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Unpacking "Honesty": Vertebrate Vocal Production and the Evolution of Acoustic Signals

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1. Introduction

When autumn arrives in northern Europe, female red deer (*Cervus elaphus* L.) begin to congregate. The mating season has begun. They are soon joined by males, who have spent the previous ten months in preparation, feeding and sparring. Some of the males herd females into groups or "harems", which they vigorously defend from other males. A prominent component of this defense is roaring, a powerful, low-pitched groaning sound made only by males, and primarily by harem holders. Why do males produce these sounds, and what effect do they have on listeners? Early observers (Darling 1937) suggested that the roars intimidated rivals, and repelled intruders without the need for a dangerous fight. However, selection should favor opponents who are not so easily intimidated, and who base their behavior solely upon a balanced assessment of their chances of winning a fight and inheriting the herd (Maynard Smith and Price 1973). In a classic paper, Clutton-Brock and Albon (1979) showed that roaring provides a source of information relevant to this decision: roaring rates of individual males are highly correlated with their fighting ability and thus provide an accurate indication of the males' ability to repel intruders. They also demonstrated, in a series of playback experiments, that rival males attend to this information, responding preferentially to high roar rates and ignoring the roars of young, small males. Red deer roaring has since become a classic example of "truth in advertising" in an animal vocalization.

"Honest signaling" in animal communication refers to signals that provide accurate information to perceivers, either about the quality or properties of the signaler itself (e.g. advertisement calls), or about something in the environment (e.g. alarm calls). The degree to which animal signals are honest in this sense has been a perennially provocative problem, and has generated significant theoretical advances, along with some empirical work, in the last few decades. Early workers in ethology were primarily interested in the historical evolutionary origins of particular communicative displays (e.g. via "ritualization" of intention movements; Cullen 1966), and devoted little attention to questions of honest or deceitful information transfer (Hinde 1981). To the extent that information is transferred, it was often implicitly assumed to be in both parties' interests that the information be accurate. However, the red deer example illustrates the weakness of this assumption. What prevents every harem holder from roaring at very high rates, and thus repelling all comers without regard to his fighting ability? Such a deceitful mutant would be spared the costs of fighting, and his genes should spread rapidly through the population (Dawkins and Krebs 1978). This in turn would generate strong selection for "skeptical" males who ignored roaring altogether (Clutton-Brock and Albon 1979, Hinde 1981, Krebs and Dawkins 1984). Thus, theory predicts that selection resulting from receiver skepticism would eliminate the potential benefits of dishonest signaling. The only communication systems which would be stable in the long run (an "evolutionarily stable strategy" or ESS) are those in which honesty is ensured by some mechanism. This search for such honest ESSs in animal communication has been a major preoccupation of the field for more than a decade.

The best-known mechanism by which honesty in communication could be insured was proposed by Zahavi (1975). Though initially repudiated by many researchers (e.g. Maynard Smith 1976), Zahavi's "handicap principle" received support from a mathematical model developed by Grafen (1990), and has now become widely cited as a possible source of honesty in communication. The handicap principle proposes that only heritable signals that bear a high cost (the "handicap"), thereby reducing their bearer's fitness, can be stably honest. Of course, all signals bear some cost (Bradbury and Vehrencamp 1998), so this statement alone has little explanatory value. In Grafen's (1990) analysis, a "handicap" signal of male quality must be more expensive for low-quality males to perform than for high-quality males. Although there has been growing

agreement that Zahavian handicaps may play a role in the evolution of honest signaling, a recent paper by Siller (1998) exposes important flaws in the Grafen (1990) model, and again casts some doubt upon the basic logic of the handicap principle. In particular, Siller (1998) demonstrates that there is no guarantee of a single ESS under Grafen's model conditions, and opens up the possibility of multiple coexisting ESSs. More generally, if there are mechanisms that allow honest communication without a handicap, these less expensive alternatives should be favored over handicap signals, which can impose an arbitrarily high cost on their creators.

Again, the roaring of red deer illustrates the point. Harem-holding males rarely feed during the rutting period and lose up to 20% of their body weight. Towards the end of this exhausting period, male fighting ability drops rapidly, with harem-holders tending to tolerate rival males and lose fights with males they had previously beaten. This decline occurs at different times for different individuals, but in each case is associated with a drastic reduction in roaring rates (Clutton-Brock and Albon 1979). This suggests that roaring rate is an honest signal of fighting ability because both are dependent on bodily condition and stamina. Clutton-Brock and Albon (1979) suggested that this results from the fact that the same thoracic musculature is used for fighting and roaring, but commented that "current knowledge of cervid physiology is inadequate" to evaluate that hypothesis. Unfortunately, this comment is still mostly true twenty years later, though recent work has revealed some interesting adaptations for sound production in red deer (Fitch & Reby 2001, see below). Resolution of such questions demands an understanding of the mechanisms used to produce sound, and their physiological and anatomical relationship to other systems. Considerations such as these have led to an increased interest in production mechanisms in recent years, and to a growing consensus that our understanding of the evolution of acoustic signaling systems will remain incomplete until the physics and physiology of signal production are better understood (Hauser 1996, Bradbury and Vehrencamp 1998, Krebs and Davies 1997).

In this chapter, we will address the production of acoustic signals from a dynamic evolutionary perspective, paying close attention to the role of physical and phylogenetic constraints on the evolution of acoustic signals and the mechanisms that produce them. This choice of perspective is somewhat atypical and perhaps requires justification. First, why focus on signal production mechanisms? For researchers in the behavioral ecology tradition, who typically seek ultimate evolutionary explanations for a given pattern of behavior, the proximate mechanisms responsible for a behavior have often appeared irrelevant. However, researchers in evolutionary bioacoustics can expect at least two benefits from a basic knowledge of sound production mechanisms. First, our ability to conduct research in bioacoustics depends crucially on our ability to analyze animal sounds precisely, and in some cases to synthesize them, both of which hinge critically on a solid understanding of the acoustic mechanisms that generate them. Second, an understanding of mechanism offers crucial insights into the adaptive landscape of a communication system: what sounds are easy, or impossible, to produce? What are the costs and benefits of a given sound type in terms of energetics, predator detection, environmental transmission, and receiver characteristics? What are the possibilities, for a given species, to cheaply produce honest signals, or to cheaply mimic honest signals? The data we will review below indicate that the laws of physics, and the structure of sound producing organs, place strong constraints on the possible evolution of acoustic signals, determining what information is available for perceivers to exploit initially, what deceptive or skeptical mutations can subsequently arise, and the costs and benefits of producing and responding to a given signal. Far from being a wide open field, the adaptive landscape for vertebrate acoustics seems to be characterized by a circumscribed range of biologically-relevant and potentially honest signals, and an even narrower range of potentially deceptive mechanisms (both morphological and behavioral). Thus, we argue, an understanding of signal production mechanisms and physical acoustics can provide crucial insights into the evolution of acoustic communication.

Second, why adopt an evolutionary perspective? Researchers interested in the mechanisms underlying vocal production and/or auditory perception might argue that the ultimate evolutionary forces structuring a communication system offer little insight into the proximate morphological and neuronal mechanisms that underlie acoustic behavior. One reason that an evolutionary viewpoint is valuable is that many aspects of animal morphology and behavior 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 developmental, physical or mechanistic constraints. No animal has wheels, despite the fact that wheels would be adaptive for large grassland herbivores. The absence of wheels results from developmental and physiological constraints operating over evolutionary time. More prosaically, small body size will forever

prevent many species from exploiting infrasonic communication, which might otherwise be optimal in terms of attracting mates but not predators. An evolutionary perspective also encourages an exploration of interspecific similarities and differences, providing a comparative framework to address many mechanistically-based questions that have already been answered by experiments of nature. Could an animal with a larynx half the size of its body still breathe and eat? The fruit bat *Hypsignathus monstrosus* shows us that the answer is yes (see Sec. 2.2.2). What is the relationship between perceptual and production systems in the evolution of acoustic communication? Ryan's (1985, 1988, and Ryan and Kime, this volume) and Gerhardt's (1982, 1991) elegant comparative work on anuran bioacoustics has increased our understanding of the coevolution of production and perception mechanisms in frogs, as well as anuran evolution more generally. Finally, certain adaptive problems are so persistent and pervasive that they have spawned numerous, independently-evolved solutions, and we need to identify these powerful evolutionary forces if we are to understand the broad patterns of diversity seen in animal behavior and morphology. Tracheal elongation in birds, which has independently evolved at least eight times, provides a possible example that will be discussed below.

1.2 Evolutionary Constraints

The notion of restrictions or constraints on evolution has been with us since Darwin (1859, Chapter 13). Although most researchers agree on their importance, detailed analysis and quantification of the role of evolutionary constraints has proved an elusive goal (see Maynard-Smith et al. 1985, Carroll 1997), and many different classifications of constraints have been proposed. In this chapter, we will distinguish functional from phylogenetic constraints. Functional constraints result from physical, anatomical and physiological factors that limit the range of possible forms and functions; e.g., physical constraints on evolution stem from properties or laws of the physical world which do not depend on properties of living organisms. For example, hydrodynamic forces have a profound influence on the shape of aquatic organisms. The functions relating pressure drag and friction drag to velocity lead to an ideal length/width ratio of 4.7 for a streamlined body (Hildebrand 1974). While this ratio is equally valid for a swimming fish and an inert object dragged through the water, it is clearly no accident that streamlined body forms of this aspect ratio have evolved repeatedly in fast swimming organisms (fish, penguins, dolphins and ichthyosaurs, Carroll 1997). The study of such physical constraints is an important component of the discipline of functional morphology.

Phylogenetic constraints, on the other hand, 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. The fact that insects have six legs is not due to any physical constraint (as the existence of quadrupeds, spiders, crabs and millipedes clearly demonstrates), but to the strong canalization of the developmental pathways that generate adult insect forms. Although small mutations can have drastic phenotypic effects (e.g. mutations of the *Antennipedia* gene lead to flies with legs in place of their antennae), the chance of such macromutational changes leading to increased fitness is vanishingly small. Another example of a phylogenetic constraint is the genetic code itself: there is no reason in principle for the nucleotide-to-amino acid code to be shared by all life on this planet, but practically speaking, any mutant with a deviant code would be eliminated very early in development. Such constraints are in some sense arbitrary results of the particular evolutionary history of a species, but nonetheless create extremely powerful limitations on the viable genotypes available by mutational changes from a given parental lineage.

A major goal of this chapter is to explore the role of physical, physiological, and cognitive constraints in shaping vertebrate communication systems over time. Because many relevant constraints are shared by all vertebrates (and physical constraints are shared by all organisms), sampling a wide range of species may allow us to uncover and understand such constraints, and outline their influence on the shape of adaptive space, with some accuracy. Thus we will cast a broad net, considering the communication systems of most terrestrial vertebrates at least briefly, though focusing on tetrapods, and birds and mammals in particular (see Ryan and Kime, this volume, for a fuller discussion of anuran communication, Bass and Clark, this volume, for discussion of underwater organisms, and Tyack and Miller, in press, for more on marine mammals). In Section 2 we will outline a set of relatively well-understood constraints that follow from the physics of sound, relating body size to signal frequencies. Using the comparative method, we show how these constraints have led to the evolution of cheap, honest signals in birds and mammals. In Section 3, we turn to perceptual and cognitive mechanisms in communication, showing how perceptual constraints can leave perceivers vulnerable to "sensory exploitation", and how learning mechanisms can allow perceivers to short-

circuit such manipulation. We conclude that an understanding of constraints in signal evolution, together with a dynamic view of evolution, can provide rich insights into animal communication systems. We hope to show that, when integrated with the comparative evolutionary perspective advocated above, the study of physical and phylogenetic constraints can provide rich insights into the evolution of acoustic communication systems.

1.3 Distinctions and Definitions

There are many important distinctions to be made in discussions of the evolution of honest signals. Here we will focus on three: arbitrary vs. direct signals, lies of omission vs. commission, and external- vs. self-reference. These distinctions do not represent hard and fast categories that exist in nature, but rather lay out a continuum upon which any given signal can be located. A signal might be intermediate or extreme along any of these continua. Thus, these distinctions must be seen as aids to communication and understanding, and not claims about dichotomies in the world.

1.3.1 Arbitrary and Direct signals

One continuum along which we can analyze acoustic signals concerns the degree to which the mapping between signal and referent is arbitrary. In human language, word meaning is generally not tied in any direct way to the acoustic structure of that sound. Thus, except for a small number of onomatopoeic or sound-symbolic words, one cannot guess the meaning of a word in a foreign language based only on its sound. It is often assumed that the information in animal calls is similarly arbitrary. There is, however, significant evidence that at least some of the information in animal calls is "direct", with a non-arbitrary mapping between sound and meaning. The most obvious example is the association between low frequency and large size. Because only large objects can produce and radiate low frequency signals effectively, there is a natural mapping between size and frequency, particularly large body size and low frequency calls (e.g., elephants and infrasound). We will argue that physical facts like the size/frequency relationship have played a pervasive role in the evolution of communication systems, and that a solid understanding of production mechanisms is necessary to uncover and understand such relationships. In contrast, the difference between the vervet monkey's leopard and snake alarm calls probably has little or nothing to do with the sounds themselves (Cheney and Seyfarth 1990). Rather, these calls are more like human words, providing an example of an arbitrary sound/meaning pairing that has been conventionalized over evolutionary time.

1.3.2 External and Internal Reference

Because "reference" in humans is typically construed to involve consciousness and intentionality, researchers wishing to remain agnostic about these issues in animals often adopt the term "functionally referential" when discussing this issue (Marler et al. 1992, Hauser 1996). We will use the word "refer" here only in a limited sense of causal correlation between an object or event and a corresponding animal signal. Thus a bee's waggle dance "refers" to flowers, in the sense that it enables other bees to locate and feed from the flowers, despite a presumed lack of self-awareness or high-order intentionality on the part of the dancing bee. Most traditional work in animal communication has concentrated on signals that indicate the signaler's species, individual characteristics or motivational state, and we will consider many such internally referential signals in the first part of the chapter. Recently, there has been much interest in signals that seem to refer to the world outside the signaler (Seyfarth et al 1980a, b, Gyger et al. 1987, Hauser and Marler 1993a, b). The classic example is alarm calling in vervet monkeys, where different calls produced by signalers viewing eagle, snake or leopard predators elicit appropriate escape reactions from listeners (Struhsaker 1967, see Sec. 3.2). These calls are externally referential in that, regardless of the state of the caller, listeners respond to them as if they indicated something about the world outside of the caller (playback experiments that simulate a predator encounter provide further evidence that the calls alone are sufficient to elicit appropriate responses from listeners). We will consider such signals in some detail in the second half of this chapter.

1.3.3 Lies of Omission and Commission

In their recent textbook on animal communication, Bradbury and Vehrencamp (1998) define deceit as "the provision of inaccurate information by a sender to a receiver". However, it is often possible to deceive by failing to provide information (e.g. failing to give food calls upon discovering food, Hauser 1992, Hauser and Marler 1993a). We thus distinguish between lies of commission (the provision of inaccurate or misleading information) and lies of omission (withholding expected information) (Hauser 1997). There is good empirical data concerning both types of "deceit" in animal communication (see Sec. 3). It may be quite difficult to locate

and identify individuals who withhold signals, which may make the evolution of lies of omission easier. The evolution of receiver skepticism is not as common as might be expected. In particular, receivers who are able to learn about signalers through repeated interactions should quickly be able to learn to identify signalers who "cry wolf", since calls typically carry information about signaler identity, along with any external referentiality. Our review of the literature will suggest that the development of such facultative skepticism is surprisingly uncommon, with clear evidence only in a few primate species. This suggests either that the cost of being deceived may be very low, or that perceptual or cognitive constraints may limit the ability of perceivers to become effective skeptics.

2. Physical and Anatomical Constraints on Signal Production: The Physics of Honesty

This section is focused on the mechanisms involved in vertebrate vocal production, and is divided into three parts. First, we briefly review the basic acoustics of vocal production, showing how a few easily-understood physical principles combine with anatomy and physiology can have profound consequences on the sounds a particular animal is able to produce. Then, we examine the morphology of vertebrate sound production systems in greater detail, surveying the vast and mostly unexplored diversity of vocal tract anatomy in terrestrial vertebrates. Finally, we attempt to make some sense of this diversity, describing how evolutionary constraints can act in some cases to enforce honest communication in the absence of any specific selection for honesty. We also describe how novel morphological or physiological mechanisms can allow the evasion of certain anatomical and physiological constraints, suggesting that many morphological oddities are best understood as constraint evasion mechanisms. For example, the "key innovation" of the syrinx has opened the door to vocal adaptations in birds that are inaccessible to other tetrapods due to their reliance on the larynx as a sound-producing source.

