

1 **Animal linguistics in the making: The Urgency Principle and titi**
2 **monkeys' alarm system**

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14 HIGHLIGHTS

- 15 • The field of animal linguistics aims to apply methods borrowed from linguistics
16 to animal communication data
- 17 • Some of the theoretical tools need further empirical testing on nonhuman
18 systems to assess their value
- 19 • We provide evidence that one of these tools, the Urgency Principle, is reflected
20 in the organization of the titi monkey' alarm call sequences
- 21 • In titi monkeys' alarm sequences, mechanisms encoding for urgent predator-
22 related information appear before those encoding for social information

23 The emergent field of animal linguistics applies linguistics tools to animal data in
24 order to investigate potential linguistic-like properties of their communication.
25 One of these tools is the ‘Urgency Principle’, a pragmatic principle postulated by
26 Schlenker et al. (2017) stating that in an alarm sequence, calls providing
27 information about the nature or location of a threat must come before those that
28 do not. This theoretical principle has helped understand the alarm system of
29 putty-nosed monkeys, but whether it is relevant for animal communication
30 systems more generally remains to be tested. Moreover, while animal
31 communication systems can convey information via a large set of encoding
32 mechanisms, the Urgency Principle was developed for only one encoding
33 mechanism, call ordering. Here, we propose to extend this principle to other
34 encoding mechanisms and empirically test this with the alarm call system of
35 black-fronted titi monkeys (*Callicebus nigrifrons*). We investigated how
36 information about the context of emission unfolded with the emission of
37 successive calls. Specifically, we analysed how contextual parameters influenced
38 the gradual sequential organization of the first 50 calls in the sequence, using
39 methods borrowed from computational linguistics and random forest algorithms.
40 We hypothesized that, if the extended Urgency Principle reflected the sequential
41 organization of titi monkey alarm call sequences, mechanisms encoding urgent
42 information about the predatory situation should appear before encoding
43 mechanisms that do not. Results supported the hypothesis that mechanisms
44 encoding for urgent information relating to a predator event consistently appeared
45 before mechanisms encoding for less-urgent social information. Our study
46 suggests that the extended Urgency Principle applies more generally to animal
47 communication, demonstrating that conceptual tools from linguistics can
48 successfully be used to study nonhuman communication systems.

49 KEY WORDS: *Callicebus nigrifrons*, vocalisations, sequences, computational
50 linguistics, formal linguistics

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57 INTRODUCTION

58 The investigation of meaning (or ‘semantics’) in nonhuman animal vocalizations
59 has played a central role in the field of animal communication since the foundational
60 work on vervet monkey alarm calls (Seyfarth et al. 1980a, 1980b). The question and
61 debate of what animal calls mean is still ongoing as shown by the recent discussions on
62 the notion of functionally referential communication (e.g., Wheeler & Fischer 2012;
63 Townsend & Manser 2013) or the debates around the specificity of animal calls (Fichtel
64 & Kappeler 2002; Schlenker et al. 2016b; Dezecache & Berthet 2018).

65 Debates surrounding the concept of meaning in animals come from practical and
66 theoretical difficulties encountered when investigating animal semantics. First, methods
67 commonly used in animal communication to reveal linguistic-like capacities in
68 nonhuman animals sometimes fail to reveal these capacities even in humans (Prat
69 2019). Second, some have discussed the use of linguistic terminology (e.g., ‘semantics’)
70 in animal communication (e.g., Seyfarth et al. 2010; Kershenbaum et al. 2014; Scott-
71 Phillips 2015; Fitch 2016), mainly because of conceptual and theoretical disagreements.
72 Third, since some species combine calls into sequences (see review in Zuberbühler &
73 Lemasson 2014) allocating meaning to an utterance becomes even more complicated,
74 due to the fact that researchers must investigate not only the meaning of the individual
75 component parts but also that of the sequences, and identify potential combination rules
76 (e.g., Engesser et al. 2016; Suzuki et al. 2020).

