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Combinatorial capacities in primates

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ABSTRACT

Do primates have syntax-like abilities? One line of enquiry is to test how subjects respond to different types of artificial grammars. Results have revealed neural structures responsible for processing combinatorial content, shared between non-human primates and humans. Another approach has been to study natural communication, which has revealed a wealth of organisational principles, including merged compounds and sequences with stochastic, permuted, hierarchical and cross-modal combinatorial utterances. There is solid experimental evidence that recipients can attend to such combinatorial features to extract meaning. The debate is whether animal communication can also be compositional, insofar as whether signallers assemble meaningful units to create more complex utterances with novel meanings.

22 INTRODUCTION

23 Syntax is one defining feature of human language and part of our uniqueness, which
24 raises questions about its nature and evolution [1] [2]. In one view, syntax refers to the
25 ability "...to make infinite use of finite means" [3], a pragmatic approach by which
26 linguistic conventions function to achieve social goals [4]. In another view, syntax is
27 the ability to organise and represent mental content in a hierarchical, recursive way, a
28 computational system that generates internal representations [5]. Syntax is also about
29 recognition, which enables humans to discriminate legal from ill-formed sentences not
30 conforming to linguistic conventions and to apply them to form novel, legal utterances
31 [6].

32 The ontogeny of syntactic skills in humans is still debated, in part because it is difficult
33 to understand the underlying cognitive operations and to determine whether they are
34 language specific (see Mueller et al.; Gervain, this volume). An early view has been
35 that human infants possess an innate, universal grammar module that drives language
36 acquisition [7]. In a recent embodiment, this module is a single powerful operation,
37 'merge', which combines lexical/conceptual objects into unordered sets [8]. When
38 infants acquire language they use this innate operation, merely adjusting the
39 parameters to their respective language based on the input they receive. Alternative
40 models propose that grammatical competence cannot be reduced to one core operation,
41 but is acquired gradually, in conjunction with an asymptotically growing reference
42 library of speech utterances, accessed by both general-purpose and language-specific
43 rule-based systems that recognise legal combinatorial structures [9] [10]. With this,
44 language learners can go beyond the utterances they have heard and create unbounded
45 linguistic schemas [6] (p. 70). The debate thus amounts to whether syntactic

46 competence is acquired by manipulations of symbols or by general purpose, including
47 statistical learning not specific to language, but closely dependent on cognition and
48 memory for acoustic or other forms of input.

49 The purpose of this position piece is to provide an update on the combinatorial
50 competence of non-human primates. How extensive are combinatorial and
51 compositional phenomena in non-human primate communication and what is their
52 importance for understanding the evolution of syntax, a core intellectual capacity of
53 humans?

54

55 Recently, there has been resurgence of scepticism about the relevance of animal
56 communication studies for understanding language evolution, and especially syntax
57 [11], but this is mainly based on the controversial assumption that the only relevant
58 feature of syntax is generativity. An alternative hypothesis suggests that everyday
59 language use is not very generative at all, but based on accessing prefabricated phrases
60 from a vast stock. Although such utterances may be described in terms of their
61 syntactic structure, language users do not normally generate any of them, but deploy
62 them ‘wholesale’ in adequate situations. If this view is correct, then evolutionary
63 investigations of syntax should primarily focus on non-generative, combinatorial
64 systems, as frequently seen in animal communication.

65

66

67 **ARTIFICIAL GRAMMARS**

68

69 One way to study the nature and evolution of syntax is to investigate how subjects
70 learn and interact with artificial grammars [12]. The basic idea is to expose subjects to

71 a training phase during which stimulus sequences are presented, but without explicitly
72 highlighting the underlying organisational structure. Subjects are then exposed to a test
73 phase, during which they can apply any acquired ‘rule-based knowledge’ of the
74 structure to unfamiliar sequences. The technique has been used to investigate cognitive
75 capacities within and across species, and in humans it can be used to understand what
76 parts of the brain circuitry are involved in (artificial) grammar processing [13]. For
77 instance, rats that have learned simple order rules, such as XYX, XXY, or YXX, can
78 determine whether or not novel stimulus sequences comply to these patterns [14].
79 Various primate studies have used other paradigms, showing, for example, that
80 monkeys can learn to use patterns akin to morphological markers (e.g., English past
81 tense), indicating that the required perceptual and memory capacities have evolved
82 prior to language [15].