2.1 Vertebrate Vocal Production: Anatomy and Acoustics

Our intent in this section is to survey vocal production in tetrapods. With 9000 species of birds, 6000 reptiles, 4500 amphibians and 4000 mammals, we could not hope to be exhaustive. Due to space limitations and the significant differences between sound production and transmission in air and water, we will have little to say about fish or cetaceans (see Bass and Clark, this volume). Furthermore, available research on terrestrial vertebrate vocal production is unevenly distributed: the best-researched groups are oscine birds (Nowicki and Marler 1988, Gaunt and Nowicki 1998), anurans (see Ryan and Kime, this volume, and Schneider 1988), and, among mammals, echolocating bats (Suthers and Fattu 1973, Suthers 1988) and humans (Fant 1960, Lieberman and Blumstein 1988, Titze 1994). Much less is known about reptile vocal production (see Gans and 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, we follow tradition (e.g. Greenewalt 1968, Lieberman 1968, Hartley and Suthers 1988) in using data from human vocal production to ground our discussion of call production in other vertebrates. Where appropriate, we point out the many significant differences between human speech and animal calls, and call attention to the importance of developing new methodological and theoretical tools to cope with these differences.

2.1.1 Generating Power: the Lungs

Voice production is the conversion of air flow into acoustic energy (that is, longitudinal pressure waves in the audible frequency range). Typically, this air flow emanates from the lungs. Tetrapod 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 crocodylians (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 air flow 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) or Perry (1989), or Lasiewski (1972) for birds.

Although most tetrapod vocalizations (e.g. human speech) are apparently generated on expiration, inspiration also plays an important role in vocalization in some anurans, 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 and 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, discussed in more detail below. 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 and Dudley 1993). The relevance of call duration to both energy expenditure and to female choice has been documented in anurans (Klump and Gerhardt 1987, Welch et al. 1998, see also Ryan and Kime, this volume), 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 et al. 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 and Tenaza 1977, de Waal 1988), as do human infant cries (Wolff 1969, Truby and Lind 1975). 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 (Calder 1970, Hartley and Suthers 1989).

2.1.2 The Voice Source

In terrestrial vertebrates, vocalizations are initially generated by a structure which converts air flow 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 (Fig. 1). In amphibians, reptiles and mammals, the source is typically the larynx. In birds, an evolutionarily 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 through the source by constricting its lumen. In the larynx, these vibrators are the vocal folds, sometimes called vocal cords. In the syrinx, the identity of the vibrators was long thought to be the medial tympaniform membranes (Miskimen 1951, Greenewalt 1968, Gaunt and Gaunt 1985). However, recent direct visualization via endoscopy suggests that the vibratory structures are the syringeal labia in passerines (Goller and Larsen 1997b) and the lateral tympaniform membranes in pigeons (Goller and Larsen 1997a). Although the medial tympaniform membranes may play some acoustic role, their complete ablation does not prevent nearly normal vocalization (Larsen and Goller 1999). In both the larynx and syrinx, energy created by the passage of air through 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 (see White 1968 for a possible exception).

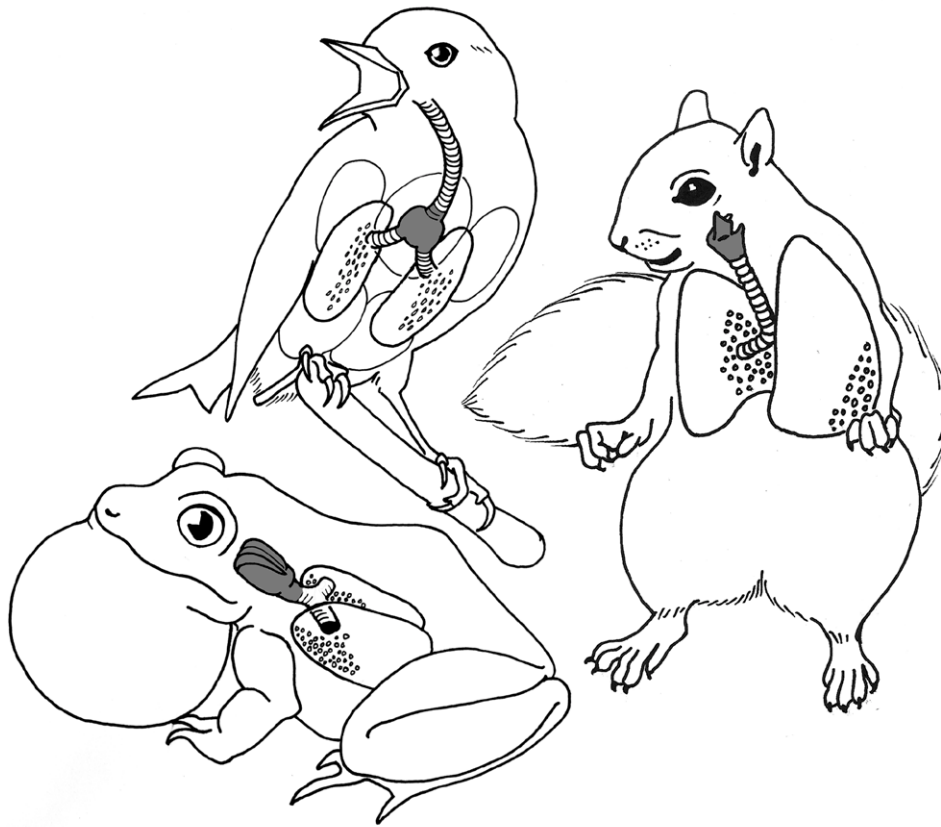


Figure 1: Representative tetrapods showing (in gray) the different anatomical sound sources in each group (schematic). Left: Anuran amphibians use a larynx with vocal folds to produce sound, and often vocalize into an inflatable vocal sac. Middle: Birds (a passerine is shown here) have an evolutionarily novel structure, the syrinx, which is located at the base of the trachea. Right: Mammals (a rodent is shown) use a larynx and vocal folds as the sound source.

There is a long history of scientific attempts to understand the functioning of the human voice source, starting with Johannes Müller's pioneering work with excised larynges (Müller 1848). The further work of van den Berg (1958, 1968) and Titze and colleagues (Titze 1994) has deepened this understanding, and we now have a detailed and accurate model of vocal production at the voice source termed the "myoelastic-aerodynamic theory". The vocal folds act as mechanical vibrators, with their own elasticity and mass, that are coupled to the aerodynamic flow from the lungs to generate self-oscillation. Before oscillation can begin, the vocal folds must be placed in an appropriate "phonatory" position, closer to one another than during normal breathing. Once this position is attained, air flow from the lungs can set up sustained oscillations. The critical factor is that energy must be pumped into the system in phase with the vocal fold oscillation: there must be a greater pressure pushing the folds apart as they are opening than while they are closing. In human speech this is made possible by a change in the vertical geometry of the folds, with a divergent glottis during closing leading to less force than the convergent glottis during opening. Although it is frequently stated that the Bernoulli force is adequate to maintain oscillation, this alone is not adequate, since it is equally strong during opening and closing (Titze 1976, 1980). Similar considerations must apply in all tetrapod sound sources; Titze (1994) is recommended as an excellent introduction to the topic.

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 and Cannitto 1995 and Mergell et al. 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 et al. 1990, Bless et al. 1998, Hirano 1991, Brown and 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 and 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 F_0). 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 and 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, van den Berg 1968; see also Yamaguchi and Kelley, this volume). All that is necessary is to place the vibrators in an appropriate state of tension and approximation, with the proper air flow, and the system will vibrate with a motion and at rates closely approximating those seen *in vivo*. The passive frequency control of the voice source of terrestrial vertebrates contrasts sharply with frequency control of the swim bladder production system found in most fish, where each pulse of acoustic energy is produced by a muscular contraction (Demski et al. 1973, Bass 1989, Bass and Baker 1997). Such a system puts a clear physiological constraint on the highest producible fundamental (though some of the fastest-twitching muscles in the animal kingdom are found in swimbladder muscles; Tavolga 1964). Only a few teleosts produce sound via expulsion of gas from the swim bladder in a manner homologous with vocalization in tetrapods (e.g. minnows through the pneumatic duct, loaches through the anus, Demski et al. 1973).

The oscillations of the source are never perfectly periodic. Even a nearly constant fundamental has small perturbations around the mean frequency, termed jitter by speech scientists (Lieberman 1961, Baken 1987), and most vocalizations involve large nonrandom changes in fundamental over time. Nonetheless, to a good approximation much of normal phonation can be idealized as periodic. In human speech, such quasi-periodic phonation accounts for the vast majority of voiced sounds, and can be understood using standard linear systems theory and Fourier analysis. However, in the past decade it has become increasingly clear that certain types of broadband vocal phenomena are the result of deterministic chaos in the (nonlinear) dynamics of the vocal source (see Herzel 1996 for an introduction). In pathological cases in adult human speech (Herzel and Wendler 1991), in human infant crying (Mende, Herzel and Wermke 1990), and in a variety of animal sounds (Wilden et al. 1998), nonlinearities in the vocal production mechanism 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 including period-doubling, biphonation (the presence of two independent frequencies) and deterministic chaos (Fig. 2). 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 (see also Tyack and Miller, in press).

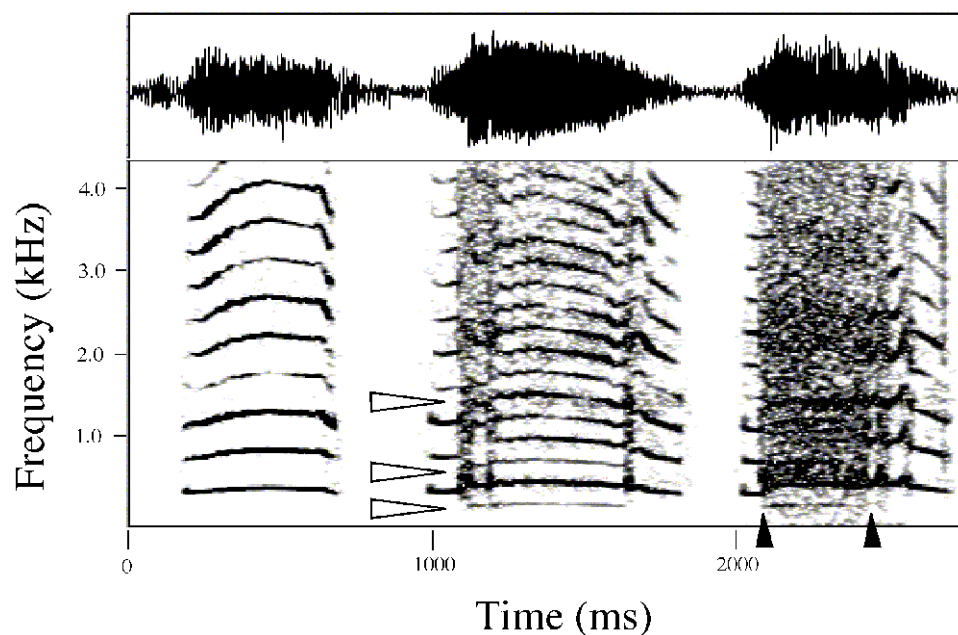


Figure 2. Nonlinearities in mammal vocalizations: Spectrogram of a series of three consecutive calls by a normal adult rhesus macaque male. The first call is a prototypical "coo" call, and the subsequent calls show intrusions of nonlinear phenomena. Call 2: after normal onset, subharmonics (indicated with light arrows) intrude. Call 3: after normal onset deterministic chaos appears (indicated with heavy arrows).

The most common example of irregularities in the voice source are provided by calls like those shown in Fig. 2, which shows calls from a normal rhesus macaque. Although the last call is "noisy" in the sense that it lacks clear periodicity, it has too much spectral structure to be caused simply by turbulent noise generated by vocal tract constrictions. Instead, such calls appear to be generated by irregular opening and closing of the glottis, due to strong non-linearities in the dynamics of the vocal folds; they are examples of deterministic chaos in glottal dynamics. This hypothesis has been confirmed in the human voice by direct observation of the vocal folds with high speed video endoscopy (Tigges et al. 1997), and is supported in the case of mammalian vocalization by abundant evidence summarized in Wilden et al. (1998). Other types of phenomena, such as period-doubling bifurcations shown in the second call of Fig. 2, lend further credence to this hypothesis. Despite the ubiquity of such calls, they have received little attention in the bioacoustics literature, perhaps because the appropriate conceptual framework to understand their production is quite new, and has until recently been confined mostly to physics journals. Fortunately, however, one of the ideal tools to analyze such calls is the familiar narrow-band spectrographic representation. Consequently, the next few years will bring a much more detailed understanding of both the acoustic production of non-linearities in animal vocalizations, and their behavioral and evolutionary significance.

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 crocodylians among reptiles, oxpeckers (genus *Buphagus*), vultures, geese, swans and ostriches among birds.

To give a concrete example of the value of mechanistic understanding in addressing evolutionary questions, we will briefly consider the role of fluctuating asymmetry in mate choice. Fluctuating asymmetry (FA),

individual deviations from physical symmetry that are hypothesized to provide an indication of developmental stability (see Møller and Thornhill 1998 for a recent review, and Houle 1998 for a critique), has been shown to play an important role in mate choice in an impressive variety of species. FA is an intrinsically unfakeable cue: the simple fact of bilateral symmetry means that most animals have paired structures, and small differences in the developmental environment of these structures can potentially have perceptible effects on the adult that can be used to evaluate FA and provide an indication of developmental stability. The use of FA in mate choice has been documented in a great diversity of species, but in all of these examples visual cues were used to evaluate FA. However, because asymmetries in the vocal folds exist (Hirano et al. 1989) and can have a perceptible effect on the vocal signals (Isshiki et al. 1977, Tigges et al. 1997, Steinecke and Herzog 1995), it is plausible that mistuned vocal folds could provide an acoustic indicator of FA. Similarly, the different lengths of bronchi in oilbirds give acoustic cues to vocal tract asymmetries in the species (Suthers 1994). Such acoustic indicators of FA could theoretically play a role in mate choice in addition to, or instead of, the well-known visual indicators. Such a supposition could be tested via tests of animals that vary naturally in FA, with calls synthesized with vocal tract models possessing varying degrees of asymmetry, or via experimental manipulation of vocal fold asymmetry (e.g., via unilateral vocal fold injections).

2.1.3 The Vocal Tract

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 supra-syringeal 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, using the term “vocal production system” to refer 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 (see next section). However, most of these papers are old and many are in German, and these morphological features have received little attention from modern bioacousticians. Furthermore, the functional importance of these features has received 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 (see Sec 2.1.4). 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. Human speech uses changes in formant frequencies to code meaning directly: formants and their movements are the most important acoustic cue in speech which typically provides external reference. 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 and Fitch 1999, Fitch and 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 and 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. Formants can vary independently of the source, and formants have little or no influence on pitch perception (which is determined by source characteristics), at least in humans (Lieberman and Blumstein 1988, Titze 1994).

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 et al. 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 and Fattu 1973, Andrew 1976, Nowicki 1987, Suthers and Hector 1988, Suthers et al. 1988, Hartley and Suthers 1988, Suthers 1994, Owren and Bernacki 1988, 1998, Owren 1990, Owren et al 1997, Westneat et al. 1993, Hausberger et al. 1991, Hauser 1992, Hauser et al. 1993, Hauser and Schön-Ybarra 1994, Fitch and Hauser 1995, Fitch 1994, 1997, 1999, 2000a, b, Rendall 1996, Riede and Fitch 1999).

For anurans 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 and 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 (see Sec 2.1.4). 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 Schneider (1988) and Ryan (1985). 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, see Sec. 2.2.5 "Air Sacs", below). Our 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 and Marler 1988, Hartley and Suthers 1988), in general there is a close correspondence between "pitch" and fundamental frequency. Thus the use of "pitch" to refer to other acoustic parameters, such as voice timbre or vocal tract resonances (e.g., Hausberger et al. 1991) is to be discouraged.

2.1.4 Independence of Source and Filter

There is a superficial similarity between vertebrate vocal production systems and wind instruments like the clarinet or trumpet, where the reed or lips play the role of the source and the column of air contained by the body of the instrument is analogous to the vocal tract. However, there is an important difference in the

physics of wind instruments and the vocal tract. In wind instruments, the vibrating frequency of the source is largely determined by the resonant frequencies of the instrument's "vocal tract", that is by the air column contained by the body. The instrumentalist manipulates the pitch of the instrument by changing the length of this air column, and thus the characteristic frequencies of the column's vibratory modes. In this case, it is appropriate to term the modes "resonances", because the source vibrates in resonance with (at the same frequency as) the air column.