77 One attempt to overcome these difficulties is the emerging field of animal
78 linguistics, which applies methods from linguistics to animal communication. This is
79 based on the vision that an interdisciplinary collaboration between biologists and
80 linguists can result in a shared terminology and methodology, and that this will foster a
81 more thorough investigation of the communicative capacities of nonhuman animals.
82 Two main linguistic domains are of particular relevance. First, computational linguistics
83 offers mathematical tools that can help to detect underlying structures in complex vocal
84 sequences (see Kershenbaum et al. 2014). Such methods have been successfully applied
85 to several communication systems (Kershenbaum 2014; Alger et al. 2016; Berthet et al.
86 2019). Second, formal linguistics provides tools to investigate the combination rules
87 linked to the meaning of individual calls, in order to determine the semantics of the
88 resulting sequences. In a series of analyses, Schlenker et al. (2014, 2016a, 2016b,
89 2016c, 2017) proposed to (1) investigate the literal meaning of calls based on the
90 circumstances of their emission (a concept otherwise redefined in Dezecache & Berthet
91 2018), (2) identify the pragmatic inferences that enrich their meanings, and (3) establish
92 the rules that structure the sequences and contribute to their semantics. Following this
93 approach, Schlenker et al. (2016b) proposed the ‘Informativity Principle’, which states
94 that if one call conveys more information than another call, then the most informative
95 call should be used whenever possible. If the less informative call is emitted, then one
96 can infer that the more informative call is not applicable (otherwise, the emitter would

97 have uttered it). A concrete example comes from the alarm system of male blue
98 monkeys (*Cercopithecus mitis*). They emit ‘pyow’ calls in a wide variety of alerting
99 situations, such as the presence of a terrestrial predator or during agonistic interactions.
100 The literal meaning of pyow is thus ‘alert’. However, when a raptor is present, pyows
101 are typically not emitted (even though the presence of a raptor is an alerting situation).
102 Rather, male blue monkeys emit ‘ka’ calls. Thus, these calls are specific to the presence
103 of aerial predators. ‘Ka’ calls are more informative than ‘pyow’ calls: while ‘pyow’
104 refers to a large set of alerts, the emission of ‘ka’ is linked to a much-restricted set of
105 circumstances (namely, the presence of a raptor). The Informativity Principle states that,
106 since individuals tend to be as informative as possible when communicating, the least
107 informative call (‘pyow’) is only emitted when its most informative counterpart (‘ka’) is
108 not applicable. As such, the enriched meaning of ‘pyow’ is ‘alert but not raptor-related’
109 (otherwise, the ‘ka’ call would have been emitted).

110 Another principle proposed by Schlenker et al. (2016b) is the ‘Urgency
111 Principle’. The principle postulates that, in a threatening situation, urgent information
112 (e.g., nature or location of the threat) should be communicated as soon as possible. As a
113 consequence, calls conveying urgent information should come before those conveying
114 non-urgent information in the call sequence (Schlenker et al. 2016b, 2016c). One
115 concrete example is the male putty-nosed monkey alarm system (*Cercopithecus*
116 *nictitans*). Male putty-nosed monkeys emit ‘hack’ calls when confronted with an aerial
117 threat (typically, a raptor), while ‘pyow’ is emitted to unspecific, general alerts. They
118 also emit ‘pyow-hack’ sequences to elicit group movements (Arnold & Zuberbühler
119 2006a, 2006b). The rules of combination of these “pyow-hack” sequences are puzzling.
120 The system does not seem to be idiomatic, since the sequences are slowly emitted and
121 not stereotyped. However, it is not compositional either, since the conjunction of a
122 raptor-related call (‘hack’) and a general alert call (‘pyow’) in no obvious way refers to
123 a group movement. Schlenker et al. (2016a, 2016b) argued that this combination might
124 be ruled by the Urgency Principle. According to this principle, if a raptor was present,
125 calls conveying urgent information about the threat (here, ‘hack’) should come before
126 calls that do not (here, ‘pyow’). On the contrary, ‘pyow-hack’ sequences can only be
127 emitted when group movement is required, but no raptor is present (otherwise ‘hack’
128 would have been emitted before ‘pyow’). The Urgency Principle is useful here to
129 determine that the meaning of ‘hack’ is not ‘raptor’, as could be expected from the
130 context of emission of individual calls, but rather ‘non-ground movement related alert’:
131 when a ‘hack’ is uttered first, it refers to the most urgent non-ground movement related
132 alert, i.e., a raptor.