83

84 One particularly influential line of research has been to devise artificial grammars
85 along the ‘Chomsky hierarchy’ with increasing grammatical complexity [16]. Here,
86 monkeys have managed to learn regularities across adjacent and non-adjacent units
87 from finite-state grammars but failed to extract patterns at higher ‘phrase structure’ or
88 ‘context-free’ grammars [17] [18]. However, an exclusive focus on primates for
89 evolutionary arguments can be dangerous, as demonstrated by a study with European
90 starlings that recognise patterns more complex than the ones with only adjacent
91 relationships (which tamarin monkeys can learn [19], [20]). Also, research with mixed
92 complexity artificial grammars has compared humans and monkeys to find that many
93 humans also struggle with non-adjacent relationships when adjacent relationships are
94 more salient [21].

95

96 Artificial grammar paradigms have been very effective in highlighting the brain
97 circuitry involved in processing sequences with different forms of dependencies. For
98 instance, EEG event-related potentials have been compared between macaques and
99 human infants and adults when responding to violations in artificial grammar
100 sequences [22] [23]. Furthermore, functional imaging has identified counterparts in
101 human and macaque brains for processing adjacent sequencing dependencies [24], an
102 initial stage of syntactic processing in some neurobiological models of language [25]
103 [26]. These studies have generally supported the notion of evolutionary continuity at
104 certain levels in combinatorial capabilities and of brain structures that support
105 cognitive domain-general processes not specific for language [27].

106 The weakness of artificial grammar studies is that they are typically based on stimuli
107 with no ecological or social relevance. Subjects are tested with simple sound
108 sequences, which require auditory pattern recognition but are devoid of meaning.
109 Although some linguistic theories stress that syntax should be investigated as divorced
110 from semantics [5], this is unlikely the case during natural acts of communication [28].
111 For evolutionary considerations, it is equally important to understand signal
112 combinations and compositions during natural social interactions.

113

114

115 **NATURAL GRAMMARS**

116

117 **Duality of patterning**

118

119 In human language, generativity is often highlighted as the pivotal feature, which is
120 visible at two different levels. First, all languages build on repertoires of (meaningless)

121 phonemes (expressed to different degrees across languages) by which meaningful
122 *combinations*, i.e., morphemes or words, are generated in compliance with language-
123 specific combinatorial rules. Second, these phoneme combinations are then further
124 assembled into higher-order *compositions*, i.e., phrases or sentences. For
125 compositionality, a key point is that the meaning of a composition can be
126 systematically derived from its parts *and* the rules that combine them [29] (see Fitch,
127 this volume). Although the ‘duality of patterning’ (or ‘double articulation’)
128 interpretation of language has been a very useful heuristic, it is also a gross
129 simplification of reality because of the deep, hierarchically layered relationships in
130 sentences [30] [7] and, crucially, of questionable use for evolutionary studies of animal
131 signals. For example, linguists have long realised that phonemes are abstract constructs
132 that are difficult to ground in the acoustic reality of speech, and that they sometimes
133 carry natural meaning by being linked to mental concepts [31]. Moreover, there are
134 countless examples of linguistic structures at intermediate stages [32], such as patterns
135 in emerging sign languages, idioms, some affixes, which further undermines the notion
136 of duality.

137

138 **Combinatoriality**

139 *Merged compounds*

140

141 One of the first systematic studies on primate ‘syntax’ was on wedge-capped capuchins,
142 reported to merge four different call types into larger compounds [33]. No systematic
143 analysis of function has been made so the current interpretation is that compounds are

144 'online' readouts of conflicting motivations. Similar reports exist on gorilla close calls,
145 which can be given singly or as non-random compounds [34, 35].

