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# Combinatoriality in the vocal systems of non-human animals

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## Abstract

A key challenge in the field of human language evolution is the identification of the selective conditions that gave rise to language's generative nature. Comparative data on non-human animals provides a powerful tool to investigate similarities and differences among non-human and human communication systems and to reveal convergent evolutionary mechanisms. In this article, we provide an overview of the current evidence for combinatorial structures found in the vocal system of diverse species. We show considerable structural diversity exits across and within species in the forms of combinatorial structures used. Based on this we suggest that a fine-grained classification and differentiation of combinatoriality is a useful approach permitting systematic comparisons across animals. Specifically, this will help to identify factors that might promote the emergence of combinatoriality and, crucially, whether differences in combinatorial mechanisms might be driven by variations in social and ecological conditions or cognitive capacities.

## Introduction

Language is considered a hallmark of the human species (Darwin, 1871; Hockett, 1960). Our ability to purposefully communicate (*intentionality*) meaningful information (*semanticity*) in an open-ended way (*generativity/productivity*) appears to set us apart from the rest of the animal kingdom (Hockett, 1960). The question of the origin of this capacity has puzzled scholars ever since Darwin drew attention towards the obvious differences between human language and animal communication (Darwin, 1871), and much effort has been put into elucidating language's uniqueness and which language-specific traits might be shared with non-human animals (Hauser, Chomsky, & Fitch, 2002; Pinker & Jackendoff, 2005). As a result, comparative studies conducted over the last decades have revealed that several language-specific components do have analogues in animal systems (Hauser et al., 2002; Pinker & Jackendoff, 2005). For example, both the ability to intentionally communicate information (c.f. vocal flexibility (Marler, Dufty, & Pickert, 1986; Zuberbühler, 2008)) and to assign acoustic labels to external stimuli (c.f. functional referential signals (Seyfarth, Cheney, & Marler, 1980; Suzuki, 2016; Townsend & Manser, 2013)) have been argued to be present in diverse animal species, providing important insights into the evolutionary drivers of these abilities (Christiansen & Kirby, 2003; Hauser et al., 2002) (but see Sievers and Gruber (2016); Townsend et al. (2016); Wheeler and Fischer (2012) for further reading and ongoing debates). However, one critical component remains obscured: the evolutionary origin of language's generative nature (Hauser, 1997; Humboldt, 1999; Nowak, 2000; Zuidema & de Boer, 2018).

Language's generativity is the product of its double articulation, which involves the combination of acoustic elements and units on two different levels (Hockett, 1960). On the *phonological layer* (*combinatorial phonology*), a limited number of meaningless speech sounds (e.g. /a/ /t/ /k/ /h/) can be (re-)combined to create a theoretically infinite array of morphemes or words, (e.g. "at", "cat", "hat"), whereby those sounds that serve to distinguish meaning are classified as phonemes (e.g. /k/ & /h/ when contrasting "cat" & "hat") (Chomsky & Halle, 1968). At the higher *syntactic layer* (*compositional semantics*) these meaning-encoding components can then be assembled into larger structures, with the structure's meaning being derived from its individual components and the rules that govern their organisation (e.g. "the cat in the hat") (Chomsky, 1957; Hurford, 2007, 2012b). Traditionally, the search for comparative examples of phonological and syntactic features outside of human

language has i) focused on song-driven systems, arguably the most obvious and complex forms of sound combinations, or ii) searched for homolog examples in primates, under the assumption that our generative capacities are adaptations of pre-existing traits shared with our closest-living relatives (Berwick, Okanoya, Beckers, & Bolhuis, 2011; Hauser et al., 2002; Yip, 2006; Zuberbühler, 2018). Only more recently has this comparative approach been extended to the discrete vocal systems of distantly related species (as opposed to song-driven or primate systems). As a result, the growing body of work suggests that the ability to combine acoustic segments into larger structures is by no means a rare phenomenon in the animal kingdom, with some combinatorial structures providing analogues to linguistic structures in human language and others lacking any apparent resemblance.