133 The Informativity Principle and the Urgency Principle have demonstrated their
134 heuristic value for the alarm calling behaviours of several nonhuman primate species.
135 Specifically, they propose principles based on competition among meaningful
136 vocalizations to help understand why one call is emitted rather than another.
137 Nevertheless, it remains unclear whether the framework proposed by Schlenker et al.
138 (2016b) represents a general principle in animal communication, which would require

139 testing it with further data. Second, the understanding of cognitive mechanisms
140 underlying call production and comprehension, which could support the authors'
141 hypotheses, is lacking. Third, the Urgency Principle is currently tailored to species
142 whose sequence structure relies solely on call ordering. However, an increasing amount
143 of evidence suggests that call sequences can convey reliable information through a large
144 set of other encoding mechanisms, such as call intervals, repetition of elements, or
145 probabilities (see review in Engesser & Townsend 2019). For the Urgency Principle to
146 be more largely applicable to animal systems, it needs to be refined to integrate any sort
147 of encoding mechanisms. Finally, these theoretical principles are post-hoc speculations,
148 which provide an interpretation of the sequences of calls once they have been produced.
149 It remains to be tested whether they are relevant to the studied species and whether they
150 account for the mechanisms underlying call production.

151 Here, we test the hypothesis that the Urgency Principle can be applied to
152 nonhuman animal communication more generally. First, we propose an extended
153 version of the Principle stating that encoding mechanisms (hereafter, 'mechanisms')
154 conveying urgent information should take place before those that do not in the
155 sequence. Second, we propose to investigate whether this extended Urgency Principle
156 reflects the organisation of the alarm sequence of a nonhuman primate, the titi monkey,
157 using methods borrowed from computational linguistics. Titi monkeys (*Callicebus*
158 *nigrifrons*) are an ideal candidate species for this exercise. Their alarm vocal system has
159 been well investigated by biologists and linguists (Cäsar et al. 2012a, 2012b, 2013;
160 Schlenker et al. 2017; Berthet et al. 2018, 2019; Commier & Berthet 2019).

161 During predator encounters, titi monkeys emit alarm sequences: the first
162 individual to spot the threat emits soft calls, and other group members join into a chorus
163 composed of soft and loud calls that can last up to two hours (M. Berthet pers. obs.;
164 Cäsar 2011). Because these long and multi-caller sequences are difficult to investigate
165 with current methods, previous studies (Cäsar et al. 2013; Berthet et al. 2019) have
166 focussed on the first 10 and 30 calls of the alarm sequence (or respectively, during the
167 first 18 and 37 sec): these calls are emitted by one caller only, and are likely to convey
168 enough information about the predatory event for kins to adopt a sound reaction. These
169 10- and 30-alarm sequences are mostly composed of two alarm soft calls, A- and B-
170 calls. Based on experimental presentations of natural predators, it was shown that these
171 sequences can encode reliable information about the type of predator (aerial vs
172 terrestrial) and its location (ground vs canopy) (Cäsar et al. 2013; Berthet et al. 2019).
173 More importantly, this information seems to be conveyed in a gradual, probabilistic
174 fashion by the proportion of consecutive B-calls (Berthet et al. 2019). Specifically,
175 sequences with a high proportion of consecutive B-calls (BB-grams) mostly refer to
176 terrestrial predators on the ground, while sequences with a low proportion of BB-grams
177 mostly refer to aerial predators in the canopy.