In contrast, the vibratory frequencies of source and filter appear to be independent in vertebrates, an independence that makes vocal acoustics fundamentally different from the acoustics of wind instruments. 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 and McChesney 1965, Greenewalt 1968, Westneat et al. 1993, Hersch 1966, Nowicki 1987, Gaunt et al. 1987, Brittan-Powell et al. 1997, Capranica and Moffat 1983, Rand and Dudley 1993, Pye 1967, Hartley and Suthers 1988).

The best evidence for source/tract independence comes from experiments with animals vocalizing in light gases. Typically researchers have used heliox, a mixture of helium and oxygen with nearly double the speed of sound in air. Because formants are dependent upon the transit time of sound waves up and down the vocal tract, raising the speed of sound shortens transit time, and thus nearly doubles formant frequencies. In a coupled system like a wind instrument, doubling the air column resonances also doubles the fundamental frequency at which the source vibrates. However, in the human voice (e.g. Beil 1962), and in those animals tested (birds: Hersch 1966, Nowicki 1987, Gaunt et al. 1987, Brittan-Powell et al. 1997; anurans: Capranica and Moffat 1983, Rand and Dudley 1993; bats: Pye 1967, Hartley and Suthers 1988) the fundamental frequency does not shift appreciably in heliox. Where formant frequencies are present (mammals and birds), they shift upward. In humans, this leads to the peculiar "Donald Duck" quality of helium speech, with a normal, low fundamental and high formants (Beil 1962). In the case of birds and bats, the formant shift often "unmasks" harmonics which are present in the source signal, but are normally filtered out as the signal passes through the vocal tract (Nowicki 1987, Nowicki and Marler 1988, Pye 1967, Hartley and Suthers 1988). The only case of which we are aware that the perceptual relevance of heliox-shifted vocalizations has been examined is the work by Strote and Nowicki (1996), who found in a two-speaker choice experiment that song sparrows respond slightly more strongly to normal calls than to helium-shifted calls. There appears to be no consistent, significant effect of helium on vocalizations in the anuran species tested to date (Rand and Dudley 1993).

Despite the consistency of these heliox data in these species, there is little information relevant to source/tract independence for the vast majority of tetrapod species. Less direct analyses suggest independence, simply because the relatively short vocal tract of non-avian tetrapods would result in formant frequencies that are high relative to the fundamental in most mammals and anurans. Thus in macaque and baboon grunts (Andrew 1976, Rendall 1996, Owren et al. 1997) and dog growls (Riede and Fitch, 1999), the fundamental frequency falls far below that of the lowest formant. Although Bauer (1987) found a correlation between fundamental and mouth opening in an adult male chimpanzee, there was no indication that the change in fundamental was causally related to changes in formants due to mouth opening, and other time-synched analyses of formant changes with mouth opening indicate that no causal connection is likely (Hauser et al, 1993, see Fitch and Hauser 1995).

Thus there is a significant body of data indicating independence of source and filter in many vertebrate species. Nonetheless, independence is best considered a working hypothesis at present, given our limited knowledge of animal vocal production. Although source/filter theory is well-tested and well-accepted in speech acoustics, independence of source and filter is only a first-order approximation even in speech, and some interactions between the two do occur (Bickley and Stevens 1986, Mergell and Herzel 1997). Early *in vitro* work in birds provided some evidence of strong source/tract coupling. For example, Rüppel (1933) found that the vibratory frequency of an excised crane syrinx was dependent upon the length of the vocal tract attached supra-syringeally. Furthermore, a recent paper looking at *in vivo* production showed no heliox effect on intact birds but a profound effect on a budgerigar with a denervated syrinx (Brittan-Powell et al. 1997). These data suggest that source and filter may be passively coupled in this species, but that the bird normally overrides this coupling via active control of the syrinx. This hypothesis would explain both the *in*

vitro results of Ruppel (1933), and the lack of evidence for source-tract coupling in the vast majority of more recent studies. Another possible type of source/tract coupling, suggested by Hartley and Suthers (1988) for an echolocating bat species, is that energy propagating back from the trachea could provide positive feedback to support high-amplitude phonation, which is critical to receiving a sufficiently strong echo from their echolocation cries. Despite its plausibility, this hypothesis remains speculative at present. Finally, there are many bird and mammal species for which the fundamental frequency is close to the predicted formant frequencies based on vocal tract length, suggesting the possibility for source tract coupling, but whose production has not been experimentally examined.

In conclusion, 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 and Gray 1976, see Owren and 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 and Bernacki 1988, 1998, Fitch and Kelley, 2000).

2.1.5 Vertebrate Vocal Production: Summary

The vocal production apparatus of terrestrial vertebrates is made up of two components. The source - typically the syrinx in birds and the larynx in mammals, reptiles and amphibians - creates the sound. When this source-generated signal is periodic, its fundamental frequency (and in some cases the spacing between harmonics) determines the perceived pitch of the signal. The term "pitch" should be used with care, and only to refer to source-related acoustic parameters (e.g. the fundamental). This source-generated energy then passes through and is filtered by the vocal tract, which includes the mouth, nasal cavities and pharynx in all vertebrates, and additionally the trachea in birds. The filtering frequencies of the vocal tract are called formants. There is no colloquial term to refer to their perceptual correlate of formant frequencies, which is nonetheless perceptually salient to humans and to all vertebrates that have been tested. 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.

2.2 *Morphological Diversity in the Vertebrate Vocal Production System*

Although all of the vocal production systems considered here work in roughly the same fashion, and are governed by the same physical principles described above, there is an impressive diversity of form in the vertebrate vocal tract. Below we will provide a selective overview of this morphological diversity, and of some of the hypotheses that have been put forward to account for this variation.

2.2.1 Dual sources: the two-voice phenomenon in birds

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 et al. 1992).

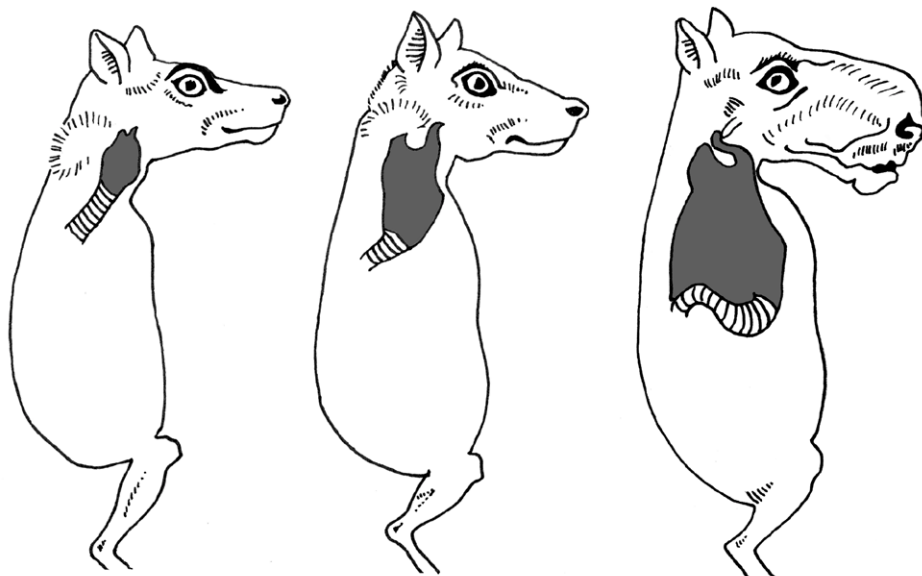
Conclusive evidence for the two voice theory was provided by Suthers' (1990) elegant experiments with mimic thrushes, which produce elaborate songs including imitations of other species songs. By implanting pressure and flow sensors in living birds, Suthers was able to definitively observe the two voice sources creating independent portions of the awake, singing birds final song. Interestingly, mimic thrushes (at least the catbirds and thrashers that Suthers studies) appear to utilize both sides of the syrinx relatively equally, although each side appears to habitually produce certain syllables and not others.

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, during breathy voice, or in pathological cases of unilateral laryngeal paralysis, the vocal folds do not collide, and have been shown to be capable of vibrating at two independent fundamental frequencies (Tigges et al. 1997). 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.

2.2.2 Hypertrophy of the voice source

In many mammalian species, the male larynx is enlarged relative to female conspecifics. Male specific enlargement of the larynx is probably common but we know of no systematic review of this topic. The best known example is provided by our own species. At puberty, the cartilages of the human male larynx increase rapidly in size (to about 150% of female laryngeal dimensions), and the length of the vibrating portion of the vocal folds increases even more (to nearly twice the female size (Hollien 1960, Titze 1994). This change in vocal fold length leads to a precipitous drop in F₀ at puberty that is one component of the pubertal voice change in males (F₀ about 50% of prepubertal values, Hollien et al. 1994). That this laryngeal enlargement is triggered by androsteroid hormones like testosterone has been known for centuries, leading to the widespread practice in medieval times of castration of boy singers to produce adult males with high-pitched voices ("castrati"). However, the details of the hormonal mechanisms mediating the pubertal voice shift have not been worked out in any species and are currently receiving intense scrutiny (Yamaguchi and Kelley, this volume).

Other examples of laryngeal hypertrophy are even more extreme. In howler monkeys (genus *Alouatta*), for example, the male hyoid apparatus and larynx are vastly enlarged, with the swollen, hollow hyoid occupying the entire space within the mandible (Schön-Ybarra 1986, 1988). The hyoid contains a laryngeal air sac, similar to that seen in many other primates, which may function as some sort of resonator (see below). It is possible that the mandible functions to limit further growth of the hyoid; it too is enlarged relative to other primates. Howler monkeys produce loud, low-pitched roars which appear to function in intergroup spacing; these calls may have provided the selective force underlying laryngeal hypertrophy in this genus. Finally, the most pronounced laryngeal hypertrophy in the animal kingdom is seen in African epomophorine fruit bats, especially the hammerhead bat (*Hypsignathus monstrosus*), in which the male larynx fills the entire thoracic cavity (more than half of their body, Fig. 3). As with the howler, the hammerhead larynx seems to have grown until it reaches a bony anatomical limit, namely the rib cage, pushing the heart, trachea and lungs down into the abdomen. The size of the larynx of female hammerheads is 1/3 its size in males. For the hammerhead bat the selective pressures underlying laryngeal hypertrophy have been quantified by the field work of Bradbury (1977), who studied mate selection in this African species. In trees along riverbanks, male hammerheads form "leks" (areas where males aggregate to attract mates), from which they emit an extremely high-amplitude advertisement call. Females fly up and down the riverine corridor, and finally choose a male to mate with. Males provide no parental care or other resources, suggesting that female choice might rely primarily on the vocal display. Bradbury found that five males in his population of 85 males accounted for 79% of the matings observed. These data suggest that sexual selection upon the vocal production apparatus of this species, and perhaps other epomophorine species, may be extremely intense.



Epomophorus wahlbergi *Epomops franqueti* *Hypsignathus monstrosus*

Figure 3: Enlargement of the larynx in the epomophorine bat *Hypsignathus monstrosus* compared to two related bat species, *Epomops franqueti* (which shows some laryngeal enlargement) and *Epomophorus wahlbergi*. The figure shows the outline of the larynx (black) and the upper portion of the trachea in each species.

These examples indicate that the mammalian larynx is not tightly constrained by body size. Although there is considerable interspecific variability in the size of the anuran larynx and avian syrinx, we are not aware of any examples of hypertrophy of the voice source as extreme as those seen in mammals. Some groups of birds that are known for having loud or low-pitched voices also have unusually large syringes (e.g. curassows and their allies, Amadon 1969, Delacour and Amadon 1973). Many studies have failed to find a correlation between body size and "dominant frequency" in anurans, but it is unclear to what extent dominant frequency depends on larynx size (see Sec. 2.1.3). Thus current data are adequate only to suggest a lack of constraint on source size, suggesting that even mild selection could disturb any primitive correlation between voice pitch and body size (*contra* Morton 1977).

2.2.3 Diversity in vocal fold morphology

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 (see Schneider 1988 for examples). Anurans also often have additions to the vocal folds which modify their oscillatory characteristics. The best-studied example is in the Túngara frog (*Physaleamus pustulosus*). This species has two components in its advertisement call, termed the "whine" and "chuck". The high-pitched, frequency modulated whine results from the oscillations of the vocal folds alone. The lower-frequency chuck is hypothesized to result from vibrations of two fibrous masses, coupled to the vocal folds, which are introduced into the airstream late in the advertisement call (Drewry, Heyer and Rand 1982, see also Ryan and Kime, this volume).

Another example of an anatomical modification of the voice source are the vocal membranes found on the vocal folds of many mammalian species. Vocal membranes, sometimes termed "vocal lips" or "sharp-edged vocal folds", are thin upward extensions of the glottal margin of the vocal folds. They vary in thickness, and in the details of their histology. They are common in microchiropteran bats, where they appear to subserve the production of ultrasonic echolocation pulses (Griffin 1958). Vocal membranes are also common in primates, where they have been hypothesized to allow individuals to generate calls with very high fundamental frequencies (Schön-Ybarra 1995) or two simultaneous frequencies ("biphonation": Brown and Cannito 1995), and perhaps to create instabilities in the fundamental (Lieberman 1968, Schön-Ybarra 1995, but see Hauser and Fowler 1991). The hypothesis of higher-frequency calling follows directly from the fact that, if the lightweight vocal membranes are free to vibrate independently of the much larger vocal folds, they will do so with a much higher frequency. Similarly, Brown and Cannito's "biphonation" hypothesis follows from the possibility that the vocal folds could vibrate simultaneously with the membranes, leading

to two independent frequencies in the vocal output. This effect was inferred from electroglottographs of the vocalizations of the Syke's monkey (*Cercopithecus albogularis*).

A recent modeling study sought to understand the acoustic role of the vocal membranes by simulating their effects in a nonlinear dynamical computer model (Mergell, Fitch and Herzel 1999). Mergell and colleagues modeled the membranes as fixed upward extensions of the upper mass in a well-studied two-mass model of the vocal folds (Ishizaka and Flanagan 1972); thus the membrane was not simply treated as an independent oscillator but as an integral portion of the vocal fold as a whole. This relatively minor geometrical change had significant effects on the dynamics of vocalization. In particular, the addition of vocal membranes enabled the model to support louder and higher-pitched vocalizations. Because echolocating bats need to produce extremely loud and high-pitched calls in order to provide a detailed, long-range "picture" of their surroundings, the functional utility of this enhancement is clear. Mergell and colleagues also found that the addition of membranes increased the possibility of source-tract coupling in the model, resulting in an increased possibility of nonlinear effects and irregularities in vocalizations of species with vocal membranes, as predicted by Lieberman (1968) and Schön-Ybarra (1995). More empirical work is needed to further test these predictions, including simple anatomical measurements of vocal membranes in different species, *in vivo* observations of vocal membranes during vocalization, and investigations of the social consequences of sounds acoustically manipulated to possess, or to lack, the characteristics caused by vocal membranes.

A second, and less common, modification of the mammalian vocal folds is essentially the opposite of vocal membranes: the addition of thick, fleshy pads to the vocal folds, rather than thin membranes. Such "vocal pads" are seen in lions and other cats of the genus *Panthera* (Hast 1989, Harrison 1995). No detailed physiological or observational data are available on their function. However, it seems quite likely that, due to their large mass, they play a critical role in the production of the low-pitched roars made by all of these "roaring cat" species (Hast 1989). Finally, there are significant differences in the histological fine structure of the vocal folds of different mammalian species, differences which will have significance in the F0 range and possibly other aspects of vocal fold dynamics (Hirano 1991).

2.2.4 Modifications of the vocal tract

Moving now from the voice source to the vocal tract, there are 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 (Fig. 4).