146

147 Chimpanzees pant hoot calls may also qualify as compound calls, consisting of four
148 units; introduction, build-up, climax and let-down, always produced in this order (fig.
149 1). Although not yet studied systematically, the calls given as part of the four units
150 almost certainly contribute to other constructions in chimpanzee vocal behaviour or are
151 produced as standalone signals (P Fedurek, personal communication). In a study using
152 machine learning, it was demonstrated that the four units convey information on caller
153 identity, rank and age, and on the external event [36]. The different call types within
154 the four units can be repeated multiple times, but it is currently unknown whether this
155 has communicative function. Juveniles and females also give pant hoots, but they
156 sometimes omit units, as do adult males when they join others for a pant hoot chorus
157 [37]. There are trade-offs within units and within the compound, in compliance with
158 Menzerath's law (the observation that as the size of linguistic constructs increases,
159 constituent size goes down, and vice versa [38]). Interestingly, the same phenomenon
160 has also been observed in vocal sequences of Gelada baboons [39], suggesting that
161 combinatoriality may further function as honest signals of physical condition.

162

163 -- Figure 1 --

164

165 Another well-studied combinatorial system is female Diana monkey contact calls. Here,
166 four vocal structures ('H', 'L', 'R', 'A' calls) can be given alone or as part of orderly
167 combinations ('HA', 'LA', 'RA'). 'A' calls function to signal identity; 'H', 'L', and 'R'
168 calls refer to on-going events [40]. In playback experiments, R and L 'event' calls were

169 artificially merged with A 'identity' calls, to which subjects responded as if both event
170 and identity information were relevant [41].

171

172 *Stochastic sequences*

173

174 Animal songs, such as in passerine birds [42], humpback whales [43] or gibbons [44],
175 have been primary targets of sequence analyses. Singing is typically a male behaviour
176 for reproduction although, in monogamous species, singing can also be as duets and
177 functions in intergroup competition [45]. Although songs are often complex, they are
178 thought to be semantically vacuous and do not seem to advertise much beyond a
179 caller's location, identity and vigour, such as to intimidate rivals or to attract partners.
180 However, sometimes song is produced to predators, such as in lar gibbons. Here,
181 predator-induced songs consist of the same units as regular duet songs, although they
182 are assembled in different ways [46].

183

184 Other examples of stochastic sequences are from chimpanzees, where about half of all
185 calls occur in combination with other calls, but also with drumming and gestures, often
186 in context-specific ways [47] [48]. Similar findings have been reported in bonobos,
187 with call combinations relating to caller movement [49] and different types of foods
188 [50].

189

190 *Permutated sequences*

191

192 In some instances, call sequences show strong order effects, in which case they qualify
193 as permutations. Putty-nosed monkey sequences are one example (see before), but

194 similar patterns have also been reported in male Campbell's monkeys, who combined
195 alarm calls into various sequences to refer to different events, such as travel, falling
196 trees, neighbouring groups, non-predatory animals, unspecific predatory threats,
197 crowned eagles and leopards [51] (fig. 2). Sequence composition follows a number of
198 rules, such as non-random transition probabilities, adding calls to existing sequences to
199 form novel ones, or combining two sequences to form a third one [51]. Playback
200 experiments have shown, for some of sequences, that they are communicatively
201 relevant [52].

202

203 -- Figure 2 ---

204

205 Amongst the New World primates, black-fronted titi monkeys have been studied well.
206 Here, both males and females produce sequences consisting of two main alarm call
207 types (A, B) that convey, in different parts of the utterance, information about predator
208 type (mammal, raptor) and location (ground, tree) [53]. B-calls appear as context-
209 specific acoustic variants (terrestrial predators vs. ground-related movements) with call
210 sequences to predators showing more regular sequential structure than ground-related
211 sequences [54]. The permutation hypothesis appears to be facing a challenge by recent
212 field work suggesting that predator type and location are encoded stochastically by
213 proportional differences in call combinations [54].

214

215 *Hierarchical sequences*

216

217 Another salient feature of signal sequences is the delivery rate (e.g., inter-call intervals,
218 call rates), and this can generate hierarchical structures. Differences in call rates have

219 been shown to refer to perceived urgency, as in male blue monkeys responding to
220 differences in threat posed by aerial predators [55] or male Campbell's monkeys
221 responding to predator vs. non-predator disturbances [56]. In some instances, signal
222 emission is clumped into bouts, which adds another perceptual dimension (fig. 3).
223 Diana monkeys, King Colobus and Guereza monkeys all use this feature to refer to
224 external events, with leopards triggering short bouts with small numbers of calls, and
225 eagles triggering long bouts with large numbers of calls [57-59], differences that are
226 recognised by recipients [60, 61].