178 To investigate whether the extended Urgency Principle reflects the organization
179 of titi monkey alarm sequences, we propose to investigate how information about the

180 context of emission of the call unfolds with the emission of a sequence. To this end, we
181 investigate how contextual parameters (predatory and social situation) influence specific
182 features of the sequence as it unfolds, using random forests algorithms. Importantly, we
183 extend the analysis window to up to 50 calls (mean \pm SD = 54.84 sec \pm 52.14). This
184 choice is two-fold. First, it allows us to ensure that, in case it is strictly encoded after
185 urgent information, non-urgent information has the opportunity to be transmitted.
186 Second, these sequences can be reliably analysed, for few callers are involved in the
187 chorus at this stage and calls do not extensively overlap. We hypothesized that, if the
188 extended Urgency Principle reflected the sequential organization of titi monkeys' alarm
189 call sequences, mechanisms encoding urgent information (i.e., information about the
190 predatory situation) should appear before mechanisms that do not.

191 MATERIAL AND METHODS

192 *Dataset*

193 We extracted data from the datasets published by Cäsar et al. (2013) and Berthet
194 et al. (2019). Both datasets were collected at the Reserva Particular do Patrimônio
195 Natural Santuário do Caraça, MG, Brazil (20°05'S, 43°29'W) from six wild groups of
196 black-fronted titi monkeys (*Callicebus nigrifrons*) habituated to human observers (see
197 more details about the field site and the population in Berthet et al. 2021). Monkey
198 groups were presented with three stuffed predators: one aerial predator (caracara,
199 *Caracara plancus*), and two terrestrial predators (tayra *Eira barbara* and oncilla
200 *Leopardus guttulus*). Each species of predator was presented twice to each group: once
201 at its usual location (i.e., in the tree canopy for the aerial predators, on the ground for
202 terrestrial predators) and once at its unusual location (i.e., on the ground for the aerial
203 predators, in the tree canopy for terrestrial predators). Focal group's vocal reactions
204 were recorded.

205 Experiments were conducted from August 2008 to July 2010 on five groups (A,
206 D, M, P and R groups), and replicated from May 2015 to August 2016 on the same five
207 groups plus the S group. Group composition varied between study periods, due to
208 births, dispersals and deaths (see details in Berthet et al. 2021). For full experimental
209 setup and trials exclusion criteria, see Cäsar et al. (2013) and Berthet et al. (2019).

210 For each recording, we collected 18 contextual parameters: (1) group identity,
211 (2) predator type (aerial or terrestrial), (3) predator species (caracara, tayra, or oncilla),
212 (4) predator location (canopy or ground), (5) predator height (i.e., its distance from the
213 ground), (6) identity of the first individual to call at the predator, (7) height of the first
214 individual to call (i.e., its distance from the ground), (8) distance between the first
215 individual to call and the predator, (9) number of individuals composing the group, and
216 (10-18) demographic features of the group, namely the number of infants, of female and
217 male juveniles, of female and male subadults, of female and male adults, of paired
218 adults and of non-paired adults. We considered individuals as adults from the age of 30

219 months, sub-adults between 18 and 30 months, juveniles between six and 18 months,
220 and infants if less than 6 months old (Cäsar 2011).

221 The final dataset comprised 58 sequences: 23 sequences were collected during
222 the first field period (August 2008–July 2010), and 35 sequences collected during the
223 second field period (May 2015–August 2016).

224 *Sequence coding*

225 We used the vocal repertoire described by Cäsar et al. (2012b), which comprises
226 two alarm call types: A-call and B-call. To assure that call types were reliability coded,
227 L. Narbona Sabaté and M. Berthet performed an inter-observer reliability test: they both
228 coded 199 calls from 12 randomly selected sequences, comprising about 7% of the final
229 dataset. According to standards (Landis & Koch 1977; Hallgren 2012), agreement was
230 almost perfect (Cohen’s $k = 0.81$).