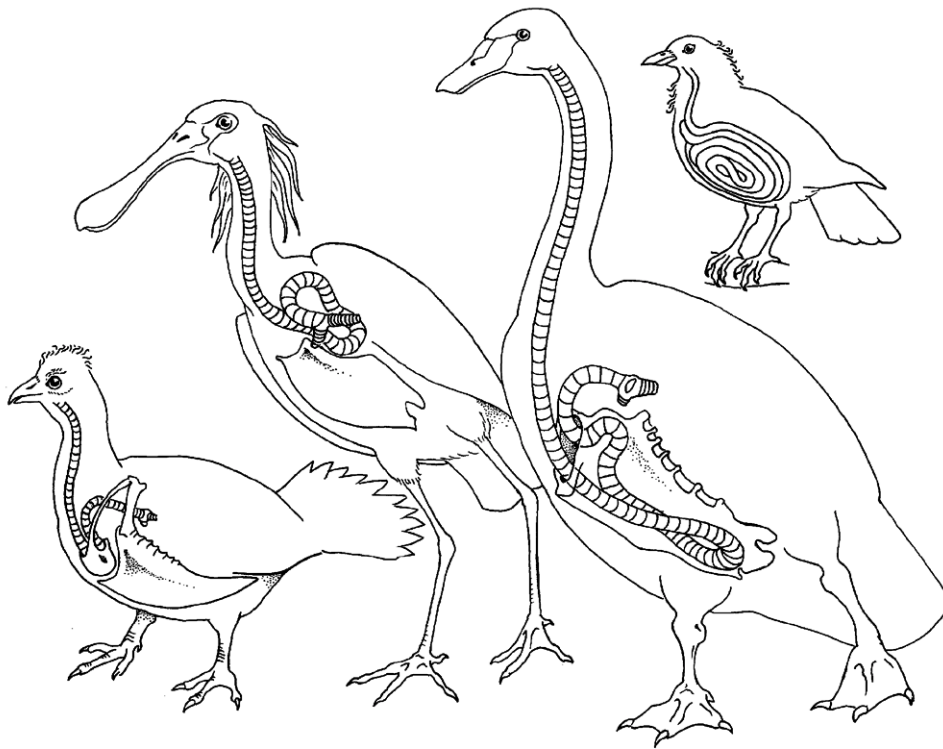


Figure 4: Tracheal elongation in birds. Species shown (left to right) are Crested guinea fowl *Guttera edouardii*, European spoonbill *Platalea leucorodia*, Trumpeter swan *Cygnus buccinator*, and Trumpet manucode *Manucodia keraudrenii* (upper right).

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, Fitch 1999). Tracheal elongation (TE) is common among curassows and allies (Cracidae), cranes (Gruidae) and swans (Anatidae), and is also found scattered among many other groups. The diversity of morphology, combined with this scattered phylogenetic distribution, suggests that TE has evolved independently a number of times. Because TE has been known for many years (the first published record, for the European crane *Grus grus*, is from Kaiser Friedrich II in 1250 AD; Niemeier 1979), a wide variety of hypotheses have been offered to explain its function (reviewed in Fitch 1999). Briefly, these can be classified into physiological hypotheses and acoustic hypotheses. "Physiological" hypotheses hold that TE serves some non-acoustic function, and include the idea that TE is a respiratory adaptation to retain CO₂, to increase non-vascular respiratory area for cooling, to retain water, etc. Because only one sex exhibits TE in many species, all of the physiological hypotheses run into immediate problems explaining the absence of a presumed physiological adaptation in one sex (typically males) and not the others. Even in non-dimorphic species, each of the various physiological hypotheses has problems explaining the presence of TE in the wide variety of species and habitats in which it is seen. For example, Schmidt-Nielsen's (1972) hypothesis that TE represents a respiratory adaptation to long, high-altitude migratory flights, while applicable to trumpeter swans and many cranes, cannot explain TE in sedentary rainforest birds such as cracids and manucodes. While TE may serve some physiological function in some species, it is unlikely to play the same role in all (or many) of them. Similar considerations to these, combined with the problem of explaining sexual dimorphism, have led most workers to dismiss physiological functions as a general explanation of TE. Acoustic hypotheses suggest that the function of TE has to do with modifying vocal output; recall that because the vocal source in birds is the syrinx, at the base of the trachea, the trachea is an integral part of the avian vocal tract. Thus, elongation of the trachea is also vocal tract elongation, and may allow an individual to deceptively mimic the vocalizations of a larger bird that lacks this feature. This acoustic hypothesis, which explicitly links production mechanisms to honest signaling, will be taken up below (Sec. 2.3.6); see Fitch (1999) for a more complete review.

A second relatively common type of vocal tract modification is widespread among geese and ducks. Many of these species show bony enlargements of the syrinx or trachea, which are often confined to males and probably play some as yet undetermined acoustic role. A good review of the anatomy and its relevance in taxonomy is given by Johnsgard (1961, 1971), but like so many of the morphological phenomena reviewed here, there has been no further work elucidating their role in sound production or the evolution of Anatid communication systems. Similarly, there are a number of possible vocal tract modifications of unknown significance among reptiles. These include elongated trachea and bronchi in some tortoises (Siebenrock 1899, Crumly 1984), tracheal diverticula in snakes (Young 1992), the narial excrescence of gharials (Martin and Bellairs 1977) and the unusual hollow bony crests of many lambeosaurine dinosaurs (Weishampel 1981).

In mammals, the supra-laryngeal vocal tract spans from the larynx to the lips or nostrils. Consequently, the vocal tract can be elongated in two ways: by elongating the nose or protruding the lips, or by lowering the larynx in the throat. Recent cineradiographic observations of vocalizing mammals reveal that in dogs, cotton-top tamarins, pigs, and goats the larynx is lowered during vocalization (Fitch 2000a). During resting breathing in mammals, the larynx is inserted into the nasopharynx. The epiglottis engages with the velum, forming a tight seal which separates the nasal/tracheal passageway for air and the oral/esophageal passageway for food. This allows many mammals to breathe and swallow liquids at the same time, and is probably particularly important for young mammals, allowing them to suckle (orally) and breathe (nasally) simultaneously. For many years it was thought that an intranarial larynx was the only normal position in non-human mammals, but the cineradiographic data indicate that in fact a lowering of the larynx during calling is typical for these mammals. This descent may subserve the production of high-amplitude calls, because the nasal passageways absorb sound much more than the oral cavity, decreasing the amplitude of nasal calls by about 15 dB relative to oral calls (Hauser 1992, Fitch 2000a).

Another form of laryngeal descent is permanent descent of the larynx. Rather than being dynamically disengaged from the nasopharynx during calling, and then reinserted, the larynx is permanently lowered. This is the situation in humans. Although human babies start life with an intra-narial larynx, and can suckle and breathe simultaneously like other neonatal mammals, the larynx begins to descend caudally starting around 3 months of age. This gives humans an unusually long pharynx, which is believed to subserve the production of a wider range of vocal tract shapes, and thus vowel formant frequencies, than attainable by other mammals (Lieberman et al. 1969, Lieberman 1984, Crelin 1987). Recent data show that there is in fact a second "descent of the larynx" in humans at puberty, limited to males, in which the larynx descends another several centimeters relative to females (Fitch and Giedd, 1999). Because adult males are not superior in speech abilities to females (indeed, available evidence suggests the opposite: Koenigsknecht and Friedman 1976, Kimura 1983, Henton 1992), this observation suggests that the function of the elongated vocal tract in humans may not be limited to its effects on the vowel space.

Although the descended larynx has long been thought to be a uniquely-human feature, a similar descent of the larynx is seen in several species of Eurasian deer, including fallow (*Dama dama*) and red (*Cervus elaphus*) deer (Fitch and Reby, 2001). In parallel with adult male humans, the larynx in adult males of these deer species is enlarged relative to juveniles or females and rests much lower in the throat. During roar vocalizations produced during the rutting period, powerfully developed sternothyroid muscles pull the larynx even lower, until it reaches the sternum in large males. As predicted by acoustic theory, time-synched audiovideo analysis shows that formant frequencies drop as the larynx descends, due to the elongation of the vocal tract.

A final possible example of vocal tract elongation is provided by the proboscises seen in a wide variety of mammalian species, including elephants, elephant seals, elephant shrews, tapirs, male proboscis monkeys and some extinct but formerly common mammal groups such as oreodonts. Such elongations of the nasal cavity would inevitably lower the formant frequencies of vocalizations emitted through the nose (though as mentioned earlier, nasal vocalizations are likely to be considerably quieter than oral vocalizations). Although there is little evidence suggesting that the primary function of proboscises in most species is acoustic, such a hypothesis may be reasonable in sexually-dimorphic species such as proboscis monkeys *Nasalis larvatus*, in which only the male has an elongated nose.

2.2.5 Air sacs

The final type of morphological modification of the vocal tract we will consider are vocal air sacs, which exist in a bewildering diversity amongst tetrapods. We distinguish "vocal" sacs, which at least may have some acoustic function, and are typically attached to the larynx or vocal tract, from the respiratory air sacs found in all birds and some reptiles (Lasiewski 1972) which are not likely to serve any acoustic function. There are many types of vocal air sacs, for which we will offer a preliminary classification into oral, nasal, laryngeal, tracheal and "other", depending on the location of the air sac opening. However, even within the laryngeal sacs (the most common type), there is great diversity of form, including soft-walled vs. hard-walled sacs, paired, midline, or asymmetric sacs, and a variety of possible opening locations relative to the glottis (sub, supra- or para-glottal). We will review four plausible hypotheses that have been advanced for the acoustic and/or respiratory function of air sacs, and give possible examples of each type (see Negus 1949, Schneider 1964 for more detail).

Although our survey of air sacs is organized by possible function for conceptual clarity, we do not mean to imply that air sacs serve a single function, in any single species or certainly across species. For example, in frogs the air sacs appear to serve both air recycling and impedance matching functions. Another good example of multipurpose air sacs is provided by the walrus *Odobenus rosmarus*. Adult male walruses have large pharyngeal air sacs that are outgrowths of the pharyngeal wall, opening just dorsal to the larynx (Sleptsov 1940, Fay 1960). These sacs appear to subservise production of the peculiar "bell" sound made by males during sexual behavior (Schevill et al. 1966), though the mechanism for this is unknown. However, the pouches can also be inflated as "life preservers", allowing the walrus to stay afloat during naps at sea: Fay (1960) reports that he observed walruses sleeping at sea at least eight times, and the pharyngeal air sacs were invariably inflated, holding the shoulders out of the water. Finally, Sleptsov (1940) reported finding the sacs of two hunted walruses filled with food (crustaceans and molluscs), and suggested a third function for the sacs as food storage devices (similar to the cheek pouches of Old World monkeys, which play no acoustic role, Schön-Ybarra 1995). However, Fay (1960) found this last suggestion unlikely, suggesting that Sleptsov's specimens had regurgitated stomach contents into the sacs in their death throes. In any case, the "bell production" and "life preserver" hypotheses are both well supported, indicating at least two functions for walrus pharyngeal sacs, and suggesting that air sacs may serve multiple functions in other species as well.

The most commonly cited possible function for vocal air sacs is that they play a role in impedance matching from the vocal tract to the atmosphere (see below for more detail). Such a role has been suggested for most anurans, as well as for the inflatable (soft-walled) air sacs of cercopithecoid monkeys such as guenons (*Cercopithecus* spp. Gautier 1971), and siamangs (*Hylobates syndactylus*, Napier and Napier 1985). Impedance matching has also been suggested as a function of the inflatable esophagus of male bitterns (*Botaurus lentiginosus*), which during the breeding season produce a loud, low-pitched booming sound (Chapin 1922). Similar observations have been made concerning the role of the swim bladder in sound producing teleost fishes (Demski et al. 1973), as well as other birds that inflate the crop or a gular air sac during vocalization (e.g. doves and pigeons, grouse, ostriches, bustards, and other species; Ziswiler and Farner 1972). There are many other species with air sacs attaching to the vocal tract that have not been studied but where a similar impedance-matching function seems plausible, e.g. in the "drumming" of emus (*Dromaius novaehollandiae*) (McLelland 1989), in some baleen whales (Quayle 1991) or in the pharyngeal sacs of the walrus described above. In several species an impedance-matching function has been experimentally verified by simply puncturing the air sacs, and observing that normal-sounding vocalization continues, but at much reduced amplitude (Gautier 1971, Gans 1973).

Another hypothesized role of air sacs is to allow air recycling, where the same volume of air is used repeatedly to excite the voice source. Air expelled through the lungs passes through the larynx in the elastic sac, which then deflates, returning the air to the lungs. Such a role is clear for anurans, where the recycling of air probably allows much higher rates of vocalization than would be possible given the relatively inefficient mechanisms available to anurans to inflate the lungs; this mechanism may also allow some conservation of mechanical energy (Dudley and Rand 1991). While most anurans appear to vocalize on expiration, members of the relatively primitive genera *Discoglossus* and *Bombina* vocalize on inspiration (Schneider 1988). An air recycling function also seems very likely for the large laryngeal air sacs seen in Mysticete (baleen) whales (Hosokawa 1950, Quayle 1991), which can vocalize for long periods under water without releasing air. Though no experimental data are available, Mysticete air sacs are heavily invested with muscle which would aid in returning the expired air to the lungs.

A related possibility, the "accessory lung" hypothesis, is proposed here for the laryngeal air sacs of the great apes. Chimpanzees, orangutans and gorillas all have voluminous air sacs (6 liters in orangs, Schön-Ybarra 1995), that can be inflated with air from the lungs. The air sacs connect to the larynx via a long thin-walled channel that opens directly above the vocal membranes and vocal folds. The air sacs extend into the subdermal space in the pectoral region, and are overlain by the sheetlike platysma muscle. Thus, an ape could inflate the air sacs via lung pressure, and then forcibly deflate them by tensing the platysma and other pectoral muscles (or by pounding the chest, as in *Gorilla*). This anatomy suggests that great ape air sacs may act as "accessory lungs", providing an additional source of expiratory air flow and thus of energy into the source. This hypothesis seems more plausible than that offered by Negus (1949), who suggested that ape air sacs act as storage sites for oxygen during vigorous activity. Because the sacs are inflated with exhaled air that has already been in the lungs, and thus will be low in oxygen and high in CO₂, such an air reserve would be of dubious respiratory value (Fitch and Hauser 1995). Air sacs are also found in some pinnipeds, where a gas storage function would be of clear value during diving (Sleptsov 1940), but Fay (1960) doubted this possibility because the additional oxygen stored in even large sacs would be trivial relative to dissolved blood O₂ in a diving pinniped.

A final class of laryngeal air sacs, found in many nonhuman primate species, are subhyoid air sacs. This type of thin-walled sac opens into the glottis, and extends into an enlarged hollow bulla in the hyoid bone. Such a hard-walled laryngeal sac is typical of cercopithecids (Old World monkeys), and is developed to the extreme in New World howler monkeys (*Alouatta* spp.). Because these sacs are surrounded by bone, they would be of little value in radiating sound out to the environment and no value as an accessory lung. We speculate that they could act as Helmholtz resonators, and that the small plug of air that vibrates in and out of the narrow neck of the sac would support vocalization at the Helmholtz resonance frequency. If true, this would constitute a form of source-tract coupling. Although the opening of these sacs directly at the glottis is consistent with this hypothesis, there are currently no empirical data (e.g. using light gases) available to further evaluate this hypothesis.

2.2.6 Morphological Diversity: Summary

As this brief review makes clear, there is 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. Advances in digital signal analysis, techniques for the visualization of the vocal tract in action, and an increasing interest in the role of proximate mechanisms in evolution suggest that progress in understanding this morphological diversity, and correlating it with social behavior and evolutionary history, will be rapid in the coming years.

2.3 *Physical and Phylogenetic Constraints on Vocal Production*

In this section we attempt to explicate some of the diversity documented above by integrating the acoustic and anatomical data into a more comprehensive functional and evolutionary framework. In particular, we argue that much of the anatomical diversity seen in tetrapod vocal tracts can be understood from the point of view of ubiquitous selective pressures operating within a framework of physical and phylogenetic constraints, together with evasions of those constraints via "key innovations".

Because this is a selective synthesis, there are two potentially relevant topics that we will not cover: 1) adaptations of calls to the transmission characteristics of the environment (Morton 1975, Wiley and Richards 1982, Brown and Gomez 1992, Bradbury and Vehrencamp 1998, see also Ryan and Kime, this volume, and Bass and Clark, this volume). and 2) adaptations of alarm call morphology that make localization difficult. This last topic was initiated by Marler's classic (1955) observation that the "seep" alarm calls of passerine birds are difficult to spatially localize and has recently been reviewed by Catchpole and Slater (1995) and Hauser (1996).

2.3.1 Syringeal Diversity and Multi-Use Constraints on Laryngeal Function

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 gatekeeping role.

In contrast, the avian syrinx appears to serve only one function: sound production. In birds, the larynx is devoted to the gatekeeping role exclusively, while the syrinx is free to create sound. We hypothesize that 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.

