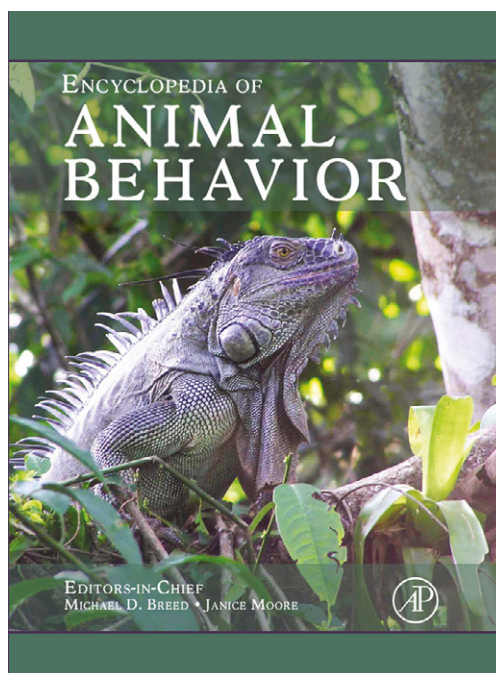


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## Syntactically Complex Vocal Systems

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### Introduction

What constitutes 'animal communication' is subject to many interpretations. Uniform among all definitions, however, is that communication, whether between humans or non-human animals, involves the transmission of information from a sender to a receiver. In this basic description, information is coded by the patterning of a physical signal. In principle, the patterning can occur in any physical dimension occupied by the communication signal. In practice, because most behaviors unfold over time, on scales ranging from milliseconds to hours, or longer, behaviorally relevant information is carried in the signal's temporal patterning.

Temporally patterned communication signals can use any available sensory modality for transmission. For example, sagebrush lizards, *Sceloporus graciosus*, engage in elaborately structured push-up displays that can vary between behavioral contexts. Likewise, honeybees, *Apis* sp., use stereotyped sequences of movements, called a 'waggle dance,' to communicate the location and distance of a food source through a combination of tactile, auditory, and airflow cues.

Auditory signals are by far the most common sequentially patterned communication signals. Sound pressure waves can be transmitted over long distances through a variety of media and can contain variations in frequency, intensity, and timbre – all of which enhance the signal's information-carrying capacity. Auditory communication signals are produced by many species across a range of taxa, including mammals, birds, amphibians, fishes, and insects. This article focuses on behaviorally relevant temporal patterning in acoustic communication signals.

Temporal patterns in acoustic communication signals may exist at many levels of complexity. In its simplest form, an otherwise static signal may either be off or on. To increase the amount of information transmitted, such a signal might be modulated across time. For example, males in several families of crickets generate courtship signals of a constant carrier frequency modulated at a species-specific rate to attract females. An unmodulated sine tone at the species-typical carrier frequency, or another carrier frequency modulated at the species-typical rate, will fail to attract females.

For communication systems to function in more dynamic contexts and/or across a wider range of behaviors, it may be adaptive for animals to use a repertoire

of communication signals. In the simplest case, the repertoire comprises a set of independent, isolated signals, each used to convey information in a specific context. For example, some guenons and other closely related species (e.g., vervet monkeys) produce acoustically distinct alarm calls that refer to different classes of predators. In this case, a different 'unit,' that is, alarm call, is necessary to convey each possible message and receiving a partial sequence of units does not necessarily improve the ability to predict the following units (but see section 'Syntactically Complex Vocal Signals in Nature').

Communication systems in which single units are mapped onto single behavioral contexts can be made more complex by allowing for specific combinations of units, with different combinations conveying different meanings. We term such systems 'syntactically complex' communication systems. These systems have two important emergent properties. First, they permit redundant encoding. If a receiver knows the syntactic structure of a communicative system, that is, how units are typically combined, it can generate expectations about the upcoming signal components, thereby reducing uncertainty. This renders the combined signal robust to interference (at least to a limit) and therefore may be adaptive in noisy environments. Syntactically complex communication systems are also, in principle, more efficient than other systems because they allow for a theoretically infinite number of meanings to be constructed from a finite number of signal elements. This combinatorial efficiency is one hallmark of human language. As we discuss later, it has been observed only in a small number of instances among animals and even then in a somewhat remedial – perhaps qualitatively different – form from that seen in humans.

