	Rock hyrax	407	2662	2607			
77.	Manatee				1055	9097	
78.	Wild Horse	55	2662	2607			
79.	Zebra	344	2008	1664			
80.	Malaysian Tapir	346	2983	2637			
81.	Black Rhinoceros	256	2972	2716			
82.	European Wild Boar	50	2660	2610			
83.	Warthog	528	869	341			
84.	Hippopotamus	41	1384	1343			
85.	Bactrian Camel	40	1155	1115			
86.	Dromedary Camel	40	588	548			
87.	Llama	453	2211	1758			

Sl. No	Common name	LFO	HF0	R	Frequency of noise		
88.	Vicuna	550	2275	1725			
89.	Roe Deer	535	701	166			
90.	Caribou	51	2810	2259			
91.	Fallow Deer	42	637	595			
92.	Barking Deer/Indian Muntjac	333	1001	668			
93.	Red Deer	50	726	676			
94.	Spotted Deer	217	877	660			
95.	White Tailed Deer	315	988	673			
96.	Dik dik	440	2983	2543			
97.	Thomson's Gazelle				1205	5975	
98.	African Buffalo	99	114	**15**			
99.	Bushbuck	445	620	175			
100.	Saiga	40	156	116			
101.	Springbok	52	2992	**2942**			
102.	Wild beast	52	2212	2160			
103.	American Bison	42	82	40			

Table 6: Lowest FO (LFO), highest FO (KFO), range of FO (R), and frequency of noise concentration in mammals.
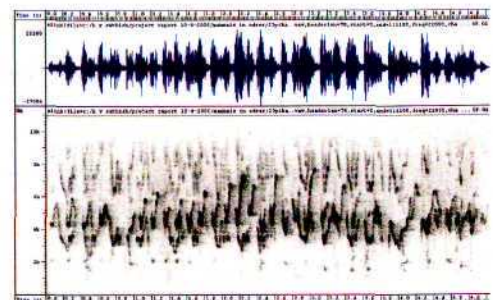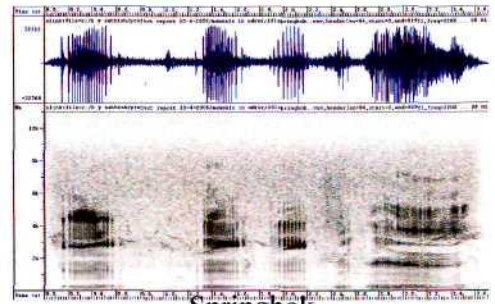
Serval
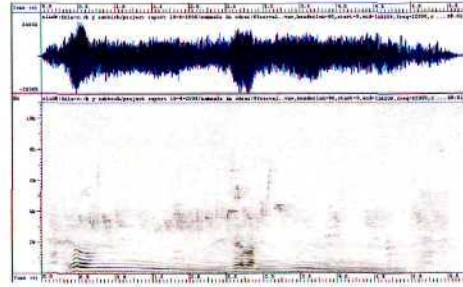
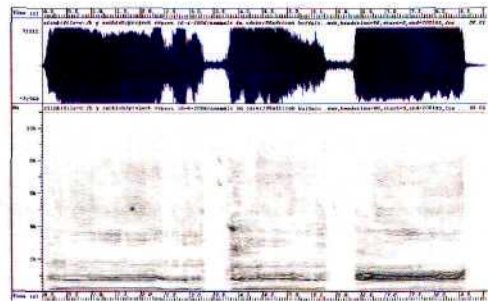Serval
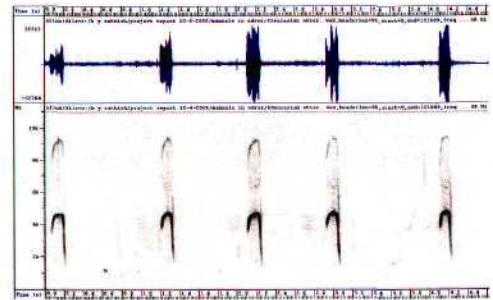
Eurasian Otter

Pika (A Rodent)

Pika

Figure 15: Photographs and wide band spectrograms of vocalizations of some mammals.