The larynx of mammals is under what can be described as a “multi-use constraint”: the same structure serves multiple functions with incompatible design requirements, and its function is thus an unhappy compromise between these functions. We suggest that one of the virtues of the avian syrinx was as an evolutionary “key innovation” (Liem 1973) that allowed birds to escape from this constraint. The evolution of a specialized sound-producing organ allowed birds to evade the conservative restrictions imposed on laryngeal anatomy and nervous control by its critical role in swallowing. This constraint was presumably in effect in the ancestors of birds; the closest extant group, the crocodylians, possess a surprisingly mammal-like larynx, including a non-homologous “epiglottis” and soft palate that allow them to form a sealed nostril-to-lung respiratory pathway, and some crocodylians use the larynx in vocalization. Although little is known about the evolutionary origins of the syrinx, we argue that its freedom from the role of gatekeeper to the trachea has been significant in the evolution of the impressive morphological diversity of the syrinx, relative to the anuran or mammalian larynx. In turn it seems plausible that morphological diversity is tied to repertoire diversity and perhaps has implications for the rapid diversification and speciation of the passerine birds, which have the most complex syrinx (but see Raikow 1986). In contrast to the syrinx, the avian larynx shows almost no functionally-significant variation throughout the entire class (McLelland 1989), consonant with its primary and unchanging role as protector of the airway.

2.3.2 Physical Constraints and the Communication of Body Size

A fundamental fact differentiating the physics of sound from the physics of light is that sound waves are about the same size as organisms. For example, an average human female's speaking voice has a fundamental frequency around 220 Hz, with a wavelength of 1.6 m, on the order of her height. In contrast, a spring peeper's (*Hyla crucifer*) 3 kHz call has a wavelength about four times its 3 cm body length. This simple fact has enormous consequences for the production and propagation of sound at an immediate mechanistic (proximate) level, and therefore, we will argue, at the ultimate evolutionary level as well. In particular, interactions between sound waves and the vocal production system place significant constraints on what sounds can be effectively generated or transmitted, thereby rendering a large class of signals that might be theoretically possible and biologically advantageous impossible, in practice, to produce. On the other hand, interactions between sound and body can in other cases provide information “by default”, without any need to invoke biological advantage or selection at all. This is particularly true for information about body size. Finally, because it is the dimensions of the vocal production system that are acoustically relevant, and not overall body dimensions, it is sometimes possible for organisms to evade physical constraints by changing dimensions of vocal structures independent of body size. Over the course of evolution, nature has been ingenious in finding ways to pack more vocal tract into less body. Thus, the communication of body size provides an ideal arena within which to explore the interactions of physical constraints with ubiquitous selective forces in the evolution of communication.

Body size is a critical parameter in virtually all aspects of biology. An animal's body mass has important implications for its physiology (Schmidt-Nielsen 1984), ecology (Peters 1983), fecundity (Smith-Gill and Berven 1980), and life history (Calder 1984). At the behavioral level, body size plays a role in aggressive interactions and/or mating success (Parker 1974, Clutton-Brock and Albon 1979, Schuett 1997, Clutton-Brock et al. 1977, Modig 1996). Thus, the accurate perception of body size is predicted to be adaptive for a wide variety of organisms for a number of different reasons, and should constitute a ubiquitous selective force in the evolution of communication systems. There is also a ubiquitous physical limitation on signals, in that the size of various components of the sound production apparatus has an important effect on the acoustic output (Fant 1960, Lieberman 1984), with larger components producing lower frequencies. Because the size of these production components may in many cases be related to the overall weight or length of the animal, there is good reason to expect that some aspects of the acoustic signal may provide cues to the size of the vocalizer. In particular, we can predict a negative correlation between body size and any of a variety of measures of call frequency (Morton 1977). Such acoustic cues to body size would be internally referential (providing information about the vocalizer itself) and direct or non-arbitrary (because the link between large size and long wavelengths is a fact of physics).

Because of the importance of body size in animal behavior, we expect that there will often be strong selection on perceivers to make use of available acoustic cues to body size. For the same reason, however, once perceivers are using a particular cue, we expect selection on senders to manipulate this cue to their own advantage (Dawkins and Krebs 1978). There may be situations (such as when retreating from a lost aggressive contest or luring in a timid mate) in which it would be beneficial for a sender to seem smaller than it is. In general, however, we expect this manipulation to be in the direction of size exaggeration; regardless of whether the receiver in question is a competitor or a potential mate, it will typically benefit the sender to seem larger than it is. Thus we will focus on constraints that might prevent the production of low frequencies, or morphological innovations that might allow it.

2.3.3 Body Size and Acoustic Impedance Constraints

The most fundamental limitation on the generation and propagation of low frequency sounds comes from impedance matching requirements. Although a small body may produce low-frequency oscillations, its ability to convert energy from these oscillations to acoustic energy in the environment is limited by the relationship of oscillator size to the wavelength of the generated sound. In general, wavelengths longer than twice the length of the vibrator will be very ineffectively transmitted to the environment, and lower frequencies will suffer even worse attenuation (Beranek 1954). A good example is provided by a tuning fork, which is nearly inaudible when vibrating freely in air, but is quite loud when placed on a large surface (a tabletop or the sounding board of a musical instrument). Mechanical vibrations set up on a large surface couple to the air much more effectively than those isolated to the moving tines of the fork itself. The difficulty in radiating low frequency sounds, termed an impedance mismatch, provides a physical constraint on the production of low frequency sounds by small animals.

The most frequent evolutionary solution to this problem appears to be the use of various types of air sacs, which are interposed between the vibrating structures (e.g. the vocal folds or the air in the vocal tract) and the environment. A detailed description was given earlier, under "Morphological diversity". Air sacs are ubiquitous in anurans, and a role as impedance matching systems appears to be undisputed (see e.g. Ryan 1985, Bradbury and Vehrencamp 1998). By increasing the size of the vibrating structure, anuran air sacs allow their bearers to more effectively radiate lower frequencies to the environment than would otherwise be possible given their small body size. However, some anurans lack sacs, which may be related to underwater vocalization where there is no impedance mismatch (Hayes and Krempels 1986). A similar example is provided by some non-human primates, in which puncturing and subsequent deflation of laryngeal air-sacs results in an attenuation of the radiated low-frequency sound but no change in pitch (Gautier 1971).

An impedance-matching function was also proposed for those cases of avian tracheal elongation in which the trachea invaginates the sternum (e.g. cranes, trumpeter swans) by Gaunt and colleagues (Gaunt and Wells 1973, Gaunt et al. 1987). Gaunt and his colleagues reasoned that the entire sternum of such birds could be like the sounding board of a stringed instrument, with the coiled trachea serving a function analogous to the bridge. The main problem with this hypothesis is a different impedance mismatch, that between the vibrations in the tracheal air column and the walls of the trachea. In a stringed instrument, mechanical vibrations in the strings are efficiently conveyed to the instrument body and sounding board, where they are

then converted to acoustic energy. In contrast, the vibrations in the vocal tract start out as acoustic pressure waves and suffer a large impedance mismatch that prevents these acoustic vibrations from being converted to mechanical vibrations in the bony tracheal walls and sternum. In fact, Gaunt et al. (1987) report that virtually all acoustic energy radiates from the mouth in cranes, not from the chest; see Fitch (1999) for further discussion.

Although impedance matching systems such as air sacs have been shown experimentally to be effective, and appear to have evolved independently multiple times, the extension of the low frequency range for a given size air sac is limited. The fully-inflated air sac of a 3 cm spring peeper substantially increases the efficiency with which its 3 kHz call is radiated to the environment, but it would have no effect on a 300 Hz call with a wavelength greater than 1 m. Thus, impedance matching air sacs ameliorate the situation without actually evading the physical constraint relating low frequencies to large bodies. We still expect this constraint to play a significant role over the large range of body sizes seen in terrestrial vertebrates.

2.3.4 Lung Volume and Acoustic Cues to Size

The lungs (along with air sacs, in birds) occupy most of the thorax in mammals, reptiles, and birds. Thus it is unsurprising that the size of the lungs is closely related to body size (Hinds and Calder 1971; Scammon 1927, Krogman 1941). If an acoustic variable directly depended upon lung volume, it would also be correlated with body size. The most obvious example is the maximum length of a single call: where one would expect longer calls to indicate larger callers. However, since a quiet call requires less air flow than a loud one, the relevant acoustic parameter might be more complex (e.g. the integral of call amplitude over an entire call). Such details aside, it is reasonable to hypothesize that the production of long, loud calls might be restricted to large individuals, and thus provide a cue to body size. We currently lack data relevant to this prediction. The nearest example comes from the classic study on red deer vocalization by Clutton-Brock and Albon (1979), discussed in the introduction.

As mentioned earlier (Sec 2.2.5), a possible function of the elastic air sacs found in many primate species, including most apes, might be as "accessory lungs" (Fitch and Hauser 1995), either prolonging vocalizations or increasing the intensity of calls, relative to those produced solely by lung deflation. There has been no experimental test of this hypothesis to date, though MacLarnon and Hewitt (1999) found that those primates with air sacs do seem to have longer maximum call durations than those without. Interestingly, humans have the longest "calls" of all primates (our inordinately long single-expiration spoken sentences), but lack air sacs, unlike all of our nearest relatives, the great apes. MacLarnon and Hewitt (1999) suggest that this is due to an increase in breathing control in our species. If this hypothesis is correct, it suggests that other species in which call length plays an important selective role might also be expected to evolve enhanced breath control.

The possible link between call length and body size, or body condition, provides a nice example of an unexplored source of cheap, honest cues in vertebrate acoustic communication. If only animals in good physical condition have larger healthier lungs and can thus sustain longer calls, or longer bouts of calling, we expect selection for discriminating perceivers who attend to this unfakeable cue. For example, females might compare the length of calls from two competing males in order to choose between them, or males might avoid picking fights with rivals who can call longer than them.

2.3.5 Source-Related Cues to Body Size

The most frequently-cited acoustic parameter which could provide a cue to body size is mean and/or lowest fundamental frequency (Darwin 1871, Morton 1977). In non-avian tetrapods, the lowest producible fundamental frequency of phonation ($F_{0\min}$) is determined by the length of the vocal folds: the longer the folds, the lower is $F_{0\min}$ (Titze 1994). Mass plays a role only if it is unequally distributed over the fold, as in *P. pustulosus*, discussed above. If the length of the vocal folds is related to the vocalizer's body size, $F_{0\min}$ will thus provide an honest cue to body size (Morton 1977, Hauser 1993). This indeed appears to be the case in some species, including some toads and frogs (Martin 1972, Davies and Halliday 1978, Ryan 1988). However, such a relationship between body size and vocal fold size does not seem to be typical in other vertebrates. For instance, there is no correlation between F_0 and body size in adult humans (Lass and Brown 1978, Künzel 1989, Cohen et al. 1980, van Dommellen 1993), red deer (McComb 1991), and other amphibian species (Asquith and Altig 1990, Sullivan 1984). This lack of correlation in adult humans may be particularly surprising given the widespread assumption that a "deep" or low-pitched voice indicates large body size.

The lack of correlation between F_0 and size seems less surprising when the anatomy of the vocal folds is considered. The folds are housed within the flexible cartilaginous larynx, which itself floats at the top of a trachea and is unconstrained in size by neighboring bony structures (the hyoid bone, though ossified, grows as a unit with larynx, Schön 1971, Schneider et al. 1967). Thus, the larynx and vocal folds can grow independently of the rest of the head or body, as indeed occurs in human males at puberty (Negus 1949, Goldstein 1980), where androgen receptors in the laryngeal cartilages respond to increased circulating testosterone with a profound growth spurt (Tuohimaa et al., 1981, Beckford et al. 1985). The result is a typical F_0 for adult males which is about half that of adult females, despite an average difference in body weights of only 20% (Hollien 1960). As mentioned in Sec 2.2.2, hypertrophy of the male larynx, out of all proportion to body size, is carried to an absurd extreme in animals such as the howler monkey (*Allouatta seniculus*, Schön 1971) and the hammerhead bat (*Hypsiprymna monstrosus*), which clearly illustrate that larynx size, within broad limits, is unconstrained by body size. Although much less is known about the relationship between body size and syrinx size in birds, it seems likely that similar considerations apply. The syrinx, like the larynx, is free from any skeletal constraints on its size, and would be expected to respond freely to selection for low voices. For example, both cranes and curassows are groups with unusually large syringes (Delacour and Amadon 1973, Johnsgard 1983, Fitch 1999), and both groups are typified by low-pitched, loud voices. In contrast, other groups such as Falconiformes (hawks, eagles, etc.) have unusually high-pitched voices for their size. These observations suggest that the syrinx is not under any strong size constraints, and can respond to selection by either increasing or decreasing size.

When such developmental flexibility is present there is clearly no *a priori* reason to expect vocal fold size (and thus F_0) to be well-correlated with body size (Fitch 1994, Fitch and Hauser 1995). Of course, between disparate enough taxa some degree of correlation is inevitable due simply to the very large differences in overall avian body size; the syrinx of an ostrich or emu could contain the entire body of a hummingbird. Thus, various researchers have found correlations between body size and some measure of vocal frequency across different avian or mammalian taxa (birds: Ryan and Brenowitz 1985; mammals: August and Anderson 1987, Hauser 1993). Similarly, in species with large size differences between infants and adults we may expect some differences in pitch between young and old animals, as indeed appears to be the case in humans, where the F_0 of infant cries average around 500 Hz and adult speech between 100 and 200 Hz (Titze 1994). However, the relevant information for many species in many communicative situations is not the size of young or of members of other species, but of conspecific adults. In this domain, and despite the common claim that voice pitch provides an accurate cue to body size (e.g., Morton 1977), the data reviewed above suggest that the voice source (larynx or syrinx) is ill-suited to provide dependable cues to body size in adult terrestrial vertebrates.

2.3.6 Vocal Tract Length and Acoustic Cues to Body Size

A different potential acoustic cue to body size comes from vocal tract length and formant frequencies. If the cross-sectional area function of the vocal tract is constant, the primary determinant of formant frequencies is the length of the vocal tract (Fant 1960, Lieberman and Blumstein 1988, Fitch 1997). In particular, a lengthening of the vocal tract tube will lead to a decrease in the average spacing between successive formants, or "formant dispersion" (Fitch 1997; Riede and Fitch 1999). Thus, if vocal tract length is correlated with body size, there will be an inverse correlation between formant dispersion and body size, and formants will provide honest cues to body size. Such formant cues are completely independent of voice fundamental frequency, or perceived pitch.

Formant dispersion is simply the average spacing between successive formants, and provides one simple metric for estimating vocal tract length. However, no single number can accurately capture all the information in a complete list of formant frequencies and bandwidths, and in some cases other statistics that rely only on higher formants, or on the most reliably-excited formants, may be preferable. It may appear that the first formant would provide an equally good estimate of vocal tract length. There are two reasons that this is not the case. The first concerns the boundary (end) conditions of an air column contained in a simple tube, which have a drastic effect on the lowest formant, but no effect on formant spacing. For example, a 17.5 cm tube that is open at both ends has formant frequencies at 1000, 2000, 3000 Hz, etc., while the same tube with one end closed has formants at 500, 1500, 2500 Hz, etc. The spacing is 1 kHz in both cases, but F_1 varies between 500 and 1000 Hz. Although the human vocal tract during speaking is often idealized as being closed at the glottal end, this approximation is only strictly correct for a portion of the glottal cycle, and may never be true in certain phonatory modes (e.g. the glottis may never close during breathy phonation). The use

of formant dispersion avoids the need for any assumptions about glottal state and phonatory mode, and is thus preferable to F1 as a measure of vocal tract length. A second reason that F1 provides a poor correlate of vocal tract length is the increased role of the yielding walls of the vocal tract at low frequencies. In much the same way as described for the anuran vocal air sac, the soft parts of the vocal tract begin to absorb significant energy from the acoustic signal at lower frequencies. This effect of the vocal tract walls at low frequencies will place a lower limit on F1, irrespective of total vocal tract length (Fujimura and Lindqvist 1970). This effect will be most pronounced for long vocal tracts, e.g. in large mammals, or in animals with vocal sacs.