In line with the accumulating evidence of animal combinatoriality, the objective of this review is to provide an overview of diverse forms of naturally produced vocal combinations found in the communication systems of non-human animals (but see also Zuberbühler (2018) for a synopsis on combinatoriality in primates; as well as ten Cate (2017) and Fitch (2018) for recent reviews on cognitive abilities related to the computation of combinatorial sequences). We aim to illustrate the diverse forms combinatoriality can take in animal vocal systems and the extent to which these might resemble linguistic structures in human language. In doing so we hope to stimulate further research investigating the selective conditions and underlying mechanisms that drive the emergence of generative vocal mechanisms characterising animal vocal systems.

## Animal combinatoriality

Within and across species, the combinatorial forms characterising animal vocal systems involve an interesting degree of structural and semantic complexity (Hurford, 2012a; Marler & Slabbekoorn, 1999). Classically, vocal sequences produced by animals have been categorised as either a form of *phonological syntax* (or *combinatoriality*) if the sequences are composed of so-called meaning*less* elements; or alternatively as a form of *lexical syntax* (or *compositionality*) if a sequence constitutes a combination of, and derives its overall meaning from, individually meaningful signals (Hurford, 2007; Marler, 1977). While this binary discrimination initially has proven useful in defining crude similarities and differences among animal and human communication systems (Collier, Bickel, van Schaik, Manser, & Townsend, 2014; Hurford, 2007; Marler, 1977), recent research indicates that many animal vocal sequences cannot easily be assigned to one or the other layer. Instead, both animals and human combinatorial systems can be decomposed into finer, transitional forms (e.g. affixation) or sometimes even feature both phonological and syntactic aspects (e.g. music) (Rohrmeier, Zuidema, Wiggins, & Scharff, 2015; Townsend, Engesser, Stoll, Zuberbühler, & Bickel, 2018).