In the context of human language, 'syntax' refers to the rules that describe the construction of sentences from classes of words, for example, nouns and verbs. Indeed, syntax has often been characterized as the uniquely defining characteristic of human language. Perhaps as a result, claims that animals might 'have syntax' often elicit intense (usually negative) responses from human language researchers. Linguists have proposed several different theories of syntax, all of which provide a framework for analyzing how words are assembled to create well-formed sentences. Debate exists among linguists, however, as to whether syntactic structure emerges from statistical regularities in word order, or whether there are innate, rule-based,

structural constraints. In either case, it is important to be clear from the outset that a divide separates the kind of 'syntactic' communication observed in humans and those behaviors observed in other animals which we discuss here. We know of no animal communication system that threatens the claim that human language, as practiced among normal adults, is unique.

Many scholars surmise that the neural mechanisms that permit language processing are separate from those underlying our ability to communicate; that is, that there are language-specific brain mechanisms. Language is not a single behavior, however, and no single cognitive process accounts for its expression. Thus, the specificity and the unique role of any brain mechanism in language are an empirical question. To address such questions, it is useful to consider all syntactically complex communication systems as at least some of the mechanisms underlying the perception of temporally patterned vocal signals may be shared among a range of species. Careful description and empirical study of these mechanisms and behaviors are interesting in their own right, and will be instructive in understanding shared processes, convergent evolutionary mechanisms, and differences across taxonomic groups.

## Historical Context and Definitions

There is a long and rich history of scientific interest in the temporal organization of animal behavior. Though not the first to consider such ideas, Lorenz's and Tinbergen's pioneering work in the middle of the twentieth century set the stage for the empirical study of how animals communicate through patterned sequences of complex, natural behaviors. Karl von Frisch was among the first to put these concepts into action in his study of the honeybee waggle dance. During the same era, laboratory scientists such as Karl Lashley began to appreciate the difficulties of using associative learning to describe serial behaviors in animals. Instead, Lashley appealed to more 'cognitive' and 'hierarchical' accounts that posited high-level knowledge about the broad sequence of behavior to be executed rather than a stimulus-response chain that simply linked successive behaviors. These conceptual advances in our understanding of temporally organized behaviors coincided with the rise in the popularity of mathematically well-defined theories of temporal patterns (i.e., syntax) in human language, most notably from Noam Chomsky.

The question of whether or not animals use syntactically complex vocalizations to communicate and whether they share any syntactic (or linguistic) abilities with humans has been a target of investigation for several decades. In 1975, Wilson noted the existence of discrete animal signaling units that could be recombined to generate sequences, but added 'no animal species communicates

in just this way.' Near the same time, Peter Marler published a seminal paper distinguishing between two types of syntactic patterning present in auditory communication signals – 'lexical' and 'phonological' syntax. Lexical syntax is the ordering of semantically meaningful functional units, analogous to words, such that the ordering of sound units carries meaning beyond that carried by the individual sound units. Importantly, to recover the meaning, the receiver must also share some knowledge of the rules used to compose the signal. Thus, in human language lexical syntax provides the mechanism for combining words into meaningful sentences, and constitutes the typically familiar definition of 'syntax.' In contrast, phonological syntax does not imply recombination of otherwise meaningful sounds. Phonological syntax may include structured rules for ordering sound units, but these sound units are often at a short timescale and have no intrinsic meaning. Phonological syntactic structure is analogous to the sets of rules underlying the arrangement of phonemes into possible words in human language. Although the phonemes of American English can be recombined to form an infinite number of sounds, many of these sequences of phonemes are not well-formed words. A native speaker would immediately recognize them as incompatible with the rules governing sound unit order in English. Likewise, there are many well-formed words that are not a part of the lexicon.

To appreciate the difference between lexical and phonological syntax, it is helpful to think of both the figurative and literal meanings of an idiomatic expression, such as 'MacDonald bought the farm.' Lexical syntax leads to the literal meaning that someone named MacDonald purchased agricultural real estate, but must be ignored in favor of phonological syntax to recover the figurative meaning that he died. A communication system with only phonological syntax is analogous to a collection of idioms, whereby certain sound sequences are mapped arbitrarily to meanings.