Is there any reason to expect vocal tract length (which determines formant spacing) to be more closely tied to body size than vocal fold length (which determines fundamental frequency)? For mammals, the answer is clearly yes. The mammalian vocal tract is made up of the pharyngeal, oral and nasal cavities, which are firmly bounded by the bones of the skull, and skull size is closely tied to overall body size (Morita and Ohtsuki 1973, Dechow 1983, Alcantara et al. 1991, Fitch 2000c). Because the facial region of the vertebrate skull is involved in so many other life-critical functions (it houses the sense organs, provides the passageway for water and air, must capture and process food, plays an important role in grooming in many species, etc.), vocal tract length should be much less free to vary independently of body size than larynx size. According to this hypothesis, mammalian vocal tract length is highly constrained by multi-use factors. Although some evolutionary modifications of facial structure may occur for the purposes of modifying vocal production acoustics (e.g. the elongated nose in proboscis monkeys or some pinnipeds, or the descended human larynx), in most species the structure of the facial skeleton is largely determined by the more basic needs of prey capture and food processing. We would expect this multi-use constraint to place stringent limits on the ways in which vocal tract structure and function can change in non-avian tetrapods. This may help explain why the vocal tract, like the skull itself, has a rather conservative evolutionary history. Thus we can expect vocal tract length and the attendant acoustic cue of formant dispersion to provide a correspondingly more robust cue to body size in mammals.

This hypothesis is supported by data from several mammalian species. Fitch (1997) used radiographs (x-rays) to measure vocal tract length in rhesus macaques (*Macaca mulatta*), and found a strong correlation between vocal tract length (from the glottis to the lips) and both body mass and length. Second, he measured formant frequencies using a spectral estimation algorithm called linear prediction, which finds the optimal all-pole (all formant) model to fit a particular spectrum (Markel and Gray 1976). Fitch found a strong negative correlation between formant dispersion and body size in these monkeys. Using similar techniques, Riede and Fitch (1999) also found strong correlations between body size, vocal tract length and formant dispersion in domestic dogs (*Canis familiaris*). In both cases, restriction of the analysis to adults still yielded significant positive correlations between body size and vocal tract length, indicating that formant frequencies can provide an honest cue to adult body size in these two species. Finally, Fitch and Giedd (1999) found strong positive correlations between body size and vocal tract length in humans, despite the fact that the human male vocal tract elongates slightly during puberty, causing an increase in vocal tract length. In this study, the sample size of fully adult humans of each sex was inadequate to evaluate within-sex adult vocal tract allometry. The correlation between body size and vocal tract length, and its acoustic correlates, provides a good example of honest, internally-referential communication that results directly from the anatomy of the vocal production system combined with basic acoustics. This honest signal does not require the invocation of any special selective forces, nor additional costs to the animal. Formant cues to body size thus appear to be an example of cheap, honest communication, at least in monkeys, humans and dogs.

In birds, the situation is quite different. Because the voice source lies at the base of the trachea, the vocal tract includes not just the oral and nasal cavities but also the entire trachea. This means that the vocal tract of a bird of a given body size is much longer than that of an equivalent mammal or reptile. More importantly, it suggests that the multi-use constraints described above, which hinder change in the mammalian vocal tract, are not applicable to birds. Fitch (1999) suggested that this provides an explanation for the phenomenon of tracheal elongation in birds. An overall correlation between body size and vocal tract length was probably the primitive state for birds, and has indeed been documented across species by Hinds and Calder (1971). Therefore, given an appropriately broadband source, formant frequencies would provide an indication of the vocalizer's body size. Once perceivers had evolved to take advantage of this information, it provided an opportunity for vocal subterfuge: a bird with an elongated trachea could duplicate the formant dispersion of a larger conspecific, and thus exaggerate its own apparent size. Unlike the case in other vertebrates, where selection for vocal tract elongation would face stiff opposing selection from multi-use

constraints, tracheal elongation in birds would be opposed only by a decrease in respiratory efficiency due to increased tracheal dead space (Hinds and Calder 1971, Clench 1976). However, due to the one way, flow-through nature of the avian respiratory tract (Lasiewski 1972, Liem 1985, Schmidt-Nielsen 1997), and the small volume of the trachea relative to the extensive respiratory air sacs system, this physiological effect may be negligible (Prange et al, 1985). Thus, little stood in the way of the acoustic exaggeration of size via the evolution of tracheal elongation in birds, which would explain its repeated independent evolution in many orders of birds, and virtual absence in all other taxa; the only other example of tracheal elongation of which we are aware is in the tortoise *Geochelone pardalis* (Crumly 1984), and is of uncertain acoustic or behavioral significance. If this hypothesis is correct, tracheal elongation in birds is a good example of size exaggeration via vocal tract elongation (Fitch 1999).

There are a number of other possible examples of deceptive elongation of the vocal tract. Weishampel (1981) suggested that the prominent crest of many lambeosaurine dinosaurs, which contained an elongated nasal passageway, functioned to lengthen the vocal tract and thus to decrease formant frequencies. The proboscises found in many non-human mammals (e.g. elephants, elephant shrews, various pinnipeds, proboscis monkeys, as well as oreodonts and other extinct taxa) have the inevitable result of lengthening the nasal vocal tract, and thus lowering the frequencies of nasal formants. Whether this serves the function of exaggerating acoustically-conveyed size remains an untested hypothesis, but seems plausible in the case of species such as elephant seals and proboscis monkeys where the proboscis is a sexually dimorphic trait. Finally, the vocal tract elongation resulting from the descent of the human larynx may have some size-exaggerating effect. This hypothesis is supported both by the fact that formant dispersion is known to be used as a cue to body size by human observers (Fitch 1994), and that an additional descent of the larynx occurs at puberty in males, simultaneous with (but anatomically and functionally independent of) the growth of the male larynx (Fitch and Giedd 1999).

We have focused in this section on acoustic cues to body size, mainly because body size 1) is easily measured, 2) is an extremely important variable in many species, and 3) has a direct and obvious effect on the production of acoustic signals. However, we would like to stress that the approach outlined above is likely to be applicable to many other types of information in animal signals as well. For example, individual differences in vocal tract anatomy may provide robust cues to individual identity (Rendall et al. 1996), and differences in the use of nasal vs. oral vocal tracts might serve as a cue to group membership (Hauser 1992). Sex hormones can bind preferentially to laryngeal tissues (Tuohima et al. 1981), suggesting that certain aspects of the voice source may provide cues to sexual readiness or other endocrinological information (Yamaguchi and Kelley, this volume). A possible example is oestrous-related calling in gelada baboons (Moos-Heilen and Sossinka 1990): could steroid-related changes in tissue hydration over a females cycle lead to vocal cues to ovulation? Finally, there may be vocal cues to age in some species. The histological composition of the vocal folds changes with age (Titze 1994), potentially resulting in vocal cues to a caller's age and experience. Similarly, the vocal tract in male plain chachalacas (*Ortalis vetula*) elongates with age (Marion 1977), presumably lowering formant frequencies. Could male rivals use such cues to avoid more experienced rivals, or might females use formants in mate choice? All of these questions are highly relevant to the evolution and structure of acoustic communication systems, but demand advances in our knowledge of proximate mechanism before they can be adequately addressed. If the above review spurs research along these lines it will have achieved its goal.

2.4 Conclusion

To summarize and conclude section two of this chapter, we have seen that physical and physiological constraints play a fundamental role in shaping the signaling systems of terrestrial vertebrates, interacting with multiple selective forces in various ways to produce an impressive variety of morphological adaptations in tetrapod vocal production systems. Physical constraints, by creating non-arbitrary mappings between behaviorally-relevant parameters (like body size) and aspects of acoustic signals (like frequency) can provide a starting point for the use of a certain parameter in a species' communication system. Physiological constraints (like the multiple functions of the mammalian larynx, or the restriction of most tetrapod vocal tracts to the skull) can play an important role in maintaining signal honesty, in lieu of any specific selection "for" honesty. Knowledge of these constraints can also provide a principled starting point for scientific analysis of a species' vocal repertoire, allowing us to precisely identify acoustic parameters that might play a role in signaling. Finally, "key innovations", such as the syrinx in birds, can allow a species to evade such constraints in evolutionary time, opening up new vistas in the adaptive landscape.

More often than not, however, new physical or physiological constraints will probably exist, even in this new adaptive space, which again will influence the evolutionary trajectory of a particular species' communication system. We now turn to the role of cognitive mechanisms and behavioral flexibility in dishonest signaling and its detection.

3. Perceptual and Cognitive Constraints on Skepticism: The Behavior of Deception

3.1 *Lies of commission*

When President William Clinton was asked about his alleged relationship with Monica Lewinsky, he claimed that he never had an illicit affair with her. As the world now knows, he lied. The public perceived Clinton's statement as a lie because they detected a mismatch between what Clinton said he did and what he actually did.

Humans are not alone in their ability to create lies of commission — actions that actively falsify information. In fact, a wide variety of animal species appear to be comparably endowed. In order for such lies to work, however, three conditions must hold. First, the species must have a signal that is tightly correlated with a particular context. Thus, for example, when an animal gives an alarm call, it must signal the presence of a predator on a significant proportion of occasions. At present, we can't say precisely how tight this correlation must be, but the signal must have relatively high predictive value with respect to the sequelae of signal and response. Second, when individuals hear such signals, they must respond in a relatively stereotyped or consistent way, and must do so on a statistically significant number of occasions. Thus, when animals hear an alarm call, they must consistently flee. Third, individuals must have the flexibility to manipulate the behavior of other group members by producing a species-typical signal in a novel context; in this sense, there must be some level of independence between signal and context. Thus, while competing over food or a mate, one animal might give an alarm call causing the competitor to dive under the bushes.

Falsifying information should theoretically be a rare event, or at least have a low cost for the deceived, in order to maintain the effectiveness of the lie. Thus, individuals might be expected to produce false alarm calls infrequently in order to avoid generating a completely ineffectual signal — "the boy who cried wolf". However, there may be considerable variability within taxa in how sensitive individuals are to being deceived, as well as in the cost of deception. To flesh out these ideas, we explore a set of observations and experiments on insects, birds and primates designed to reveal how lies of commission are enacted, and sometimes foiled by skeptical receivers. In each case, we evaluate the evidence in light of the three conditions discussed, and where possible, lay out a series of experiments that might take our understanding further.

Lies of commission appear relatively often during inter-specific interactions. Thus, in the non-vocal domain, we know of plovers that dupe their predators by performing the injury feigning display, predatory *Photuris* fireflies that mimic the mating flash patterns of their congeners thereby providing the mimic with a meal, snakes that play dead in order to avoid being eaten, fish, birds, and mammals that enlarge some portion of their body in order to look bigger, and insects and frogs that evolve coloration patterns that resemble a sympatric, but poisonous species (Burghardt, 1991; Hauser, 1996; Hauser, 2000; Lloyd, 1984; Mitchell and Thompson, 1986; Ristau, 1991). In the vocal domain, there are fewer examples, but Charles Munn's (1986a; 1986b) study of a mixed-species flock in Peru is perhaps one of the more compelling examples.

In a Peruvian rainforest, Munn noted that among the members of a mixed-species flock of birds, some species appeared responsible for finding food, whereas other species appeared responsible for alerting the flock to danger. The fluidity with which these species interacted was spectacular, but perhaps more intriguing was the fact that the alarm-calling species — the bluish-slate antshrike and the white-winged shrike tanager — sometimes produced alarm calls when there were no predators in view. These were not mistakes. Rather, the alarm calls were given almost exclusively when the antshrike or tanager were in direct competition with the food-finding species over insect prey. As they approached the insect, the antshrike and tanager produced an alarm call, causing the food-finding species to look up and thereby forfeit his access to the insect. Surprisingly, perhaps, this was not a rare event. Out of 104 alarm calls recorded from the tanager, Munn found that 55% were false alarms. Although this rate is high, we can't conclude that it

accurately represents the rate of deceptive alarm calls. It is entirely possible that in some cases, the bird detected an animal it considered to be (or confused with) a predator when there was no predator at all. The alarm call is a false alarm in the signal detection sense — a perceptual error that is likely to occur when sensitivities are set high, as are the costs of a miss (i.e., of failing to detect the predator when it is present).

Is there any evidence that antshrikes and tanagers are capable of creating lies of commission? Let us return to our three conditions. First, the antshrike and tanager's alarm call is often given during encounters with predatory birds of prey. Thus, there is a correlation between the signal and a specific context. Further, playback experiments of alarm calls given to actual predators as opposed to virtual predators revealed no differences with respect to the food-finding species' responses; in both situations, they looked up and fled. This shows that the false alarm call sounds like the true alarm call, and thus, should be equally evocative. Although there may be other acoustic cues that have been overlooked in the analysis, these possible differences don't appear to be perceptually salient to listeners. Second, when the food-finding species hears the alarm call, they respond by looking up and fleeing. Thus, the alarm call reliably elicits a response from the target receiver. Finally, the antshrike and tanager have the flexibility to produce the alarm in the absence of a predator. Thus our conditions for a lie of commission have been met.

False alarm calls by antshrikes and tanagers are relatively common. Thus, there is no support for the prediction that lies of commission must be rare. One explanation for this high rate of deception comes from an economic analysis of the interaction. For both species, the benefit comes from capturing an insect. For the food-finding species, the potential cost comes from ignoring the alarm call. Looking at the trade-offs, it never pays the food-finding species to ignore the alarm call because the benefit of eating an insect is greatly outweighed by the costs of being eaten by a predatory bird. Because of this imbalance, the antshrike and tanager can give false alarm calls at high rates. Within this snapshot of an evolutionary arms race, the antshrikes and tanagers have the upper hand.

Several questions emerge from Munn's studies for which we have no answers. For example, how often do antshrikes and tanagers make mistakes in terms of detecting a predator? Establishing the error rate is important because it sets up a more accurate measure of the rate of deceptive alarm calls. When a false alarm call is sounded, how often do tanagers and antshrikes manage to capture the insect? How do other antshrikes and tanagers respond when they hear a deceptive as opposed to an honest alarm call? Can they detect a difference? Or do they go along with the prank in order to preserve the trick on a subsequent occasion when it is their turn? How often do antshrikes and tanagers produce deceptive alarm calls to the same individuals? Although the overall rate of deceptive alarm calls is quite high, one might expect that a sufficiently high rate with one individual, over a short period of time, would cause the receiver to begin ignoring the call. Finally, how do antshrikes and tanagers acquire the ability to deceive by producing deceptive alarm calls? Do young birds make mistakes, giving deceptive alarm calls to other members of their species? Do they give deceptive alarm calls in contexts outside of food competition? Answers to these questions are certainly attainable by manipulating the contexts in which each species encounters the other, by exploring the acoustics of deceptive and honest alarm calls in greater detail, and by selectively playing back deceptive alarm calls under controlled conditions. For example, one could play back deceptive alarm calls at higher rates than what is given naturally in order to determine when members of the food-finding species habituate. Given the level of description already provided by Munn, the mixed-species flocks in Peru provide an ideal situation for looking at the dynamics of inter-specific deception.

The dynamics of inter- and intra-specific interactions may be quite different with respect to the necessary and sufficient conditions for evolving the capacity to generate lies of commission. Most studies of intra-specific deception have focused on the use of false alarm calls or food calls to exploit the behavior of other group members.

For many avian species, the winter months are difficult due to the relative scarcity of food. As a result, competition over food is more intense. Anders Møller (1988a) noticed that great tits regularly produced alarm calls in the absence of predators, suggesting that they might use such signals to gain access to limited resources. To test this possibility, Møller collected observations of alarm calling by great tits at feeding stations where food was either concentrated or dispersed. Out of the total number of alarm calls recorded, 63% were given in the absence of a predator. Great tits produced such false alarm calls when the feeding stations were occupied by either other great tits or other birds (e.g., house and tree sparrows). Specifically,

the non-feeding great tit gave an alarm call and then flew straight toward the feeding station. The feeding birds flew away upon hearing the alarm call, thereby yielding access to the food station.

To determine whether both conspecifics and heterospecifics perceived the false alarm calls as similar to the real alarm calls, playbacks were conducted. Both great tits and sparrows responded to the playbacks of real and false alarm calls in the same way: they fled the feeding station and headed for shelter. This suggested that real and false alarm calls carry the same message.

Møller also found that the use of false alarm calls was contingent upon weather conditions as well as the relative dominance rank of the bird at the feeding station. Thus, great tits produced more false alarm calls during adverse weather conditions (e.g., snow storms) as well as when the bird feeding at the station was dominant; when subordinates were present at the feeding station, dominants did not use false alarm calls, but rather, approached and quietly displaced the subordinate. Further, great tits were more likely to give false alarm calls when sparrows were present at a concentrated spread of food than at a dispersed spread of food, and when the heterospecifics were from a flocking than a non-flocking species; similar results have been presented by Matsuoka (1980) working on marsh tits and willow tits.