In the following sections, we review and categorise current examples of animal vocal combinations, in turn enabling a more precise classification of the existing diversity of animal vocal constructs (see Fig. 1 for graphical illustration). Acoustic segments will be referred to as meaning*less* if they represent distinguishable elements that are not emitted in isolation, and hence are unlikely to transfer functionally relevant information, or meaning*ful* if their production is context-specific and elicit predictable responses in receivers suggesting they serve a distinct function (Marler, 2000).
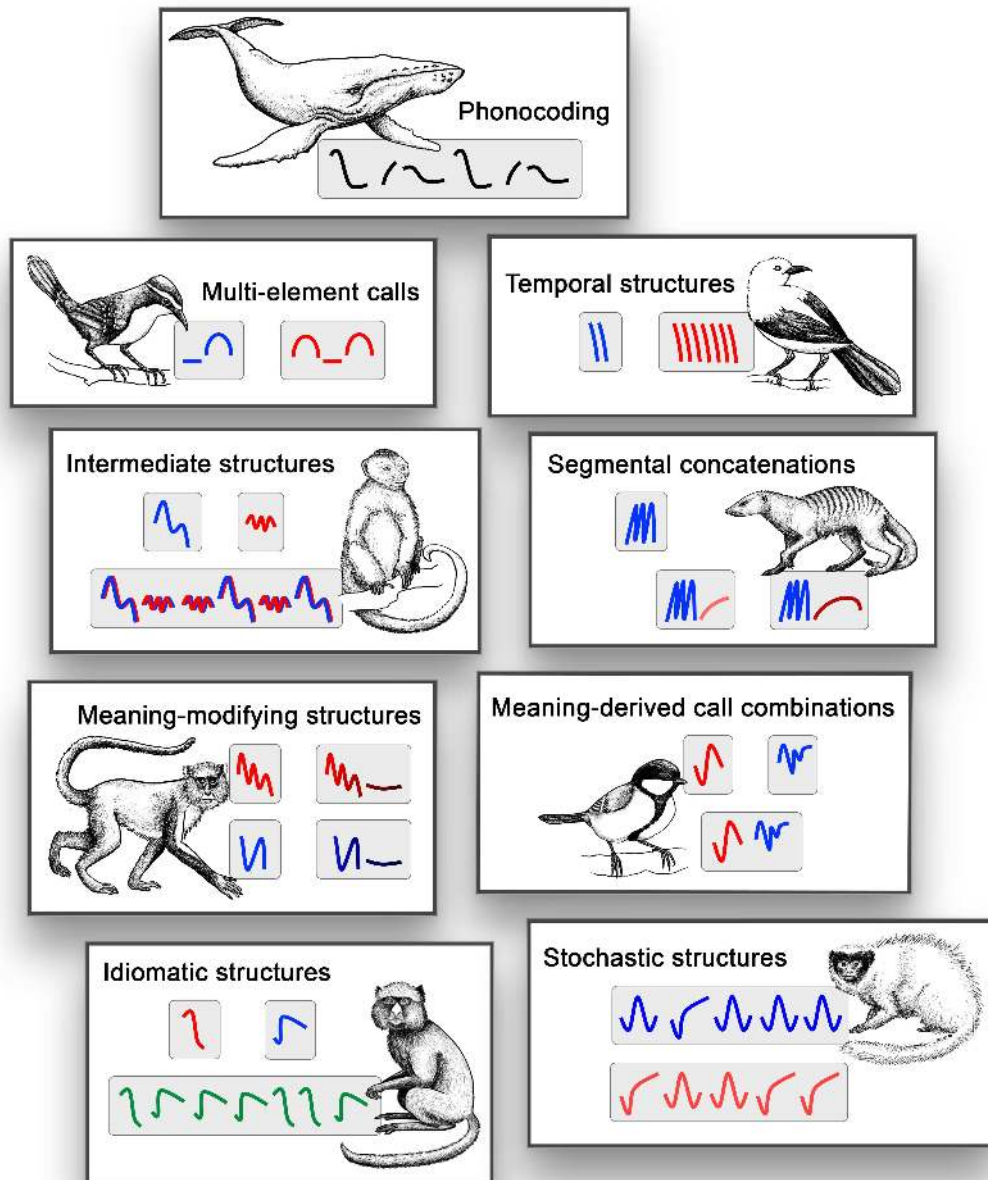
**Fig. 1: Graphical illustration of combinatorial structures in non-human vocal systems.**
Each combinatorial structure shows one representative species. Shapes distinguish sound
elements, colours distinguish meaning (black indicates absence of functional- or context-
specific meaning). **Phonocoding**: combination of meaningless elements into sequence that
lacks functional- or context-specific meaning (e.g. whales, songbirds). **Multi-element calls**:
combination and reuse of meaningless elements to generate context-specific/functionally
meaningful calls (e.g. chestnut-crowned babblers). **Temporal structures**: meaning-
differentiating temporal variation (e.g. number of element repetitions) within a string of
repeated sounds (e.g. pied babblers, Mexican free-tailed bats). **Intermediate structures**:
combination of meaningful calls into sequence reflecting intermediate stages experienced by
the caller (e.g. wedge-capped capuchins, gorillas). **Segmental concatenations**: concatenation
of invariable, stand-alone segment (generally identity-encoding) with variable, bound segment
(generally motivation/behaviour-encoding) (e.g. banded mongooses, Diana monkeys).
**Meaning-modifying structures**: combination of individually meaningful (variable) call with
(invariable) meaning-modifying affix (e.g. Campbell's monkeys). **Meaning-derived call
combinations**: combination of meaningful calls into sequence with derived meaning (e.g.
Japanese tits, pied babblers). **Idiomatic structures**: combination of meaningful calls into
sequence with unrelated meaning (e.g. putty-nosed monkeys). **Stochastic structures**:
sequence whose meaning is encoded by proportional sound/call contribution at particular
parts of the sequence (e.g. black-fronted titi monkeys). Animal drawings by Zinaida
Bogdanova.