Much of the evidence for syntactic patterning in animal communication can be interpreted within the context of phonological syntax. It is only in very rare cases that researchers have been able to implicate the ordering of otherwise meaningful sound units in changing the meaning of a communication signal, which may provide evidence of lexical syntax. Although there is strong evidence for phonological patterning in animal vocal communication, we stress the limitations in our use of the term 'phonology.' In human language, phonology implies several related skills including categorical perception and the discrimination of minimal phoneme pairs. Although categorical perception has been observed in several species, the perceptual limits of non-human animal phonology have not been adequately tested, and so drawing direct homologies to human phonological abilities remains an important challenge for future research.

## Measuring Syntactic Complexity

A major difficulty inherent in parsing the syntactic structure of animal communication systems is that investigators may not know the structure a priori, and structural patterns may exist at multiple timescales. Determining the smallest relevant unit for production and/or perception remains a challenge in many communication systems, and findings from one species have not always generalized to others. Short timescale sounds units, for example, notes in birdsong, are often produced in longer stereotyped patterns. In some species, these patterns are further combined into longer sequences consisting of several such sound units. Thus, like phonemes, these short sound units are the constituents of larger communication structures.

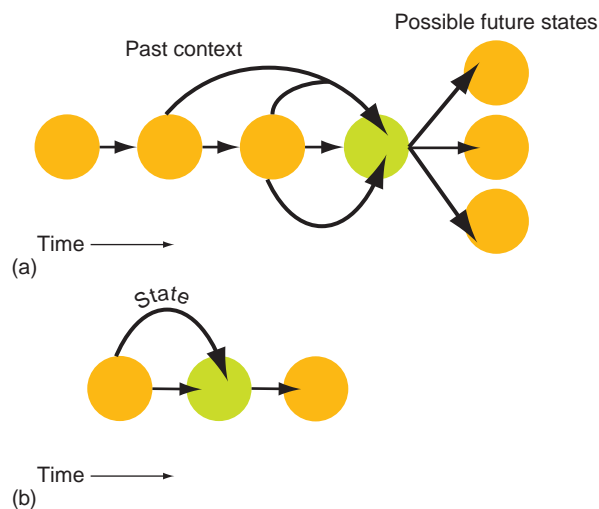
Several studies have attempted to model the generation of communication sequences by first choosing a model and then using observations to estimate the model parameters. Markov chains provide one intuitive class of sequence-generating models in which the probability of observing a certain signaling unit (known as its transition probability) is defined in terms of a finite number of observed preceding units. Markov models have been applied to the structure of animal communication signals since the early 1970s – particularly the songs of oscine birds (songbirds).

Using Markov models to evaluate complex syntactic structure is intuitively appealing, but is often difficult to implement with limited behavioral data. As the number of relevant preceding units in the Markov model increases, the number of possible transitions increases exponentially. Even with relatively large samples, many of these higher-order transitions may occur infrequently (or not at all), making it difficult to accurately estimate their likelihood. Moreover, Markov models are restricted to incorporating recent context, and so cannot capture complex structures in which meanings are changed by units separated by a large number of intervening units within a sequence. Recent results suggest that vocal communication in some species fails to support this limitation in Markov models: non-human primates have perceptual access to long-range dependencies in patterned strings of sound. Thus, the representational capacities to process structures beyond the level of a Markov process appear to be conserved, at least within some primate lineages.

Recently developed information theoretic methods provide additional frameworks for estimating the amount of temporal pattern structure present in animal communication signals. When applied to the songs of humpback whales, *Megaptera novaeangliae*, these techniques indicate a long timescale temporal structure that cannot be captured by Markov models. Although the precise form of this structure remains unclear, it requires a hierarchical syntax that constrains more than the local structure of the song. Thus, while Markov models can provide powerful descriptions of syntactic complexity (particularly for

complete repertoires), they are likely insufficient to capture the full complexity of such signals.

'Formal grammars,' or automata, define another class of models capable of capturing the structure of syntactically complex vocal communication signals. Unlike Markov models, formal grammars do not operate on the probabilistic relationships between adjacent elements in a string. Instead, a formal grammar is a collection of rules that operate on a set of symbols, termed a 'vocabulary,' to produce a set of patterned strings, termed the 'language.' Conversely, any grammar, once known, can be used to decide whether a given string is acceptable (i.e., grammatical) within a given language. A full review of syntax and compositional semantics in human language is well beyond the scope of this article. There are, however, many types of formal grammars and these can be classified according to the complexity of the patterns they can produce or recognize. Finite-state grammars are the most limited, that is, simplest, type of formal grammar. Finite-state grammars are deterministic and can be modeled with finite-state automata. Unlike Markov processes, transitions to the next state can be completely described by rules that depend only on the input symbol and a limited memory (known as the 'state') of the machine. Human languages minimally require a grammar more complex than finite-state, called a context-free grammar (Figure 1).