231 L. Narbona Sabaté extracted the first calls up to 50, and labelled each of them as
232 A-, B-call, or ‘other’ (undetermined call or other call type), based on listening and
233 visual inspection of the spectrograms. L. Narbona Sabaté also measured each inter-call
234 silence interval. Labelling and measurements were conducted using the PRAAT
235 acoustic analysis software (version 6.1, Boersma & Weenink 2009).

236 The final dataset comprised 58 sequences. Fifty-two sequences were 50-call
237 long. Five sequences were shorter than 50 calls, because monkeys stopped calling
238 before the emission of 50 calls (four sequences were one-call long and one was 43-call
239 long). Finally, one sequence was only 20-call long because it could not be entirely
240 recorded due to logistic issues (Appendix I in Supplemental Data).

241 *Metric extraction*

242 This study aimed to investigate how semantic information unfolds within titi
243 monkey alarm sequences. The first step of this analysis was to unroll the sequence, and
244 describe how its organization and structure changed with the emission of new calls. To
245 do so, each sequence was cut into subsequences, so that a sequence of x calls was
246 decomposed into x subsequences starting with the first call of the sequence and ranging
247 from one to x calls long. Our final dataset was thus composed of 58 sequences,
248 comprising a total of 2,667 subsequences.

249 We characterized each subsequence by a set of 24 quantitative variables
250 (henceforth, ‘metrics’), following the procedure used in Berthet et al. (2019). Metrics
251 comprised: (1) the mean call interval, defined as the mean of the inter-call silence
252 durations in the subsequence, (2) the coefficient of variation of call interval, defined as
253 $CV = \text{standard deviation}/\text{mean of inter-call silence durations}$, (3–4) the proportion of
254 each A-call and B-call in the subsequence, (5–8) the proportion of each possible two
255 consecutive calls, or 2-grams (AA, AB, BA, BB) in the subsequence, (9–16) the
256 proportion of each possible combination of three consecutive calls, or 3-grams (AAA,

257 AAB, ABB, ABA, BBB, BBA, BAA, BAB) in the subsequence, (17,18) the N-gram
258 slopes (here, 2-gram and 3-gram slopes), to test whether a N-gram is more present in the
259 subsequence than the others. To compute this metric, we drew a graphic representation
260 of the probability of each N-gram (either 2- or 3-gram) sorted by decreasing probability,
261 and we extracted the coefficient of regression: if it was different from 0, then one N-
262 gram was more represented in the sequence, (19) the slope of entropy, calculated using
263 Shannon entropy, to measure the organizational complexity of a subsequence. To
264 compute this metric, we plotted zero-, first- and second- order entropies (McCowan et
265 al. 1999) and extracted a coefficient of regression: a negative slope indicated an
266 important sequential organization and high communication capacities, while a null slope
267 indicated a random organization, with low communicative capacities, (20-23) the
268 probability of transitions between each call types (A to A, A to B, B to A, B to B), (24)
269 the last call emitted as a proxy of call order. More details can be found in Berthet et al.
270 (2019).

271 When calculating proportions of 2- and 3-grams, we ignored calls that were
272 coded as ‘other’: since this label refers to a large set of cases (non-identifiable calls,
273 calls given by naïve individuals in the background, or non-alarm calls), we remained
274 conservative and removed them from the analysis. Concretely, the computation of 2-
275 and 3-grams stopped before the ‘other’ call and re-started from null right after. For each
276 occurrence of one of these calls, two less 2-grams and three less 3-grams were
277 computed in the analysis.