*Phonocoding (meaning-devoid sound combinations)*

A wide range of animals, including songbirds, bats, gibbons, hyraxes and whales, combine meaningless sound elements into higher-order, often hierarchically structured, sequences or songs (Bohn, Smarsh, & Smotherman, 2013; Catchpole & Slater, 1995; Geissmann, 2002; Kershenbaum, Ilany, Blaustein, & Geffen, 2012; Payne & McVay, 1971). Such combinatorial sequences predominantly function in territorial or courtship display (Catchpole & Slater, 1995; Marler & Slabbekoorn, 1999; Mitani & Marler, 1989), to facilitate recognition between individuals or groups (Antunes et al., 2011; Briefer, Rybak, & Aubin, 2013; Holland, Dabelsteen, & Paris, 2000; Nousek, Slater, Wang, & Miller, 2006; Schulz, Whitehead, Gero, & Rendell, 2011), or to strengthen the bonding among partners or groups (Janik & Slater, 1997; King & Janik, 2013). Although, songs have traditionally been defined as phonological syntax (Marler, 1977), a more detailed analysis would suggest they neither qualify as phonology nor as syntax. Firstly, albeit composed of meaningless elements, songs lack a functionally- or context-specific meaning (i.e. songs lack propositional semantics), but instead serve to more broadly signal caller attributes (independent of context and content), hence contrasting with human phonology (Berwick et al., 2011; Rendall, 2013). Secondly, although on the surface level, a song's internal structuring (notes being arranged into syllables, motifs, phrases etc.) resembles language's syntactic architecture, songs lack the combinatorial semantics of language's syntactic layer with the precise arrangement of sounds being irrelevant for a song's informational content (Rendall, 2013; Rohrmeier et al., 2015). Nevertheless, intriguing parallels can be drawn between animal songs and human music, both being rich in structural complexity, yet, with combinatorial variation being unimportant for meaning-differentiation (Bowling & Fitch, 2015; Rohrmeier et al., 2015). As such, animal songs are suggested to offer a model system to study the evolutionary origins of human music and its structural complexity, as well as music's developmental and neural basis (Berwick et al., 2011; Rohrmeier et al., 2015).


*Multi-element calls (meaningful sound combinations)*

In contrast to the meaning-*devoid* sound combinations characterising songs, some species have been described to also combine meaningless sound elements to generate *functionally relevant* vocalisations. Among the best known; chickadees, tits and titmice (Paridae family) produce multi-element "chick-a-dee" or "chicka" calls, with supposedly meaningless elements being arranged in a stereotyped order, and with omissions or duplications of individual sounds generating dozens of call variants (Ficken, Hailman, & Hailman, 1994; Hailman, 1989; Hailman, Ficken, & Ficken, 1985; Suzuki, 2013). Although there seems to be a degree of context specificity with some call variants being more likely produced during certain behaviours, potentially linked to locomotion and movement (Ficken et al., 1994; Hailman & Ficken, 1986; Hailman et al., 1985; Suzuki, 2013) or eliciting different responses in receivers (Clucas, Freeberg, & Lucas, 2004; Freeberg & Lucas, 2002), the extent to which the variants encode qualitatively different information remains to be tested (Ficken et al., 1994; Freeberg & Lucas, 2012; Hailman et al., 1985). Outside the Paridae family, chestnut-crowned babblers (*Pomatostomus ruficeps*) produce a pair of functionally distinct vocalisations composed of two meaningless sounds: AB-flight calls that function to coordinate group movement, and BAB-prompt/provisioning calls that serve to stimulate nestling begging. Specifically, both calls are composed of two perceptibly distinct, meaningless sounds (A and B), with the meaning-differentiation among the two calls being the result of a modification at one position of the calls (i.e. ~~B~~AB) (Engesser, Crane, Savage, Russell, & Townsend, 2015). While this bears analogies with the phonemic-structuring of

words in human language (smallest contrasting elements distinguish semantic meaning; Yip (2006)), of perhaps greater relevance for studies on the combinatorial power in animal communication systems is the shared use of meaningless elements to generate qualitatively distinct signals. Future work should address whether the meaningful vocalisations of other species can be similarly decomposed into smaller, shared elements. It is worth noting that, although vocalisations composed of acoustically isolated elements offer an easy tractable system, calls composed of uninterrupted, meaningless acoustic streams deserve equal consideration.