227

228 -- *Figure 3* ---

229 *Cross-modal sequences*

230 A number of studies have looked at cross-modal sequences, mainly call-gesture
231 combinations in apes. In chimpanzees, such combinations are relatively rare and
232 mainly occur during affiliative and agonistic interactions [48]. In bonobos they also
233 occur and one finding has been that gestures can function as semantic modulators of
234 vocalisations [62], revealing the social goal of an individual. In a related study,
235 bonobos were observed to use different signal combinations to clarify their sexual
236 intentions. For example, females used 'screams' and 'hand reach' most frequently
237 when using sex in appeasement functions, but 'pout moans' when using sex for social
238 bonding [63].

239 Another series of studies has shown that differences in signal combinations can reveal
240 something about the common ground between signallers and recipients. For example,
241 if orang-utans were made to believe that a human partner providing food did not
242 understand their requests, they adjusted gesture combinations accordingly [64].

243 Bonobos exposed to the same problem were more likely to repeat gestures if they
244 interacted with a familiar keeper but elaborated their gestures when interacting with an
245 unfamiliar one, as if taking into account differences in the shared interaction histories
246 [65].

247 **Compositionality**

248 Despite its weaknesses, ‘duality of patterning’ has been applied to animal
249 communication, with the conclusion that signal combinations are common but signal
250 compositions absent (e.g., [66]). A possible exception is the vocal system of pied
251 babblers, a social passerine that combines alert and recruitment calls into sequences
252 when encountering terrestrial predators. Recipients respond differently to sequences
253 than to component calls (presumed to have distinct meanings) and it has been argued,
254 controversially, that this qualifies as compositionality [67]. But for a sequence to be
255 (non-trivially) compositional, its meaning must be derived, in some way, from the
256 meaning of the two components *and* the two components cannot be interpreted
257 separately within the sequence [68]. In a related study on Japanese tits, this problem
258 has been addressed by using compositions of artificially inverted call sequences [69],
259 but this raises other issues relating to birds reacting to novelty and non-natural stimuli,
260 requiring further work (see Griesser et al., this volume).

261

262 The distinction between limited (trivial) and genuine (non-trivial) compositionality is
263 not straightforward. In English, the sentence “It’s humid” qualifies as trivial
264 compositionality because there is no need for a semantic operation: ‘It’s’ and ‘humid’
265 are separate utterances in the sentence. In contrast, the sentence “It’s very humid”
266 qualifies as genuine compositionality because it is not possible to analyse this as two

267 separate utterances. Instead, the meaning of ‘very humid’ is derived from the meanings
268 of ‘very’ and ‘humid’ (P Schlenker, personal communication).

269

270 A relevant example in primate communication is male putty-nosed monkeys
271 assembling two basic call types (pyows, hacks) into sequences with different meanings
272 [70]. Series of hacks indicate eagle presence, series of pyows are general alarms
273 (including leopard presence), while pyow-hack permutations (small numbers of pyows
274 followed by small numbers of hacks), given on their own or in combination with hack
275 or pyow series, predict forth-coming group travel [71]. Importantly, recipients
276 understand the differences in meaning of different combinations, as judged by their
277 behavioural reactions [72]. Strictly, the system does not qualify as compositional
278 because it is difficult to assign discrete meanings to individual pyows and hacks, and
279 because the meaning of pyow-hack combinations appears to be completely unrelated to
280 pyows and hacks, more akin to an idiom [66]. However, Schlenker et al. [73] have
281 proposed a (limited) compositional explanation by assuming that calls possess weak
282 meanings (pyow: general alarm; hack: non-ground movement, including by eagles) and
283 that call order obeys an urgency principle, such that calls referring to dangers come
284 first. Since pyows come before hacks, hacks cannot refer to eagle but to (less urgent)
285 non-ground movement. This, in turn, enables listeners to make pragmatic inferences,
286 i.e., that the caller has raised a general alarm and initiates non-ground movement.