With respect to our definitional conditions, Møller's results indicate that the great tit's alarm call is commonly given during predator detection. We don't know, however, how often great tits make errors of predator detection, and thus, we can't assess whether the documented level of false alarm calls is accurate. Second, the alarm call elicits a reliable flight response in both conspecifics and heterospecifics. This claim is supported by both the natural observations as well as the playback experiments with real and false alarm calls. Third, individuals clearly have the flexibility to exploit the manipulative power of the false alarm call, as evidenced by the contexts in which they use them. Great tits certainly do not use false alarm calls reflexively. Rather, their use of false alarm calls appears to be under voluntary control as revealed by their sensitivity to the dominance rank of conspecifics, current weather conditions, and whether or not heterospecifics are flock or non-flock feeders.

Paralleling Munn's results, Møller's findings also violate the intuition that for deception to be effective, the deceptive act must be rare: great tits produce false alarm calls at extremely high rates. However, the great tit data are a bit less clear than those collected on antshrikes and tanagers because Møller only presents the overall rate of false alarm calls. Some of these calls are given in the presence of heterospecifics and some in the presence of conspecifics. To assess whether the rate of false alarm calls differs for conspecifics and heterospecifics, it would be necessary to break down the pooled data.

Møller's results raise many fascinating questions, several paralleling those raised for Munn's work on antshrikes and tanagers. Specific to the biology of great tits, however, it would be interesting to determine how often individuals produce false alarm calls during the breeding season when resources are more abundant, and whether individuals are less likely to produce such calls prior to the mating season given that they might be deceiving a potential mate. One could test this hypothesis by making a male extremely deceptive, playing back his alarm calls at high rates when no predator is present and contrasting this situation with one in which a male is made extremely honest — play back his alarm call and simultaneously present a hawk. Given these two male types, one could then look at differences in mate choice by females during the breeding season.

Møller (1990) followed up on his great tit work by looking at a comparable problem in barn swallows, a species that has been carefully studied with respect to its breeding biology and the selective forces operating on male-male competition and female choice (Møller, 1988b; Møller, 1989; Møller, 1993). Like great tits, barn swallows also give alarm calls in the absence of predators, leading to the hypothesis that they are generating lies of commission. In contrast to great tits, barn swallows most often produced false alarm calls when their fertile mates left the nest area apparently in search of extra-pair copulations. Observations revealed that females engaged in extra-pair copulations stopped upon hearing their mate's alarm calls.

To determine whether males produce alarm calls deceptively, Møller conducted two experiments. In the first experiment, he chased females away from their nest in order to determine whether such departures elicit false alarm calls in males. Females were chased away at the start of nest building, during egg-laying, and during the incubation period. When males returned to the nest and detected the female's absence, they

rarely gave alarm calls during the nest building and incubation periods, but produced false alarm calls on about 95% of all experimental trials in the egg-laying period. Observations revealed that the false alarm calls were functionally equivalent to the real alarm calls in that other swallows either flew away or gave alarm calls. Further, whereas solitarily breeding swallows produced a constant, low rate of false alarm calls across the breeding period, colonially breeding swallows — who are more vulnerable to being cuckolded — produced high rates of alarm calls almost exclusively during the egg-laying period when females are most likely to engage in extra-pair matings.

To determine whether the difference between solitarily and colonially breeding swallows reflects a behavioral polymorphism, Møller conducted a second experiment involving the presentation of a model male swallow. Males were more likely to produce false alarm calls to a model male swallow during the nest building and egg laying period than in the incubation period, and were more likely to produce false alarm calls to the model swallow than to the control, a model willow warbler. This shows that solitarily breeding male swallows are sensitive to the risks of extra-pair copulations, and are most responsive to this risk when their mates are fertile.

Once again, Møller's observations and experiments on barn swallows fit our three definitional conditions, but appear inconsistent with the prediction of rarity. The barn swallows' alarm call is generally given in the context of predator detection and elicits a flight response. Males have evolved the capacity to use this signal to manipulate the responses of their mates, thereby fending off the threat of extra-pair copulations. False alarm calls therefore provide barn swallows with a mechanism to decrease paternity uncertainty. Like Munn's antshrikes and tanagers, it appears that the cost of ignoring the alarm call is high relative to the benefit of an extra-pair mating. Even if the male has made an error, falsely signaling the presence of a predator, it is to the female's advantage to flee, and then return at a later time to mate. This economic imbalance may enable males to produce false alarm calls at high rates.

Møller's experiments reveal that barn swallows are not acting reflexively. The use of false alarm calls appears to be under facultative control, sensitive to the risks of extra-pair copulations and the female's reproductive cycle. Several questions remain, however. For example, although the male's false alarm call temporarily breaks up a covert mating, does the female in fact obtain fewer extra-pair matings? If a male produces a false alarm call, and the female fails to return to the nest, does he try again, perhaps even more frenetically? Ristau (1991), in her work on the broken-wing distraction display in plovers, has noted that when a predator ignores the plover's first try with an injury feigning display, the plover tries again, and does so more dramatically, swooping at the predator in order to grab its attention. Although male barn swallows distinguish between a model swallow and a model warbler, do they distinguish between a model male swallow who is in the company of a model female swallow? Do they perceive a potentially mated pair as a lower risk? What about an anesthetized swallow who looks dead? There is clearly no risk, but only if swallows make a clean distinction between living and dead. If we artificially escalate the rate of false alarm calls, and do so in a situation where the female can see her mate, will she abandon him in search of a more honest mate? What are the acoustic cues to individuality and context, and can they be perturbed so that false alarm calls are no longer effective?

All of the work described thus far focuses on animals using alarm calls to deceive others during competitive interactions over food or mates. Domestic chickens, however, deceive each other in the context of mating opportunities by producing food calls in the absence of food. Marler and his colleagues (1986a; 1986b) first showed that roosters produce characteristic vocalizations when they discover food, with rate of call production positively correlated with food quality. They further observed that roosters give food calls in the absence of food, and are most likely to do so when a female is present; roosters are silent when another rooster is nearby, regardless of the presence or absence of food.

One explanation for the chicken's calling behavior is that rather than providing external reference by calling attention to food, the call reflects the signaler's willingness to engage in social interactions. In other words, chickens might often call in the context of food, the call does not refer to food but to something more general. To explore whether food-associated calls refer to food or to the intent to engage in social interactions, Marler and his colleagues (Evans and Marler, 1994; Evans and Marler, 1995; Gyger and Marler, 1988; Marler et al., 1986a; Marler et al., 1986b; Marler et al., 1991) carried out experiments with chickens living in a semi-naturalistic environment. If food-associated calls refer to food, then calls produced in the

absence of food would represent lies of commission. Results showed that 45% of all calls were produced with no identifiable object present. When calls were produced in the presence of food, changes in call rate were related to food quality, but not to the distance between mates or the probability of performing the waltzing display, a behavior used by males as an invitation to mate. In an experiment using an operant procedure, males pecked for food most when a light indicated that food was available. Food calling was considerably lower when the light was off even when a receptive female was present; waltzing was highest when the female was first introduced. These two experiments suggest that the call refers to food, even though it is mediated by social context.

Given that the call refers to food, its production in the absence of food appears to represent a case of deception. Support for this claim comes from looking at the relationship between food call production and inter-individual distance. Males were more likely to produce food calls in the absence of food when the females were far away than when they were close. This makes sense if a male's vocal behavior is sensitive to the female's visual perspective, and in particular, the probability that she will notice the absence of food. Thus, males should call honestly if females are sufficiently close that they can see whether the male does or does not have food. In contrast, they should act deceptively when females are sufficiently far away to prevent a clear view of the potential feeding area.

To function as a deceptive signal, calls produced in the absence of food must sound like those produced in the presence of food, and must have an equal probability of eliciting an approach from females in hearing range. More specifically, for the act of deception to work, females must recognize the call as a food call, must perceive the call as an indication that a male has discovered food, and must then approach the male. Results show that females approached males 86% of the time when they called in the presence of food, but only approached 35% of the time when males called in the absence of food. Further, females were more likely to approach males who called in the absence of food when their call rates were high than when they were low, and were more likely to approach when they were close to the male than when they were far. When females failed to approach in response to a male calling in the absence of food, males often approached females. These results suggest that males attempt to use food calls to attract females, and that females assess the veridicality of the signal by using the rate of calling as well as contextual information. It may be that the lower rate of approach to deceptive calls is due to perceptible differences in the acoustic morphology of the calls, but no acoustical analyses of honest vs. deceptive calls has yet been performed.

The chicken food call system satisfies our definitional conditions. Once again, however, it appears to violate the prediction of rarity. Specifically, the food call is primarily given in the context of food and as recent production and perception experiments suggest, it functionally refers to food rather than to a more generic event or context such as the willingness to engage in social interactions (Evans and Evans, 1999; Evans and Marler, 1994). When chickens produce food calls, they elicit characteristic responses that are distinct from the responses elicited by contact or alarm calls. Chickens apparently take advantage of the referential properties of the food call as well as the behavior it elicits in females to produce such calls in the absence of food. For reasons that are currently unclear, males appear to get away with such lies at relatively high rates. Almost 50% of all food calls are given in the absence of food, and when given, elicit female approach approximately 33% of the time.

In terms of a mismatch between signal and context, the chicken study provides an example of a lie of commission. What is unclear, especially when contrasted with the previous examples of avian deception, are the costs and benefits of this putative case of deception. Thus, males presumably gain some benefit by eliciting an approach from a female. However, Marler and his colleagues have yet to demonstrate that the female's approach translates into a reproductive advantage for the male. In terms of costs, females lose by disrupting their current activity and by traveling a distance to the male. At present, it is unclear whether there are costs that would constrain or limit the frequency with which males give false food calls. For example, is it the case that females are less likely to mate with a male who has given a food call when no food is available? One could test this possibility with a design that we have already mentioned. Specifically, make one male completely dishonest (100% of his calls are produced in the absence of food) and one male honest (100% of his calls are produced in the presence of food). Once a female has been exposed to these two males, set up a mate choice experiment and record the female's preferences. These experiments, accompanied by others that focus more specifically on the costs and benefits of honest as opposed to deceptive

food calls, will help us understand how male chickens can get away with such high levels of deceptive behavior.

The piece of this story that has been neglected is the skepticism of the receiver. Most of our discussion has focused on how individuals can manipulate the behavior of receivers by using functionally deceptive acoustic signals. However, selection will favor both mechanisms that facilitate deception, and those that enable accurate skepticism. Is there evidence of skepticism? The honey bee dance language represents an exquisite example of a functionally referential signal. As decades of research have revealed, when honey bees dance, attentive listeners extract information about the location, quality and distance to food using visual, acoustic, olfactory and tactile cues (Dyer and Seeley, 1989; Gould and Gould, 1988; Gould and Towne, 1987; Michelsen et al., 1992; Seeley, 1992; von Frisch, 1967). No other signaling system in the animal kingdom is this precise with the exception of human language (Hauser, 1996). To assess whether individuals are ever skeptical of the information conveyed in a dance, Gould (1990) conducted an ingenious experiment. Using a hive with a long history of experience in one location, he removed a group of foragers and trained them to move back and forth from a point on land to a second point on land where a pollen-filled boat was located. Over time, he increased the distance between these two points, and also moved the boat from a position on land to a position out in the middle of a lake; throughout the training period, Gould prevented the bees from returning to their hive. Once the bees reliably traveled to the boat and back, he allowed them to return to the hive and dance.

When the trained foragers returned to the hive, they danced, indicating that a rich food source could be found out in the middle of the lake. Although the bees watched the foragers dance, relatively few of them flew off to the boat. Why? Because, as Gould argued, food has never been found out in the middle of this lake, or presumably, any lake, and thus the information in the signal was unreliable, inaccurate. The hive members refused to move, treating the signal skeptically. This interpretation is quite reasonable when one takes into account the results of a control experiment. Specifically, Gould trained a second group of foragers to find food in a boat located on the water, but along the edge of the lake. When the foragers returned and danced, other individuals immediately left the hive and flew to the pollen-filled boat; presumably, the edge of the lake represents a more likely place to find bee food.

What we don't learn from Gould's work is the nature of the information stored in the bee's brain, the extent to which an individual's own knowledge of pollen location can override the social message. For example, if a bee knows that a field of flowers has been burned down, leaving no pollen behind, would they accept or reject a dance indicating pollen at this location a week after the burn? What about one year after the burn, giving time for new growth? If an experimenter brings the bees to the lake and allows them to feed from the boat, would they then follow the dancer to this location? If a bee repeatedly lies about the location of pollen, does she lose respect? Is she punished for falsely "crying" pollen?

We don't have answers to these questions. However, the critical aspect of Gould's work for the present discussion is that bees, and perhaps other animals, can check on the veracity of a piece of information by comparing what they are told with what they have experienced, or are currently experiencing. If this interpretation is correct, then we should be able to turn reliable animals into unreliable ones as we have already suggested.

Over the past ten years, primatologists have accumulated a large number of anecdotes of potentially deceptive behavior. These observations are, as pointed out by Andrew Whiten and Dick Byrne (Byrne and Whiten, 1990; Whiten and Byrne, 1988), strikingly different from other cases of deception in the animal kingdom in that they are rare events — they satisfy the prediction of rarity. Among the many examples catalogued, several are of the form: a monkey or ape uses a false alarm call to gain access to a resource (food or mate) or to deflect an aggressive attack. These observations suggest that non-human primates may have the capacity to create lies of commission. To address the problem of skepticism, Dorothy Cheney and Robert Seyfarth designed an experiment with vervet monkeys, adopting a classic technique from cognitive psychology — the habituation-dishabituation paradigm. Taking advantage of detailed acoustic analyses of the vervets' vocal repertoire, the general procedure started with a habituation series involving repeated playbacks of a single call type from one individual. Following a fixed number of habituation trials, they then played back either a different call type from the same individual or the same call type from a different individual. Although these experiments were primarily designed to examine the problem of referentiality, the nature of the design was ideally suited to explore the problem of deception and skepticism. Specifically,

the habituation series represents a case of experimental slander: repeatedly playback an individual's call in the absence of an appropriate context. For example, in one set of experiments, Cheney and Seyfarth contrasted the vervets' response to two calls given in the context of inter-group encounters, the "wrr" and "chutter". Although these calls are acoustically distinctive, they are given in the same general context, and thus, convey the same general message: that a competitive group is nearby. In one condition, subjects were repeatedly played A's wrrs and then tested with A's chutter. In another condition, subjects were played A's wrrs and then tested with B's wrr or chutter. Subjects habituated to repeated exposure to A's wrr, showing less response with successive playbacks. When they were then tested with A's chutter, they transferred the level of habituation. In contrast, when they were tested with B's wrr or chutter, they dishabituated, showing a renewed, strong response. In other words, if A is unreliable with respect to the information conveyed by wrrs, she is also unreliable when she produces chutters, because these two calls are produced in the same general context. However, the fact that A is unreliable about inter-group encounters does not mean B is unreliable, as revealed by the vervets undiminished response to B's chutter or wrr.

These results show that the attribute "unreliable" is assigned to individuals, not contexts. Moreover, experimenters can create unreliable individuals by simply playing back their vocalizations over and over again in the absence of the relevant context. Because individuals habituate to repeated vocalizations in the absence of a relevant context, a mechanism — "skepticism" — is in place for challenging lies of commission. Comparable evidence has been found for vervet and diana monkey alarm calls, as well as rhesus monkey food and contact calls (Cheney and Seyfarth, 1988; Hauser, 1998; Rendall et al., 1996; Seyfarth and Cheney, 1990; Zuberbühler, Noe and Seyfarth, 1997).

The habituation-dishabituation paradigm is ideally suited to push the issue of skepticism further. For example, all of the playback experiments take place over the course of less than an hour. What is lacking, from all of these experiments, is the extent to which such experimental slandering affects the individual's subsequent social interactions, and for how long. Thus, if we make A unreliable about the presence of an eagle by repeatedly playing back his eagle alarm call, will others continue to ignore his eagle alarm call if it is played back after an hour of silence? How about a day later? Two weeks? If we play A's eagle alarm call and then pair it with the presence of an eagle, will this reinstate his reliability? If not, how many times do we have to play back A's alarm call in the presence of a predator before the rest of the group trusts A? Moreover, we do not yet understand the acoustic basis for distinguishing between call types, or between individuals. An understanding of these factors (see Part 1) will put us in a much stronger position regarding design and implementation of playback experiments. These sorts of experiments are needed if we are to better understand the nature of deceptive interactions, the factors that lead to skepticism, and ultimately, how individuals acquire reputations as reliable or unreliable signalers.