**Figure 1** Schematics of a Markov model and a finite-state grammar. In the Markov model (a), transitions to the next symbol are described probabilistically, whereas in the finite-state grammar (b), symbols that follow are described with a deterministic set of rules. In each model, the current symbol is marked in green. There are several possible future symbols in the Markov model, the probability of each of which depends on what has been observed in the past two states. In this depiction, arrow thickness denotes probability. In the finite-state model, there is only one possible future symbol, which is completely determined by an input symbol and the current state. The state persists until it is changed, and functions as a simple form of memory.

In principle, almost all of the vocal communication signals modeled well by low-order Markov processes are likely to have temporal patterning structure that can be captured by finite-state grammars. Empirically, finite-state grammars have been used to model the phonological syntax of calls in several species of chickadee, *Poecile* sp., and the songs in Bengalese finches, *Lonchura striata domestica*. Indeed it is likely that the structure of temporal patterning in most naturally produced animal communication signals can be computed by using a finite-state grammar, though humpback whales present one notable exception and a more careful documentation of syntactic complexity is needed.

Although finite-state grammars describe the temporal structure of most syntactically complex vocal signals, one should not interpret this as a definitive statement on the upper bound on the capacities for non-human animals to perceive syntactic structures. Multiple factors beyond perceptual abilities, such as production constraints, may limit the emergence of syntactic complexity in natural signals. European starlings, *Sturnus vulgaris*, a species of songbird, can learn to classify temporal patterns of song motifs generated by both a finite-state grammar and a simple context-free grammar (CFG). In contrast, cotton-top tamarins do not appear to be sensitive to CFG-generated patterns. By itself, the ability to process simple context-free syntactic structures may be of little functional significance or adaptive value – perhaps arising with vocal learning – and may represent a necessary but insufficient precondition to the use of unbounded signal sets observed in humans. *Saguinus oedipus*, a species of non-human primate that does not show vocal learning, appear unable to recognize patterns generated by a CFG. In any case, pattern-rule learning capacities in non-humans are under active research, and the upper bounds of such abilities across species remains an open question.

### Syntactically Complex Vocal Signals in Nature

Coincident with understanding the upper limits of syntactic processing capacities, it is important to assess the range of syntactically complex vocal signals observed under natural conditions. A variety of interesting syntactically complex vocal behaviors have been documented by careful observations and experiments over the last 35 years. Here, we concentrate on the two groups of animals that have received the most attention: birds and non-human primates.

Important differences between birdsong and non-human primate communication signals affect how patterning of sound units can be interpreted. Birdsong is important for mate attraction, individual recognition, and territoriality. Although birdsong can be potentially meaningful (e.g., to

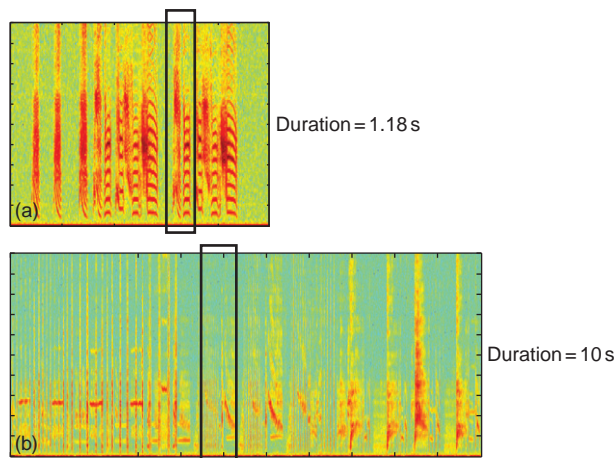
female birds), it is not possible to identify distinct meaning with any individual sound units. So, it has not been possible to identify lexical syntax in the patterning of song units. In contrast, many non-human primates use alarm calls where sound units have specific semantic meaning. The referential nature of many of these vocalizations makes investigations of the interface between phonological and lexical syntax more empirically tractable than in songbirds where meaning is often tied to individual characteristics.