Discussion

The results indicated no linear increase in the fundamental frequency with the hierarchical positions in taxonomic classification. Anuran vocal folds have a wide variety of cross-sectional shapes: they can be T- or L-shaped, or rounded more like the vocal folds in mammals (Schneider 1988). This may be the reason for the wide difference in fO among amphibians. The reasons (birds and mammals) may also be because of physical environment and other ecological factors. These factors play

important roles in shaping vocalizations in most species, so that distantly related populations occupying similar habitats may possess vocalization more similar than those of closely related populations in different habitats (McCracken & Sheldon, 1997). For instance vocalizations of species that live in dense vegetation tend to have lower frequencies and narrower frequency ranges than those of species that inhabit open areas. This is because longer wavelength propagates energy more efficiently through vegetation than shorter wavelengths, which attenuate due to the scattering effects of leaves and branches (McCracken & Sheldon, 1997). Vocalizations in birds are also constrained by syringeal, morphology, which is the product of genetic and developmental influences. These physical, ecological, behavioural, and morphological forces can cause vocal characters to be similar by convergent evolution or chance, thus limiting their usefulness for inferring phylogeny. Although these problems make systematic studies of avian vocalizations particularly difficult, they are simply homoplasy, which potentially affects all types of phylogenetic characters (McCracken & Sheldon, 1997). An analysis of frequency used by birds in this study and the height to which they fly indicated no correlation between two parameters. Table 7 shows the height (flying or habitat) and frequency range of 5 birds.

SI. No.	Name	Height in feet	Frequency range in Hz
1.	European Kestrel	6500	555-2137
2.	Bald Eagle	6500	1208 -2971
3.	House martin	7200	1034 -2982
4.	Fish Eagle	8050	648 -1654
5.	Blue rock thrash	13000	1964 - 2977

Table 7: Height (flying or habitat) and frequency range of 5 birds.

An evolutionary perspective proves valuable both for identifying functional problems that are solved by communicators, and for using phylogenies and the comparative method as tools to identify and understand widespread selectiye.

pressures and functional constraints. Today's species are the outcome of a long dynamic process of co-evolution and interaction. Signalers' ability to avoid, repel or attract predators, competitors and potential mates has played a critical role in the evolution of their acoustic signals, including the mechanisms that produce them. A comprehensive answer to the question "why do birds sing?" or "why do deer roar?" will always go beyond the proximate mechanisms to the ultimate function, the selective value that allowed singing or roaring animals to out-reproduce their mute conspecifics (Fitch & Hauser, 2002). As pointed out long ago by Tinbergen (1963), these two perspectives, proximate and ultimate, are complementary. Each provides a rich source of insights and testable hypotheses that the other does not. It is believed that vertebrate acoustic communication provides numerous model systems that are ideally suited to integrate these two perspectives, and that such integration will prove vital in understanding the remarkable diversity of acoustic signals and the mechanisms that produce them.

The non-linear variations in fO can also be attributed to considerable variability in the anatomy of the tetrapod vocal production system. Unfortunately, little of this impressive morphological diversity has received enough concentrated empirical attention for any firm conclusions to be reached about its proximate, much less ultimate, function. This is particularly true regarding the significant morphological diversity in the vocal tract. Compared with the relatively conservative tetrapod larynx, there is a bewildering diversity of vocal tract morphology, but the functional significance of this diversity is only beginning to be explored (Fitch & Hauser, 2002). Advances in digital signal analysis, techniques for the visualization of the vocal tract in action, and an increasing interest in the role of proximate

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mechanisms in evolution suggest that progress in understanding this morphological diversity, and correlating it with social behavior and evolutionary history, may become rapid in the coming years.

In a variety of animal sounds, nonlinearities (noise) in the vocal production mechanism were observed. This can play an important role in structuring the acoustic morphology of calls. In these cases, quasi-periodic phonation is replaced by one or more of a variety of irregular or aperiodic phenomena. While research into nonlinear phonation is still in its infancy, it appears likely that such vocalizations play an important role in the communication systems of many species. The next few years may bring a much more detailed understanding of both the acoustic production of non-linearities in animal vocalizations, and their behavioral and evolutionary significance.