3.2 Lies of omission

Before President Clinton's affair with Monica Lewinsky emerged into the public's awareness, it was a secret. By not mentioning their affair to other interested parties (e.g. the First Lady), both the President and Ms. Lewinsky committed lies of omission.

Non-human animals are also capable of committing lies of omission, and in fact may commit them more often than lies of commission (Cheney and Seyfarth, 1985; Hauser, 1996; Hauser, 1997; Marler et al., 1991; Mitchell and Thompson, 1986). One reason for this difference in frequency is that it is more difficult to catch someone who simply remains silent than someone who actively falsifies information. From an empirical perspective, however, researchers working on lies of omission are faced with a far more difficult problem for they are forced to interpret the absence of a response or behavior. To show that an animal has committed a lie of omission, the same conditions as discussed earlier must hold, plus an extra one. Thus, as for lies of commission, there must be a reliable association between a call type and some organism internal or external event; receivers should show a reliable response to such calls; and there must be some behavioral flexibility on the part of callers such that call production is not rigidly triggered by the relevant stimulus. The fourth condition for a lie of omission, is that situations which reliably lead to calling in some circumstances fail to do so in a different social context. Given this, studies of withholding information are necessarily tied to studies of what Marler and colleagues (1986a; 1991) have described as "audience effects", analyses of the social conditions mediating call production as opposed to suppression.

An important goal in studying lies of omission is to document the costs associated with withholding information. If animals have mechanisms for punishing those who are caught withholding information, this would indicate that lies of omission are perceived as such by conspecifics. Thus, if an animal fails to announce the discovery of food, and is then caught by another group member, there should be a penalty imposed on the silent discoverer. For example, a male caught withholding information about food might be attacked by a dominant animal, denied shared food in the future, or rejected by a female in future mating attempts. While the first possibility is nearly immediate, and thus easily observed, the latter requires long term studies of social reciprocation.

To flesh out these ideas, we return to some of the themes discussed above, exploring when animals attempt to withhold information, how they benefit from such lies, and the costs incurred if caught. We focus on cases where animals withhold food and alarm calls because the absence of production can be contrasted to the many contexts in which such calls are typically given. To broaden the diversity of contexts, we also discuss calls given by animals during mating and the contexts in which animals are selectively silent about their sexual behavior.

When domestic chickens find food, they give a distinctive food call. When domestic chickens detect an aerial predator, they give a different sounding alarm call than when they detect a ground predator. Such calls are functionally referential in that they appear to be highly correlated with particular contexts, and when receivers hear these calls, they respond in highly specific ways, approaching food calls, looking up to aerial predator alarm calls, and scanning the horizon in response to ground predator alarm calls. Playbacks of these calls show that they reliably elicit different, adaptive responses (Gyger et al., 1986; Gyger et al., 1987; Karakashian et al., 1988; Marler et al., 1992; Marler et al., 1991). As Marler and his colleagues have documented over the past ten years, whether or not a chicken produces a food or alarm call depends on who is around — its audience (Evans and Marler, 1995; Karakashian et al., 1988; Marler et al., 1986a; Marler et al., 1986b; Marler et al., 1991).

When cockerels were presented with food (e.g., mealworms), they announced their discovery 100% of the time in the presence of a familiar female, 95% of the time in the presence of an unfamiliar female, 75% of the time when alone, and never called in the presence of another cockerel. Thus, the presence of a hen potentiated food calling, whereas the presence of a cockerel apparently suppressed food calling. The pattern of calling and suppression is, however, slightly different when cockerels are presented with a non-food item such as a peanut shell. When peanut shells were present, cockerels produced food calls about 50% of the time in the presence of a strange female, but only about 20% of the time in the presence of familiar females. Cockerels almost never called when they were alone or in the presence of another male.

The food calling system of the chicken provides evidence for the definitional conditions set out above. Several studies have shown that when chickens find food, they give a characteristic call that functionally refers to food; the rate at which chickens give food calls appears to reflect the individual's preference for the particular food type. Given the fact that the signal functionally refers to food, we must then ask why chickens sometimes suppress their calls, committing a lie of omission. The results obtained by Marler and his colleagues suggest that chickens assess the costs and benefits of withholding information by attending to the composition of the audience. When another male is present, cockerels are silent because calling would increase the costs of food competition while bringing no benefits. In contrast, when females are present, calling to food increases the costs of food competition, but returns the benefits associated with sexual access or opportunity. Importantly, however, cockerels fail to call to non-food items if a familiar female is nearby, but often call if an unfamiliar female is present. Marler and colleagues offer the intriguing speculation that this pattern results from the fact that cockerels can tolerate the potential costs of a lie of commission — giving a food call to a non-food item — when the female is unfamiliar, but can't afford such costs when the female is familiar.

The data that Marler and his colleagues have collected clearly show that chickens are sensitive to the contexts in which a lie of omission pays. At present, we have no understanding of the costs associated with being caught committing a lie of omission. For example, do dominant cockerels attack subordinate cockerels who have withheld information about the presence of food? Do unfamiliar females reject the mating advances of cockerels who have withheld information about food? In addition to addressing these questions, studies of the chicken food call system might also profitably explore additional manipulations of both the

audience, food, and the signaler's motivational state. Thus, for example, all of the studies conducted to date have used audiences consisting of a single individual. Presumably, this is a relatively rare situation in nature where several individuals are likely to be in view of a cockerel finding food; minimally, there will be several individuals in hearing range. How would a cockerel's food calling behavior be affected by the presence of its mate and an unfamiliar female, or its mate and a cockerel? In addition to audience composition, it would be useful to look at the interaction between the cockerel's hunger level and the composition of the audience. If a cockerel is extremely hungry, and only a limited amount of food is present, do they remain silent even if a female is nearby? Finally, does the probability of remaining silent change as a function of whether the food is shareable as opposed to non-shareable? Are cockerels more likely to call if the food is spread out, thereby reducing the potential costs of competition should other individuals approach?

Showing that animals are sensitive to an audience is a critical component in investigations of lies of omission. Cockerels are not only sensitive to the presence or absence of another chicken, but are also sensitive to whether the audience is male or female, and if female, whether they are familiar or unfamiliar. A crucial question, then, is whether such sensitivity is preserved, in kind, across contexts. If it is, then the system is quite rigid. Marler, Evans and their colleagues have investigated this problem in considerable detail and the results indicate considerable flexibility rather than rigidity. In striking contrast to the effects of an audience on food calling behavior, alarm calls are potentiated equally by hens and cockerels. That is, the rate of alarm call production is the same for male and female audiences, and this is true of real audiences as well as audiences simulated by video playbacks (Evans and Marler, 1991; Evans and Marler, 1995). The rate of alarm call production is higher in the presence of either a cockerel or hen than it is when there is no audience present, or when the audience is comprised of a different species such as a bobwhite quail. The decrease in alarm call rate in the presence of bobwhite quail is not due to their smaller size as chickens produce a higher rate of alarm calls to chicks who are even smaller than quail. Finally, cockerels call more to a sexually receptive mate than to a broody hen with and without chicks, and also call more when testosterone levels are elevated.

In summary, chickens have the capacity to withhold information in the context of food and predation. Chickens are capable of committing lies of omission, but the social consequences of such deception remain unclear.

Cheney and Seyfarth's work on the alarm call system of vervet monkeys in Amboseli National Park, Kenya represents one of the best studied functionally referential call systems (Cheney and Seyfarth, 1981; Cheney and Seyfarth, 1990; Hauser, 1996; Marler, 1985; Seyfarth et al., 1980a; Seyfarth et al., 1980b; Struhsaker, 1967). These vervets produce a suite of acoustically distinctive alarm calls in the context of predator encounters. Of the set produced, the best studied are those given to snakes, eagles, and leopards. These three predator types exhibit different hunting strategies, and such differences appear to have led to the evolution of different alarm calls and escape strategies in vervets. Thus, in terms of the first condition for exploring lies of omission, vervets are ideally suited. These three alarm calls are primarily heard in the context of predator encounters, and in particular, snake alarm calls are given to snakes, eagle alarm calls to eagles, and leopard alarm calls to leopards. When such calls are heard, listeners respond in highly specific ways, suited to the style of predation. Two field observations suggest that, like chickens, the social context also mediates alarm call production in vervets. First, Cheney and Seyfarth (1988) noted that when lone vervets detect a predator, they remain silent. Second, low ranking animals produce far fewer alarm calls than do high ranking animals. The difference in alarm call rate between high and low ranking animals is not due to differences in the number of kin or in the probability of detecting a predator. Rather, the observations suggest that low ranking animals may actively suppress their alarm calls, committing lies of omission.

To test the prediction that vervet monkey alarm calls are mediated by social context, Cheney and Seyfarth (1985) conducted an experiment with captive vervet monkeys. Using a human dressed up as a predator (a graduate student in a monkey mask and lab coat, carrying a net), adult females were tested in the presence of their offspring or an unrelated but age-matched infant, while adult males were tested in the presence of an adult female or another adult male. Results demonstrated flexibility in alarm calling in vervets, with both males and females producing calls in some circumstances and suppressing them in others. Females produced significantly more alarm calls in the presence of their offspring than in the presence of unrelated infants, and males produced more alarm calls in the presence of adult females than in the presence

of adult males; adult males were virtually silent in the presence of other males. For females, therefore, kinship appears to play an important role in the mediation of alarm calls, whereas for males, mating opportunities and intra—sexual competition play a role.

As with studies of chickens, these experiments clearly show that both wild and captive vervets have the capacity to withhold information. They do not, however, allow us to assess the costs and benefits of such omissions. To better assess the economics of withholding information one would need to perform similar experiments over a longer time course, assessing how individuals respond to those who have concealed information about predators, food and so forth. We now turn to such a study.

Many primate species produce distinctive calls in the context of food (Benz, 1993; Dittus, 1984; Elowson et al., 1991; Hauser and Marler, 1993; Hauser and Wrangham, 1987; Wrangham, 1977). Like chickens, food commonly elicits such calls, and in many species, the rate of call production covaries with the quality of the food or the individual's preference for a particular food type. When individuals hear food associated calls, they typically orient and then approach the caller, and sometimes call back with the same call type.

Hauser and Marler (1993) investigated the food associated calls of rhesus monkeys living on the island of Cayo Santiago, off the coast of Puerto Rico. When individuals discover food, they give one or more of five acoustically distinct vocalizations. Three of these call types are given when high quality, rare food is discovered, while the other two call types are given when lower quality, common food is discovered. Playback experiments reveal that these call types are classified on the basis of their putative referents, and not on the basis of acoustic morphology (Hauser, 1998).

Given that rhesus monkeys are sometimes silent when they discover food, experiments were conducted to provide a more precise quantification of the necessary and sufficient conditions for call production as opposed to suppression. A lone individual was presented with the same quantity of either monkey chow (low quality/common food) or coconut (high quality/rare food), and their behavior recorded. On approximately 50% of all trials with individuals who were members of a social group, the food was consumed, but there were no vocalizations. Paralleling our naturalistic observations, males called less often in the context of a food discovery than did females. However, there were no differences in call rate between high and low ranking discoverers. Independently of rank or sex, individuals who called obtained more food, and received less aggression, than individuals who were silent and caught with the food by other group members. That is, silent discoverers were chased and physically attacked, and as a result, obtained less food. However, individuals who were silent and never caught at the food source obtained more food than anyone else. These results suggest that rhesus monkeys have the capacity to commit lies of omission, and that there are measurable social costs and benefits to such deception.

What makes the rhesus case particularly interesting is that the dynamics of this kind of deception change as a function of the discoverer's group status. All of the results reported above were obtained from individuals resident within a social group. When the same experiment is conducted on peripheral males — individuals who have yet to join a social group — such males never call and when they are caught with food, they are never attacked (Hauser, 1997). Rather, when members of a social group catch a peripheral male, they supplant him from the food, or chase him away without making physical contact. Thus, peripheral males can get away with lies of omission without paying the costs. One explanation for this difference between resident and peripheral males may be that only resident males are involved in subsequent social interactions.

The rhesus food call system satisfies the conditions for an analysis of lies of omission, and furthermore provides some evidence of an immediate punishment for those who commit them. Food calls are generally produced in the context of finding food and when individuals hear them, they approach. Thus, there is a strong association between call and context, and the call elicits a predictable response. When animals withhold information about the discovery of food, they incur the costs of targeted aggression if caught, but otherwise benefit if no one discovers them. However, like the other studies, research on rhesus monkey food calls fails to address the long term consequences of withholding information. For example, when silent peripheral males are caught at a food source, how does their silence affect the odds of joining a social group? If an estrous female finds a silent male at a food source, is she less likely to initiate or accept a sexual consortship with him? Are males less likely to withhold information about food in the presence of an estrous

female as opposed to a non-estrous female? Are males more likely to remain quiet when no one is around or when an adult male is nearby?

One last example illustrates that lies of omission are possible outside the contexts of food and alarm, and provides suggestive evidence of more long term costs and benefits for deception. Like many other primates (Hauser, 1996), rhesus monkeys produce distinctive vocalizations during copulation (Hauser, 1993). These copulation screams are among the loudest calls in the repertoire, are acoustically different from all other call types, and are highly distinctive by individual. Thus, when a rhesus monkey gives a copulation call, listeners know what the caller is doing and who he is. Focal animal samples of 47 adult males and 59 estrous females during the mating season indicated that males were more likely to call during copulation when the number of estrous females was high than when it was low. Thus, males often copulated in silence. Interestingly, silent males generally produced the facial expressions that accompany the copulation call, suggesting that they can inhibit the vocalization but not the facial gesture. When the data are divided according to male dominance rank, high ranking males called more often than expected, low ranking males called less often than expected, and middle ranking males called at the average rate.

To assess the consequences of calling as opposed to withholding information about mating behavior, we carried out analyses of the relationship between mating success and call frequency. Results showed that for a given female, the male who obtained the most copulations was a male who called during copulation. Moreover, calling males copulated more overall than did silent males. Thus, there may be a long term cost to withholding information, at least in terms of behavioral measures of mating success. The benefits obtained from calling were, however, associated with costs. Analyses revealed a statistically significant, positive, relationship between the number of copulation calls produced and the number of aggressive attacks received. Withholding information about mating is therefore associated with lower benefits than calling, but is also associated with lower costs. It would seem that the benefits of increased mating opportunities outweigh the costs of intra-sexual competition.

Thus studies of rhesus copulation calls also satisfy the conditions for lies of omission, and provide suggestive evidence for punishment. Copulation calls are strictly associated with the context of mating, and often, males produce such calls when they copulate. Given that males were more likely to remain silent when competition for estrous females was high, and that both high and low ranking males have the capacity to remain silent during copulation, these data indicate the ability to withhold information about mating. Although such lies of omission are associated with reduced aggression, they are also associated with increased costs due to the fact that silent males obtain fewer opportunities to mate than do vocal males. It would be interesting to follow up this work with studies in captivity that explore more carefully the mechanisms underlying mating decisions, and whether females copy the mating preferences of others. Thus, one could set up a situation in which one female watched a male copulate and vocalize with female A and a second male copulate and remain silent with female B. Given a choice, which male will the observer female select? On Cayo Santiago, some females cycle in and out of estrous several times during the mating season. Sometimes females mate with the same male on each cycle, and sometimes they mate with different males. When females switch males, it would be interesting to determine whether they switched from a silent to a vocal male. Such studies would help our understanding of why rhesus monkeys sometimes choose to vocalize when they mate, and sometimes choose to remain silent.

4. Summary and Conclusions

In this paper we have argued that the study of the proximate mechanisms underlying vocal behavior, both physiological and cognitive, is a necessary part of the study of the evolution of communication, and in particular for analyzing honesty in communication. In the first part we surveyed basic principles of vocal production in terrestrial vertebrates, and the morphological diversity of their production systems. We then provided some examples of the interactions between acoustics and anatomy that can enforce honesty, or subvert it. In the second part we examined the evidence for cognitive mechanisms that allow animals to produce deceptive calls, as well as "retaliatory" perceptual mechanisms that allow perceivers to accurately identify and ignore (and in some cases even punish) the deceivers. Both vocal production mechanisms, and cognitive mechanisms controlling vocalization, play a crucial role in determining what is possible or impossible in a particular species' communication system. A better understanding of these mechanisms can lead to rich insights into the evolution of acoustic communication.

For the reader already interested in mechanism, the chapter also provided illustrations of the value of an ultimate evolutionary viewpoint. 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 selective pressures and functional constraints. The species we observe today are the outcome of a long dynamic process of coevolution 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. 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. We believe 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.

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