*Temporal structures*

Besides the combination of *different* sounds, animals further encode information by varying the temporal arrangement of the *same* repeated sound element within a sequence. The most commonly described functions of such temporal modifications is to transfer information on an individual's arousal level experienced during aggressive or predatory encounters (Blumstein, 2007; Courter & Ritchison, 2010; DuBois, Nowicki, & Searcy, 2009; Lemasson, Ouattara, Bouchet, & Zuberbühler, 2010; Mahurin & Freeberg, 2008; Manser, 2001; Rek & Osiejuk, 2012; Sieving, Hetrick, & Avery, 2010; Templeton, Greene, & Davis, 2005; Wheatcroft, 2015). Therefore, information is generally encoded through gradual changes in the number or the rate of repeated elements or changes in the inter-element intervals (Blumstein, 2007; Courter & Ritchison, 2010; DuBois et al., 2009; Lemasson et al., 2010; Mahurin & Freeberg, 2008; Manser, 2001; Rek & Osiejuk, 2012; Sieving et al., 2010; Templeton et al., 2005; Wheatcroft, 2015). Recent work has also demonstrated that temporal changes cannot only encode *quantitative changes* in arousal, but also more qualitative information. For example, work on the alarm call system of colobus monkeys (*Colobus guereza* & *C. polykomos*), as well as on the social calls of Mexican free-tailed bats (*Tadarida brasiliensis*) and pied babblers (*Turdoides bicolor*) has shown temporal structures can further encode *categorical information* (Bohn, Schmidt-French, Ma, & Pollak, 2008; Engesser, Ridley, & Townsend, 2017; Schel, Candiotti, & Zuberbühler, 2010; Schel, Tranquilli, & Zuberbühler, 2009). Colobus monkeys cluster repeated "roar"-sounds into bouts of different lengths, with bouts then being emitted at different time intervals. Long bouts emitted at larger time intervals are indicative of eagle presence, while short bouts - each introduced by another "snort"-sound - emitted at shorter time intervals are associated with leopard presence (Schel et al., 2010; Schel et al., 2009). However, since the "snort"-element may equally serve in distinguishing the alarm sequences it is unclear to what extent the temporal arrangement is relevant for differentiating the structures' meaning. Mexican free-tailed bats and pied babblers, on the other hand, produce two qualitatively different vocalisations which are solely discriminated based on the number of element repetitions composing each call. Specifically, Mexican free-tailed bats emit *mono*-syllabic "click"-calls when investigating novel stimuli, and *multi*-syllabic "click"-calls when interacting with conspecifics, with the two call variants potentially serving different functions (Bohn et al., 2008). Similarly, pied babblers produce "cluck"-calls composed of 2-3 repetitions of a short broadband sound, and "purr"-calls composed of 17±10 repetitions of the same sounds. While "clucks" appear to induce a collective group movement based on a decision-making process, "purrs" serve to attract offspring to food sources (Engesser et al., 2017; Radford & Ridley, 2006). Overall, given modifications of a call's temporal characteristics are assumed to be less constrained than changes of frequency-related features (Janik & Slater, 1997), it is surprising that temporal modifications encoding discrete, categorical information have so far only been demonstrated in few species. One reason may be because such structures do not resemble language's combinatorial layers, and thus temporal aspects have generally been neglected. Nevertheless,

we propose that their simplicity might actually make it a valuable and widespread mechanism applied by animals to encode diverse information.

### Intermediate/readout call structures

Potentially more widespread, but so far also described in only a handful of species including wedge-capped capuchins (*Cebus olivaceus*), mountain and western gorillas (*Gorilla beringei beringei*, *G. gorilla*), and potentially chimpanzees (*Pan schweinfurthii*) and meerkats (*Suricata Suricatta*), are combinations of calls that might be interpreted as "online readouts" of the caller's current motivational state (Collier, Townsend, & Manser, 2017; Crockford & Boesch, 2005; Fedurek, Zuberbühler, & Dahl, 2016; Hedwig, Mundry, Robbins, & Boesch, 2014; Robinson, 1984; Zuberbühler, 2018). While, in these instances individual call types can be associated with certain motivational states, combinations appear to reflect intermediate or conflicting interests experienced by the caller during production (e.g. submission vs. aggression) (Cheney & Seyfarth, 1990). Although this does not require signallers to deliberately produce combined structures for informational purposes, receivers may still be able to relate the call's individual messages and to retrieve potentially relevant information on the conflicting circumstances the caller faces.

### Segmental concatenations

A few mammalian species concatenate acoustic segments in a seemingly systematic way. For example, Diana monkeys (*Cercopithecus diana*), Campbell's monkeys (*Cercopithecus campbelli campbelli*), banded mongooses (*Mungos mungo*) and dingoes (*Canis lupus dingo*) produce identity-encoding segments which can be given in isolation or concatenated with other distinct or graded elements that correlate with the animal's motivational/emotional state (e.g. socio-positive/negative context) or its behaviour (e.g. foraging – moving - running) (Candiotti, Zuberbühler, & Lemasson, 2012; Coye, Ouattara, Arlet, Lemmasson, & Zuberbühler, 2018; Coye, Zuberbühler, & Lemasson, 2016; Deaux, Allen, Clarke, & Charrier, 2016; Jansen, Cant, & Manser, 2012). From a linguistic perspective, such segments may resemble morphemes (smallest meaningful units), with the individually distinct elements representing free morphemes that can be produced as a standalone segment, or be conjoined with the behaviour- or motivation-coding (bound) segment (Collier et al., 2014).