Also, in addition to the larynx or syrinx, there are other possible sources of acoustic energy available in all terrestrial vertebrates. Given adequately high flow, a narrow constriction anywhere along the path from lungs to lips or nostrils can produce turbulent noise (as in human whispers or "s" sounds, or snake hisses), thus providing a set of other possible sources of broadband noise. Such a turbulent source can operate alone or simultaneously with the laryngeal or syringeal source. For example, the English sound "f" is produced by a turbulent noise source alone, generated at a constriction between the teeth and lips. In contrast, the "v" sound is created by phonating simultaneously with "f" , and thus is a dual-source sound. Both non-laryngeal sources and dual-source sounds are common in human speech, forming a significant portion of the consonantal repertoire. Much less is known about the use of

turbulence in animal communication, though hissing is obviously a widespread type of vocalization among tetrapods. Examples include llamas, cats, viverrids and sloths among mammals, many snakes, turtles and crocodilians among reptiles, oxpeckers (genus *Buphagus),* vultures, geese, swans and ostriches among birds. Some groups of birds that are known for having loud or low-pitched voices also have unusually large syringes (Amadon 1969, Delacour & Amadon 1973).

Another reason for variations in fO may be attributed to numerous morphological adaptations of the vocal tract in tetrapods. Many (or most) of these can be interpreted as vocal tract elongation. These include proboscises and descended larynges in mammals (deer and humans), but perhaps the most widespread example is tracheal elongation in birds. At least 60 species of birds have an elongated trachea that forms loops or coils inside the thorax, coiled between the ventral skin and breast musculature, or invaginating the sternum or clavicle (Niemeier 1979).

The accumulated data for terrestrial vertebrates, direct and indirect, suggest that independence of source and filter should be assumed as the working hypothesis of researchers in vertebrate bioacoustics as it is in human speech. Specific data (e.g., derived from vocalizations in heliox) would have to be adduced before rejecting this hypothesis and positing source/tract coupling. This is worth stressing, because many physicists and bioacousticians, particularly in the older literature, adopt wind instruments, and therefore coupling between source and filter, as their default model of acoustic production. All current data suggest that the wind instrument analogy is dangerously misleading as a model of vocal production. Moreover, independence of source and filter has an important practical consequence for researchers interested in

studying call perception: using well-developed techniques from speech science such as linear prediction (LPC) or cepstral modeling, it is possible to pull a signal apart into source and filter components and independently modify one specific parameter of interest (Markel & Gray 1976, see Owren & Bernacki 1998 for a bioacoustically-oriented review). Such analysis/synthesis techniques provide an extremely powerful way to isolate the relevant acoustic parameters in bioacoustic communication systems; these are only starting to be explored (Owren & Bernacki 1988, 1998, Fitch & Kelley, 2000). Broadly speaking, formants are one correlate of the percept of "timbre" in animal sounds; in no case are formants correlates of pitch. The frequencies of the source signal appear, in normal situations, to be completely independent of formant frequencies. This is in contrast to the situation in wind instruments, where source and filter are strongly coupled.

Finally, the results of this study have generated some data on frequencies used by vertebrates. No particular calls or songs are considered in this study. Calls have been analyzed irrespective of situations. A detailed study of calls in specific situation may provide further detailed analyses and perhaps construction of a dendogram from such data.

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Comparative Anatomy and Performance of the Vocal Organ in Vertebrates

	Vocal organ	Sound production	Skeletal part	Description of larynx
Amphibians	Larynx - Two slender cartilaginous rods embedded in the walls of the sphincter			Laryngeal box - arytenoid and cricotracheal portion
Anura (Rana)	A fold rising from the inner aspect of the arytenoid and covered with a mucous membrane, the vocal band.	Buccal air sacs, inflated during vocalization, help in producing a loud sustained voice even under water		

	Vocal organ	Sound production	Frequency	Skeletal part	Description of Larynx
Birds	Well developed larynx. Constrictor - cricoarytenoids and interarytenoids, Dilators - cricoarytenoideus dorsalis. Lacks vocal cords. The separate parts of the larynx have little mobility. Syrinx - Located in most cases at the bifurcation of the trachea. Trachea forms loops which lie in a groove of the stream. These loops elongate the trachea in such a way that the number of tracheal rings can rise to 300. surrounding the syrinx is the air sac	Larynx does not produce sound. Syrinx and the airsac produce sound.	20-4800 cps Prevalence of low tones - 75-3000 cps.		**Syrinx** - Sternohyoid and sternotrachealis and mylo-hyoideus pull the trachea up and down
Singing birds	Nine parts of the syrinx muscles regulate the position of the uppermost bronchial rings. The bill, oral cavity, tongue, hyoid bone, larynx constitute an effective mechanism for modulation of the sounds produced in the syrinx.	No mute birds Call notes True song			