278 We calculated proportions and probabilities using a Bayesian correction, in
279 order to estimate the occurrence of rare events despite our small sample size (Alger et
280 al. 2016). Briefly, we calculated each proportion of event i as $\text{proportion } i = (y_i + \alpha) / (\text{total number of events} + k * \alpha)$, with y_i the number of events i before
281 Bayesian correction, k , the number of possible events, and α , the prior distribution. We
282 chose $\alpha = \text{total number of events} / (k * 100)$ as prior distribution, so that we simulated
283 that each subsequence comprised 1% more events i . For example, to calculate the
284 proportion of A-calls in a subsequence of 10 calls, y_i is the number of A-calls in the
285 sequence, the ‘total number of events’ is the number of calls in the sequence (here, 10)
286 and k is the number of possible call types (here, two: A and B-calls). More details about
287 the method can be found in Alger et al. (2016), Berthet et al. (2019), and in the online
288 scripts.
289

290 These analyses were conducted using R version 3.6.1 (R Core Team 2020) and
291 the cfp package (Neumann 2018).

292 *Statistical analysis*

293 In order to investigate semantic information as the sequence unrolls, we
294 analysed how the structure of the sequence (its metrics) varied with the number of calls
295 already emitted and the contextual information. To this end, we investigated what
296 contextual parameters (if any) influenced the metrics’ values of each subsequence using

297 random forests algorithms. Random forests are machine learning algorithms that predict
298 the value of a variable to explain (here, each metric) based on explanatory variables
299 (here, the contextual information), using a set of multiple decision trees.

300 We split the dataset into 50 subsets, one for each subsequence length. For each
301 subset, we conducted the following analysis: first, for each metric, the explanatory
302 variables that accounted for most of the metric's variance, if any, were extracted. To
303 this end, we used a Variable Selection Using Random Forest (VSURF) method: for
304 each metric, we ran 50 random forests, each composed of 2,000 decision trees built
305 using six randomly selected contextual parameters as explanatory variables. We then
306 used a three-step variable selection procedure to eliminate contextual variables that
307 were redundant and/or irrelevant to the metric (Genuer et al. 2015). Remaining
308 contextual variables were the most likely to impact the metric for this subsequence
309 length. In other terms, these contextual parameters were likely to be encoded by the
310 metric at this time of the sequence.

311 Second, for each metric, we ran a random forest containing 500 decision trees
312 built using the contextual variables selected during the previous analysis. We extracted
313 the percentage of variance explained (here: pseudo R-squared) for each random forest:
314 this value, ranging from zero to 100, indicates the robustness of the prediction. The
315 complete statistical analysis (i.e., the extraction of relevant contextual variables and the
316 computation of random forests) was repeated for each subset, so that we computed
317 1,197 random forests.

318 After computing all 1,197 random forests, we selected those whose predictions
319 were the most robust. We plotted all the values of variance explained (sorted by
320 increasing order) and extracted the inflexion point. Random forests with a value of
321 variance explained strictly greater than the inflexion point were considered the most
322 robust and included in the results: they indicated, for each subset, what metric(s)
323 encoded information, and what type(s) of contextual information they encoded, or in
324 other words, how encoded information varied as the sequence unrolled.

325 The analyses were conducted using R version 3.6.1 (R Core Team 2020), the
326 tidyverse package version 1.3.0 (Wickham et al. 2019), the VSURF package version
327 1.1.0. (Genuer et al. 2015), the randomForest package version 4.6-14 (Liaw & Wiener
328 2002), and the inflection package version 1.3.5 (Christopoulos 2019). The full dataset
329 and the associated statistical scripts are available on a Figshare depository
330 ([https://figshare.com/projects/Animal_linguistics_inthe_making_The_Urgency_Princip
331 e_and_titi_monkeys_alarm_system/121914](https://figshare.com/projects/Animal_linguistics_inthe_making_The_Urgency_Principle_and_titi_monkeys_alarm_system/121914)).

332 RESULTS

333 After the variable selection step and the robustness step, the inflexion point
334 occurred at 45.76% of variance explained (Appendix II in Supplemental Data). Random
335 forests with a greater percentage of variance explained were considered robust, which

336 was the case for 398 out of 1,197 random forests. While random forests were built with
337 a total of 24 metrics as variables to explain, only 11 metrics were present in the retained
338 random forests (Appendix III in Supplemental Data). Similarly, 12 contextual variables
339 composed the retained random forest, out of the 18 contextual variables proposed. Each
340 retained random forest included 1.11 ± 0.36 (mean \pm SD) contextual variables (a
341 schematic summary can be found in Appendix IV in Supplemental Data).