287

288 Possibly a stronger case for compositionality is suffixation in Campbell’s monkey
289 alarm calls. Males give krak calls to leopards and hok calls to eagles, but both calls can
290 be merged with a suffix –oo to either krak-oo (wide range of disturbances) or hok-oo
291 (non-ground alerts). In playback experiments, both natural and artificially suffixed and

292 unsuffixed ‘krak’ calls caused reactions that suggested suffixation was meaningful,
293 which further implies that (limited) compositionality is an evolved function of primate
294 communication [74] (fig. 4). This is because the meanings of krak-oo and hok-oo are
295 plausibly derived from the meanings of krak/hok and the meaning of –oo, but -oo does
296 *not* form a separate utterance (analogous to ‘very’) but functions as an optional affix to
297 alarm calls [68].

298

299 -- Figure 4 --

300

301 **CONCLUSIONS**

302

303 Research on primate cognition has become a major force to enlighten the origins of
304 human uniqueness. The focus of this paper has been on the evolution of syntax, a core
305 capacity of the language faculty. Artificial grammar experiments suggest that primates
306 share certain combinatorial processing capacities with humans and utilise comparable
307 brain circuitry to analyse speech sounds and statistical regularities in artificial stimulus
308 sequences (e.g., Kikuchi et al, this volume). In natural communication, primates
309 produce and understand signal combinations as merged compounds, as well as
310 stochastic, permuted, hierarchical and cross-modal sequences. One outstanding
311 question is whether any of the reported combinations qualify as compositional.

312 Another outstanding question is whether human syntax evolved gradually from animal
313 combinatoriality or whether it appeared as a functional change from non-linguistic
314 operations during the more recent hominid evolution [75] (also see Fitch this volume).

315 If syntactic competence develops from learning and use, rather than from an innate

316 grammar module, then it may be sufficient to explain syntax as a by-product of the
317 massive brain expansion that took place from Homo habilis to early H sapiens over
318 little more than 1 million years, which have led to massively powerful acoustic storage
319 and pattern searching devices.

320

321

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326

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333 Field study on a primate vocal system demonstrating experimentally the presence of
334 meaningful, permutated call sequences with limited compositionality. In particular,
335 free-ranging putty-nosed monkeys combine two vocalisations into different call
336 sequences linked to specific external events, such as the presence of a predator and
337 the imminent movement of the group. These findings indicate that non-human
338 primates can combine calls into higher-order sequences, which has been interpreted
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346 Landmark opinion paper challenging the commonly accepted notion of linguistic
347 universals amongst cognitive scientists. The authors argue that empirical research in
348 language typology has not supported the hypothesis that human languages can be
349 characterised by universal grammar and similar notions. Instead the current picture is
350 one of maximal linguistic diversity, fundamentally variable at all levels of sound,
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352

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359 'context-free') grammars. In particular, monkeys mastered regularities if sound
360 patterns were between neighbouring units but not patterns with more complex
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362

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373

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392 primate and human brains. Key regions in the human ventral frontal and opercular
393 cortex, associated separately with the initial stages of syntactic processes, were found
394 to have functional counterparts in the monkey brain. Results suggest that certain
395 ventral frontal neural systems, originally evolved to support domain-general abilities of
396 sequence processing, underwent a functional change towards syntactic functioning in
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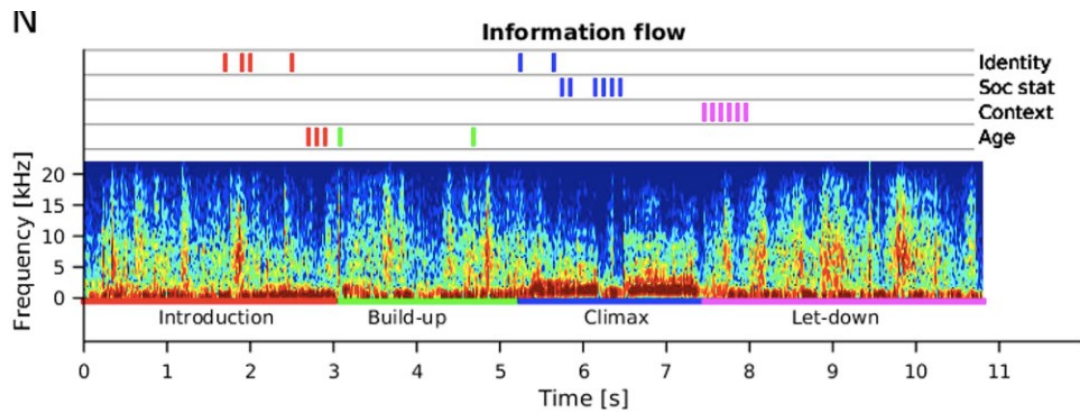
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- 558
- 559