### Birdsong Syntax

Many songbird species produce songs with organization at multiple timescales. Short spectro-temporally continuous events (called notes) are organized into longer functional units that are rarely interrupted (called motifs or syllables). These longer units are arranged in bouts of singing that can last, in some cases, up to several minutes. Structured organization exists both in the arrangement of notes to form motifs or syllables, and in the ordering of motifs to form song bouts.

Ordering of sound units in birdsong varies considerably in its flexibility. Some species sing highly stereotyped songs, with little flexibility in their temporal patterning. Each sound unit follows the other with regularity and there is only a very small probability that this ordering will be violated. Adult male zebra finches, *Taeniopygia guttata*, produce a single song that varies only slightly from bout to bout (hear audio example [Figure 2\(a\)](#)). Even in these cases where there is little flexibility in song structure from one rendition to the next, songs may end at different points in the ordering of sound units, for example in Nightingale wrens, *Microcerculus philomela*. Like zebra finches, Nightingale wrens can sing different numbers of songs from bout to bout.

Substantially more variability is observed in other songbirds. Species such as the European starling, *S. vulgaris*, and winter wren, *Troglodytes troglodytes*, produce stereotyped sequences of notes, called 'motifs,' which are unique to an individual (hear audio [Figure 2\(b\)](#)). While the pattern of notes within a given motif is largely (though not wholly) stereotyped from rendition to rendition, the ordering of motifs varies quite flexibly among song bouts. Even though there is substantial flexibility in motif ordering, transitions between motifs are not uniformly distributed (i.e., not every transition is equally likely) and some motifs are more likely to occur at a certain section of a song (beginning, middle, or end). For example, European starling song motifs can be classified into four types on the basis of their acoustic properties. One class of motifs, called 'whistles,' is typically found at the beginning of song bouts, while 'high-frequency' motifs tend to occur at the ends of complete bouts. There are also systematic differences in the number of times a given motif may be repeated with some motifs repeated many times, while



**Figure 2** Spectrograms of (a) zebra finch (*Taeniopygia guttata*) song (duration = 1.18 s and frequency range = 0–22 kHz) and (b) excerpt of European starling (*Sturnus vulgaris*) song (duration = 10 s and frequency range = 0–22 kHz). See audio examples for sound files. Zebra finch song is characterized by short, highly stereotyped bouts of song. Starling song, in contrast, consists of flexible sequences of motifs, which are often repeated. In both figures, time is represented on the horizontal axis and frequency is represented on the vertical axis. A single motif, which is repeated three times, is marked in the starling song, and a single note is marked in the zebra finch song.

others are rarely part of lengthy repetitive sequences. Thus, at least in starlings, there are multiple scales of temporal organization in song.

Markov sequence models have been applied to song production in several different species of North American thrushes, cardinals, *Cardinalis cardinalis*, rose-breasted grosbeaks, *Pheucticus ludovicianus*, and American redstarts, *Setophaga ruticella*. In these species, as in European starlings, most song sequences are best fit by Markov chain models that take into account transition probabilities between ordered pairs of events. Laboratory studies demonstrate that at least in the European starling, sequential transition probabilities between ordered pairs and ordered triplets of motifs aid significantly in the perception and recognition of familiar songs. Sensitivity to song element ordering has also been observed in the field, where for example, swamp sparrows, *Melospiza georgiana*, can recognize differences in syntactic structures of songs from different geographical regions. These studies of song perception are consistent with the idea that perceptual sensitivity of the receiver covaries with the syntactic information content of the signal. Sender–receiver matching is a common property of communication systems.

The phonological syntax of song appears to be culturally transmitted in some species. White-crowned sparrows, *Zonotrichia leucophrys*, normally produce songs composed of three to six ‘phrases,’ and can learn to sing species-typical songs from tape recordings. When male white-crowned

sparrows are tape tutored with single-phrase song models, the birds learn the phrases and assemble them into species-typical phrase sequences, but not into whole songs. Tutoring white-crown sparrows with phrase-pairs is sufficient for full, species-typical song syntax to emerge. Moreover, birds tutored with reverse-ordered phrase pairs sing songs with reversed phrase order. Thus, phrase sequencing information must be part of the song model experienced during early development. Thus at least in this species, the phonological syntax of song appears to be learned.