### Meaning-modifying segmental structures (affixation)

Other than the combination of identity- and context-encoding segments, contextually meaningful vocalisations can also be concatenated with meaning-*modifying* acoustic segments (or affixes). Both pied babblers and Campbell's monkeys affix individually meaningful signals with acoustic segments. Although these acoustic segments are never produced in isolation (i.e. are *individually* meaningless), once combined they modify the signal's meaning in a quantitative way and have therefore been argued to carry more of an abstract (intensity-modifying) meaning (Engesser, Ridley, Manser, Manser, & Townsend, 2018; Ouattara, Lemasson, & Zuberbühler, 2009b). More precisely, pied babblers produce two variants of a longer sequence that is either composed of repetitions of "A"- or "AB"-note elements. While the single-note structure functions to induce a recruitment of receivers over a short distance to the callers broadcast location, the recruitment-request is intensified through the suffixation of A-notes with B-notes, with the double-note structures inducing a follow of the caller over longer distances (Engesser et al., 2018). However, unlike in human language

where affixes modify a signal's meaning in a *predictable* way, the unproductive use of the modifying segment in pied babblers (B is only ever produced in combination with A, but no other sound), renders interpretations regarding its semantic content problematic. In contrast, Campbell's monkeys appear to productively combine a meaning-modifying "-oo" segment with *two* predator specific alarm calls. While in isolation the calls encode leopard or eagle presence, their affixed variants encode general disturbances or unspecific aerial threats respectively (Coye, Ouattara, Zuberbühler, & Lemasson, 2015; Ouattara et al., 2009b). Accordingly, the "-oo" affix appears to modify the predator-specific alarm calls' meaning in a systematic way (i.e. the affix's productive use facilitates predictability), by broadening the calls' meaning (Schlenker et al., 2014; Schlenker, Chemla, & Zuberbühler, 2016). The Campbell's monkey structure therefore qualifies as a form of basic compositionality, with the modifying segment carrying an abstract meaning, and the combined structure's meaning reflecting the meaning of its individual parts (Collier et al., 2014; Townsend et al., 2018).

### Meaning-derived call combinations (semantic compositionality)

Cases where animals combine *stand-alone* meaningful vocalisations into a higher-order structure, whose overall meaning reflects the meaning of its individual parts, are currently only found in birds: specifically, Japanese tits (*Parus minor*) and pied babblers. Both produce alert and recruitment calls, which are combined when mobbing predators (Engesser, Ridley, & Townsend, 2016; Suzuki, Wheatcroft, & Griesser, 2016). In Japanese tits, alert calls elicit vigilance- and recruitment calls approach-behaviour in conspecifics, with the combination eliciting a mixture of both behaviours (Suzuki et al., 2016). Similarly, pied babblers give alert calls to low-urgency threats, and recruitment calls when recruiting group members during collective group travels. Both calls are combined when recruiting group members to mob a terrestrial predator (Engesser et al., 2016). Critically, in both cases the meaning of the combination can be deduced from the meanings of its (individual meaningful) parts, therefore presenting a rudimentary, two-call, compositional structure (Townsend et al., 2018).

### Idiomatic structures (semantic combinatoriality)

Some monkeys further assemble discrete acoustic units into larger sequences to encode information that appear to be unrelated to the components' meaning. A textbook example is putty-nosed monkeys (*Cercopithecus nictitans*), which combine two meaningful alarm calls associated with eagle presences and general disturbances, respectively, into longer sequences that elicit group movement in non-predatory contexts (Arnold & Zuberbühler, 2006, 2008, 2012). Notably, the resultant structure does not appear to be produced and processed in a compositional way, since the meaning of the whole cannot be derived from its compounds. As such the sequence is suggested to constitute a semantically *combinatorial* or *idiomatic* structure (Arnold & Zuberbühler, 2012; Hurford, 2007, 2012a).