560 *Figures*

561



562

563 Figure 1. Information flow in chimpanzee pant hoots across the four vocal units, each
564 consisting of a variable number of acoustically distinct calls. The x-axis shows the time
565 (s), the y-axis frequency (kHz) (reprinted from [36]). Information flow determines the
566 time point in the sequence that was most associated with a given attribute of the caller.
567 In the introduction phase both ‘identity’ and ‘age’ were associated most strongly with
568 the middle of the phase. In the build-up phase, ‘age’ was apparent most strongly early
569 in the phase, while in the climax phase, ‘identity’ and ‘social status’ were apparent
570 early on. For the let-down phase, ‘context’ was apparent in very early stages.

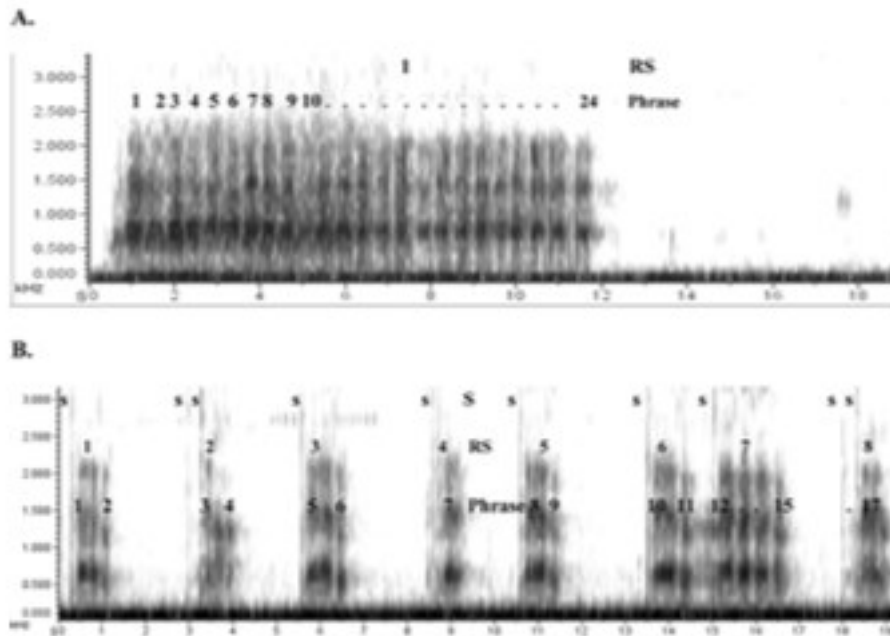
571

| Sequence composition | Context | | | | | | | | | | | N total | | | | |
|----------------------|-------------------|-------------|-------------|---------|-------|-------|-------|---------------|-------|-------|-------|---------|----|---|---|----|
| | Non-predatory | | | Leopard | | | | Crowned eagle | | | | | | | | |
| | Cohesion & Travel | Tree/Branch | Inter-group | Real | Model | Calls | Alarm | Real | Model | Calls | Alarm | | | | | |
| | | | | | | | | | | | | | | | | |
| 1 | B | | | | | | | | | | | | 13 | | | |
| 2 | B | | K+ | | | | | | | | | | 53 | | | |
| 3 | B | | K+ | | H+ | | | | | | | | 76 | | | |
| 4 | | K | | | | | | 3 | 6 | | | | 9 | | | |
| 5 | | K | K+ | | | | | | 4 | 8 | 5 | | 17 | | | |
| 6 | | | K+ | | | | | | | 2 | 11 | | 18 | | | |
| 7 | | | K+ | | | | W+ | | | | | 3 | 2 | 5 | | |
| 8 | | | K+ | H | | | W+ | | | | | 3 | 2 | 5 | | |
| 9 | | | K+ | H | H+ | | W+ | | | | | 11 | 10 | 3 | 4 | 28 |

572

573 Figure 2. Composition of call sequences by male Campbell’s monkeys in different
 574 behavioural contexts. B = non-vocal booms produced by air-sacs, K = krak; K+ = krak-
 575 oo; H = hok; H+ = hok-oo; W+ = wak-oo (see fig. 1). Depicted sequence composition
 576 does not reflect call order, apart from boom calls, which are always given in pairs and
 577 precede other calls; and apart from krak-oo calls, which tend to terminate call
 578 sequences. ‘Alarm’ indicates leopard or eagle alarm calls given by sympatric Diana
 579 monkeys.