Syntax has been extensively studied in the chick-a-dee call of chickadees, *Poecile* sp., which has considerable flexibility in the sequential ordering of its notes. Again, the variability in ordering is not random. Rather, each type of call note, denoted ‘A,’ ‘B,’ ‘C,’ and ‘D,’ may be repeated a variable number of times or omitted, but the overall sequence of note types is strictly maintained. Calls that violate the note type order are extremely rare, occurring less than 0.5% of the time. This rigid ordering structure in chickadee calls provides a concrete example of a formally computable syntactic rule for call production, and is observed in a number of chickadee species (black-capped Chickadee, *P. atricapillus*, Carolina chickadee, *P. carolinensis*, mountain chickadee, *P. gambeli*, and the Mexican chickadee, *P. sclateri*) and the taxonomically related titmice (e.g., tufted titmouse, *Baeolophus bicolor*). Moreover, violations in the typical call syntax appear to be perceptually salient to receivers, as they often elicit substantially different or no response compared to calls that follow the syntactic rule.

The temporal patterning in the chickadee call system provides a clear example of phonological syntax, as different, well-formed, call sequences can elicit different behaviors. Whether the system meets the criterion for lexical syntax is not clear. Reports from at least two chickadee species suggest that information about the sex and geographic origin of the singer is carried by single notes, but it is not clear how such information is related to the overall meaning conveyed by call syntax. It is possible that such information is coded in the acoustic characteristics of the vocalizations imparted by individually specific morphological variation in the vocal apparatus, and thus cannot be varied by the singer. However, some acoustic properties are probably dynamically regulated, as indicated by changes in some spectral properties of chick-a-dee notes when chickadees form flocks. In either case, spectral information represents a special semantic case. In humans, voice characteristics do not appear to overlap with linguistic components of speech, and they are not altered by syntax under normal conditions.

### Primate Vocal Syntax

In contrast to the primarily nonreferential function of songbird vocalizations (i.e., mate attraction, aggression, territoriality, etc.), there is ample evidence that some

primate vocal communication signals contain specific referential information, apart from individual identity. Acoustically distinct vocal calls serve as alarms for different predator types, and nearby conspecifics use these alarms to initiate defensive action appropriate to the predator's mode of attack. Acoustically distinct alarm calls can also refer to environmental dangers such as falling branches or trees.

Several species appear to use combinations of alarm (or other) calls in different behavioral contexts. Black-and-white colobus monkeys, *Colobus guereza*, sometimes use a two-call combination made up of a 'roar' introduced with a brief 'snort' to maintain spacing between nearby groups. By itself, the snort serves as an alarm call. Likewise, the 'pant-hoot' given by chimpanzees, *Pan troglodytes*, has components that acoustically resemble a mild alarm call. Male and female titi monkeys, *Callicebus moloch*, incorporate several call types into sequences that differ between behavioral contexts.

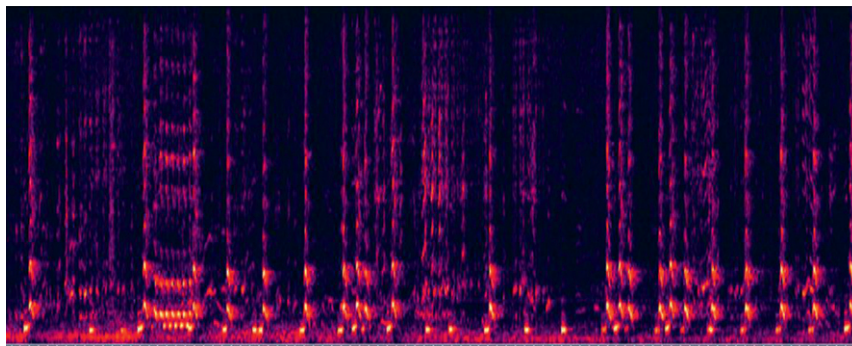
Using a variety of behavioral assays, several studies have demonstrated that primates are sensitive to the temporal ordering of sound units. Playback studies indicate that wedge-capped capuchin monkeys, *Cebus olivaceus*, are sensitive to the ordering of sound units in their calls. When calls are arranged so that sound units are ordered naturally, listeners produce fewer moans than when they are arranged in unnatural combinations. Gibbons, *Hylobates* sp., which unlike other non-human apes produce acoustically elaborate songs – typically as duets between mated pairs – appear to show similar characteristics (hear audio [Figure 3](#)). White-handed gibbons, *H. lar*, produce complex song sequences in response to terrestrial predators and during other normal daily routines. Although composed of the same call note repertoires, the predator-induced songs are assembled differently than other songs. These differences, and potentially their referential meaning, are salient to receivers. The ordering of song in other gibbons, *H. agilis*, is thought to follow a rudimentary set of structural rules, and so further study of vocal syntax in this genus will be very important.