	Vocal organ	Sound production	Frequency	Skeletal part	Description of Larynx
Mammals	**Larynx is the vocal organ. *Thyroid cartilage is the exclusive possession of mammals*. From the viewpoint of phonation the *retrovelar or retropalatinal position of the epiglottis is of importance. The rigid nasal chambers are directly connected with the larynx, and the separation of food from the air passage is complete.***				
Marsupials	Thyroid and cricoid are fused and the arytenoids are grown together dorsally. There is no mechanism to stretch the vocal cords	Voice is not made use of. Piercing cries or grunts			
Monotremes	Large arytenoids, but thyroid and cricoid cartilages are fused. The rigidity caused by the fusion of thyroid and cricoid is not favorable to laryngeal voice production.	Mostly voiceless,			
Primates Monkeys	High degree of development Intralaryngeal reinforcement by resonance in lateral intralaryngeal air columns.				
The new world monkeys an	Short, not valvular ventricular bands, and very long and sharp edged vocal cords, supported by long and deep ventricles and reinforced by an osseous dilatation of the hyoid body	Roar			

	Vocal organ	Sound production	Frequency	Skeletal part	Description of Larynx
Old world monkeys (Baboons)	The middle portion of the hyoid body is inflated, and encloses the bony portion of the air sac which is continued in the membranous portion. The epiglottis is perforated, offering a communication between larynx and air sac. Pharynx is developed with differentiation of a uvula.	Inspiratory sounds		Skeleton of larynx is built with a superior elasticity. The vocal cords jut only moderately in to the lumen. The free edge of the vocal cord is directed orally. The rest of the elastic fold remains embedded entirely in to the lateral wall.	
Gibbon	Lx stands on a sideline on the road leading to human conditions. In spite of a very high degree of differentiation it is not on the straight line which leads from the low mammals to primates. For the first time glottis can be closed to its fullest extent. Double vocal cord - Superior one can be considered as homologue to a vocal fold proper. The inferior fold, although jetting even farther against the laryngeal lumen, does not find room for its insertion on the arytenoid, and runs backwards to insert below the level of this cartilage.	Tones at fixed frequency can be sustained for a longer duration because of complete glottal closure. Finer fO modulation is questionable as the accessory vocal cords does not insert on the vocal process of the arytenoids.			
Gorilla	Remarkable is the development of the inner laryngeal musculature (muscle thyroarytenoideus	Terrific roar, but silent in captivity - a low murmur.			

	Vocal organ	Sound production	Frequency	Skeletal part	Description of Larynx
Chimpanzee	Larynx is still in a high position pressed against the lingual base, and as in Orang and Gorilla there is still some difficulty in separating the soft palate and the epiglottis. The vocal lip, the sharp upward-turned edge of vocal cord moves inward with displacement of the vocal process of the arytenoid.	This accounts for the absence of long drawn out sounds This is well suited to create inspiratory sounds.			
Man	Sites of junction where larynx, pharynx, oral and nasal cavities join each other are of outstanding interest, as they influence the configuration of the resonant tube. These sections how considerable variety within the animal range. Continuity, characteristic of the human vocal organ, is attained in a roundabout way, by intercalation of regions without phonetic role in man, or in the opposite way, by elimination of parts which were previously of decisive importance. Only in man is the voice modifiable by muscular control of the upper air passages by palatal, lingual, nasal, and other facial movements in a way to permit articulated speech. The voluminous processi of the arytenoids in the laryngeal aditus are reduced in man to the tiny corniculate cartilages. The steep rise of the glottis from dorsal to ventral, a more primitive condition, was eliminated already in Orang, Gibbon, and Chimpanzee. Also, the incorporation of muscular bundles had advanced gradually with finer, more exact control of the vocal apparatus.				

Vocal cords of Evolution of larynx is frequently *out of step.*
species

Kangaroo, an aplacental, shows already a *tiny vocal cord.*
Atherura, a rodent and consequently higher classified than the Kangaroo, shows merely a *small,* soft, not differentiated protuberance.

In Felides, the vocal cords rise *high* up to the aditus of the larynx.
In Seals, the vocal cords *step back* completely.

Double vocal cords appear at different points of the phylogenetic sequence, to disappear through long intervals, as between Swine and Gibbon.

Te larynx of the Felides is more primitive than the larynx of the Hare or of the Antelope, but the vocal production in the latter is very much poorer.

These testify the difficulty of constructing a straight, ascending scale by tabulating the vocal capacity. Study of structure and of performance show many deviations from the straight evolutionary lines.