580

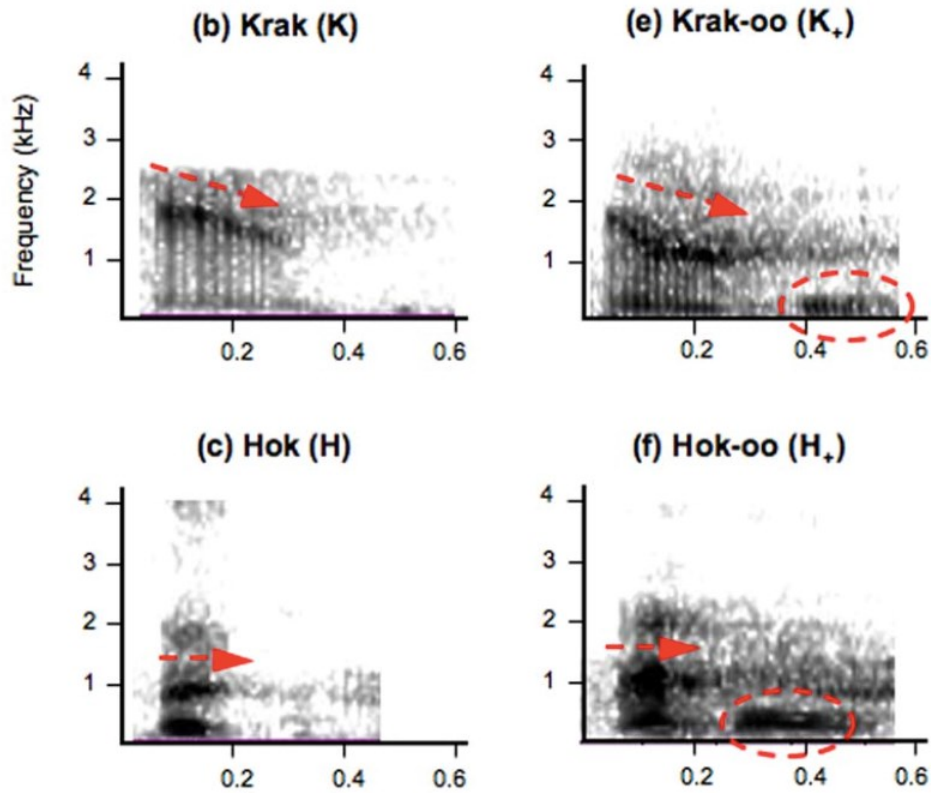


581

582 Figure 3. Spectrographic illustrations of the main structural differences characterising
 583 the vocal responses of King Colobus monkeys to eagles and leopards. A: continuous
 584 recording of an adult male responding to an eagle with a roaring sequence of 24
 585 phrases. B: continuous recording of an adult male responding to a leopard, starting
 586 with 6 snort-introduced two-phrase roaring sequences, followed by a snort-introduced
 587 four-phrase sequence, followed by a single snort and another snort-introduced one-
 588 phrase sequence. The *x*-axis represents time (s), the *y*-axis frequency (kHz). S stands
 589 for snorts, RS for roaring sequence. Reprinted from [59].

590

591



592

593 **Figure 4.** Spectrographic illustrations of the different alarm calls produced by male
 594 Campbell's monkeys. (b) 'krak' call [K], a loud vocal utterance with a decreasing main
 595 frequency band; (c) 'hok' call [H], a loud vocal utterance with no frequency
 596 modulation; (e) 'krak-oo' call [K+], a 'krak' call followed by the 'oo' suffix; (f) 'hok-
 597 oo' [H+], a 'hok' call followed by the 'oo' suffix. Reprinted from [77].

598