Recent studies provide evidence consistent with lexical syntax in wild primate species. The behavioral

response of the wild Diana monkey, *Ceropithecus Diana*, to the alarm call of the Campbell's monkey, *Cercopithecus campbelli*, can be modulated in urgency by introducing boom sound units before the alarm call. These alarm calls are initiated by Campbell's monkeys in response to approaching predators and cause other monkeys to take evasive action appropriate to the predator. Likewise, Putty-nosed monkeys, *C. nictitans*, are sensitive to particular ordered sequences of two loud alarm calls, 'pyows' and 'hacks.' By themselves pyows are a common response to leopards, and hacks (or hacks followed by pyows) are given to eagles. Males sometimes give a series of one to four pyows followed by one to four hacks, either alone or at the start of other call sequences, and these pyow–hack sequences reliably predict group movement. Lexical syntax requires not only that meaningful sound units combine into larger meaningful sequences, but also that the meaning of the sequence is dependent on the ordering of units. Thus, the fact that pyow–hack sequences appear to have a different meaning than hack–pyow sequences and that pyows and hacks are meaningful by themselves is consistent with a rudimentary form of lexical syntax.

### Vocal Syntax in Other Mammals

Surprisingly, relatively little work has examined the presence of syntactic complexity in the vocal communication systems of mammals other than primates. Playback studies with Richardson's ground squirrels suggest that the ordering of sound units has little effect on behavior. Some syllables with unique acoustic elements enhance behavioral responses, but do so regardless of where in the call they occur. Mexican free-tailed bats, *Tadarida brasiliensis*, have rich vocal repertoires. While some syllables are unique to specific calls, others are shared among multiple calls, and entire calls associated with one behavior can be embedded in more complex vocalizations used in different behavioral contexts. It remains to be seen whether or not different combinations of simpler call components convey different meanings. It is worth noting that many



Duration = 10s

**Figure 3** Spectrogram of a gibbon song excerpt (duration = 10 s and frequency range = 0–10 kHz).

other species of bats have rich vocal repertoires, and bats are one of the few mammals in which vocal learning has been documented. Thus, the characterization of syntactic complexity in this order is important.

## Conclusion

There is great diversity in the kinds of temporal patterning exhibited in the natural communication systems of non-human animals. Birdsong and the alarm calls of non-human primates have been particularly well studied, and several classes of models have been applied to extract structure in the combination of sound units. Temporal patterning commonly imparts structured combinations of sound units, but only rarely can we clearly identify that variation in this structure carries meaning within the communication system. At present, there is only limited evidence of lexical syntactic structure in animal vocalizations. Interestingly, all such evidence appears to come from a small set of non-human primate species. In contrast, there is abundant evidence for phonological syntactic structures in many species.

Comparative study of how sound units are combined can provide a rich source of evidence for investigating the evolution and neural basis of important cognitive skills involved in language perception and production. And, having emphasized in this article the distinction between phonological and lexical syntax, it may be tempting to view these descriptions as residing along a single continuum of behavioral complexity. We caution against such thinking. It may be that the lexical processes (and associated neural mechanisms) that underlie referential communication are wholly different from those that support temporally sophisticated phonological syntax. As such, lexical syntax may not be the derived form of phonological syntax, but rather may require the rare integration of typically distinct temporal patterning and lexical capacities. Thus, we find one group of very successful animals, namely oscine birds, exploiting

phonological syntax without a rich referential lexicon, and another group, non-human primates, using referential signals but in heavily restricted temporal patterns. From this perspective, the human syntactic system might be considered as the rare example of what can happen when complex auditory sequence production and perception co-occur with the use of referential units. The most productive future research is likely to come from work that highlights syntactic and referential characteristics shared among different communication systems, and which is followed by the close study of biological mechanisms as appropriate in each organism.

*See also:* Acoustic Communication in Insects: Neuroethology; Acoustic Signals; Alarm Calls in Birds and Mammals; Apes: Social Learning; Communication and Hormones; Dance Language; Hearing: Vertebrates; Information Content and Signals; Mammalian Social Learning: Non-Primates; Referential Signaling; Social Recognition; Sound Production: Vertebrates; Vocal Learning.

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