### Stochastic/proportional structures

Lastly, black-fronted titi monkeys (*Callicebus nigrifrons*) produce sequences composed of two main sound types, with resultant sequences conveying information about the type (raptor vs. carnivore) and location (canopy vs. ground) of a predator (Cäsar, Byrne, Young, & Zuberbühler, 2012; Casär, Zuberbühler, Young, & Byrne, 2013). One analysis is that each of the two sounds might potentially encode a particular meaning, with sequences then representing simple readouts of the current environmental circumstances experienced by a

signaller (c.f. *intermediate/readout call sequences*) (Schlenker, Chemla, Cäsar, Ryder, & Zuberbühler, 2016). Alternatively, the overall meaning of a sequence might be derived from the proportional contribution of the individual sounds at particular parts of the sequence (Zuberbühler, 2018). Accordingly, the individual components might lack meaning, but once combined in a rule-governed (i.e. proportional) way, generate meaning (Cäsar et al., 2012; Casär et al., 2013). Similar mechanisms might underlie bonobo (*Pan paniscus*) food call sequences, with sequences potentially encoding the type and quality of food items (Clay & Zuberbühler, 2009, 2011). Though, in both cases, further work needs to investigate whether stable proportions of call contributions can predict context and vice versa.

More ambiguous and less clearly definable vocal sequences that neither seem to fall in line with a compositional, idiomatic or proportional analysis are produced by gibbons and Campbell's monkeys. For example, white-handed gibbons (*Hylobates lar*) build structurally distinct sequences specific to social and predatory context from the same acoustic units (Clarke, Reichard, & Zuberbühler, 2006). However, whether the individual units encode meaning, and exactly how the information is derived from the sequences' (potentially "stochastic"; Zuberbühler (2018)) overall structure remains unclear. Campbell's monkeys, on the other hand, generate sequences from recombinations of individually meaningful calls and acoustic segments that are only found as part of the larger sequences (Ouattara, Lemasson, & Zuberbühler, 2009a). While the sequences are produced in various contexts, information appears to be encoded through the transition probabilities between, and co-occurrences among, the constituent, permutated parts (Zuberbühler, 2018) (see also  Schlenker et al. (2014) for a formal semantic analyses of Campbell's monkey vocal sequences and alternative interpretations).

## Conclusion

A major question in the field of language evolution is the origin of language's generative nature. Tracing its origin, however, poses major difficulties due language's cumulative evolution not leaving any fossil traces (Hauser et al., 2002; Lieberman, 1984). The comparative approach therefore constitutes a promising method to circumvent this problem (Hauser et al., 2002) and accordingly, much effort has been put into investigating combinatorial capacities in primates (Zuberbühler, 2018). Although studies on our closest living relatives can provide insight into the phylogenetic origins of linguistic traits, they are less useful for informing what factors may have promoted the emergence of our generative capacity (since features could be either homologue/derived or analogue/independently evolved traits). Expanding the comparative approach to include more distantly related species (e.g. birds and non-primate mammals) can help to investigate and identify convergent evolutionary mechanisms, and hence selective conditions, that drive the emergence of combinatorial abilities.

Here, we provided an overview of the current evidence of combinatorial structures in non-human animals and show that sound and call combinations can be found across diverse (avian and mammalian) species. Given the structural diversity combinatoriality can take, we propose that a crude division of vocal structures into combinatoriality/phonology versus compositionality/syntax might be an over-simplification trivialising the intriguing complexity of animal vocal structures (c.f. Zuberbühler (2018)). Ultimately, distinctions and subsequent comparisons of combinatorial mechanisms appear to be central to resolving outstanding

questions including i) whether we can reveal universal principles that generally drive combinatoriality, and ii) whether different combinatorial mechanisms might be the result of variations in social and ecological conditions or cognitive capacities.

To conclude, there exists a considerable diversity in the types of combinatorial structures produced by non-human animals. Such a patchwork of different combinatorial strategies across the animal kingdom implies that different combinatorial mechanisms can emerge independently. From a language evolution perspective, such a finding might suggest language's generative system also represents an assemblage of individually evolved traits (Townsend et al., 2018), rather than a "package" evolved in a sudden evolutionary transition with no similarities in other species (Bolhuis, Tattersall, Chomsky, & Berwick, 2014). Accordingly, with more data on animal combinatoriality (including insights on their distribution, diversity, and the underlying computational processes) a systematic comparative approach may eventually generate intriguing insights into the evolution of communication systems, and ultimately the emergence of language's generative system.

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