342 *What information is conveyed, and when*

343 Twelve main contextual variables were retained. Two contextual variables
344 (namely the type of predator and the predator species) were predominantly encoded
345 throughout the sequence: they were relevant for subsequences of all lengths and
346 accounted for most of the variance of 148 and 246 of the retained random forests,
347 respectively (Fig. 1, Table 1). Three other contextual variables were of lesser
348 importance in the sequences: they accounted for most of the variance of eight to 11
349 retained random forests (Table 1). These included the height of the predator (relevant
350 only for subsequences of one to three calls long), the number of juvenile females
351 (relevant for subsequences of eight to 18 calls long), and the number of individuals
352 (relevant for some subsequences from eight calls long) (Fig. 1). Finally, other
353 contextual information, like the location of the predator, the distance between the caller
354 and the predator, the height of the first caller, the group identity, the number of unmated
355 adults, the number of juveniles and the number of subadult males, were sporadically
356 present along the later sequence (from eight to 50 calls long, Fig. 1, Table 1).

357 *How information is conveyed*

358 Eleven metrics were selected by the statistical analysis (Fig. 2). Five of these
359 metrics were relevant to all subsequences' length: the proportion of A- and B-calls, the
360 transition probability from B- to B-calls, the proportion of 2-grams BB, and the
361 proportion of 3-grams BBB. Three other metrics were relevant for more than 70% of
362 subsequences lengths: the transition probabilities from A- to A-calls (relevant for 39
363 subsequences), the proportion of 2-grams AA (relevant for 37 subsequences) and the
364 proportion of 3-grams AAA (relevant for 45 subsequences). Finally, the last call was
365 relevant for 27 subsequences mostly comprised within the first 20 calls, and the
366 proportions of 3-gram BAB and BBA were only relevant for two subsequences each
367 (nine to 10 and eight to nine, respectively). Interestingly, predator's type, species and
368 height were encoded by all metrics except the proportions of 3-grams BAB and BBA.
369 These two metrics exclusively coded for social information and were relevant for
370 subsequences of eight to 10 calls long (Table 1, Fig. 1). The number of juvenile females
371 was encoded by a metric that also coded for predator type and species: the proportion of
372 3-grams AAA (Table 1).

373
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375
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Table 1.

Information type encoded by each metric. Numbers: subsequences for which a metric (in line) encoded for a type of information (in column), based on the outcome of 398 robust random forests.

		Information about the predatory event						Social information					
		Type of predator	Predator species	Height of the predator	Location of the predator	Distance to the predator	Height of the first caller	Group	Number of individuals	Number of unmated adults	Number of juveniles	Number of subadult males	Number of juvenile females
M e t r i c s	Last call	12	15	1	3	1	1	3	4	1	6		
	Proportion of A-calls	18	32	3									
	Proportion of B-calls	18	32	2									
	Transition probability from A to A	17	22										
	Transition probability from B to B	16	33	2									
	Proportion of 2-grams AA	18	19										
	Proportion of 2-grams BB	15	34	2									
	Proportion of 3-grams AAA	16	29										11
	Proportion of 3-grams BAB								2			2	
	Proportion of 3-grams BBA								2			2	
	Proportion of 3-grams BBB	18	30	1									
	Total	148	246	11	3	1	1	3	8	1	6	4	11

377

DISCUSSION

378

379 Schlenker et al.'s (2016b) Urgency Principle states that calls conveying
380 information about the nature or location of a threat should come first. This principle
381 helped draw satisfactory conclusions about the formal properties of a specific primate
382 call system, but it has not been further tested with other species. This study investigated
383 whether the Urgency Principle reflected the organization of another animal
384 communication system, the titi monkey alarm calls. Since some species (including titi
385 monkeys) do not only rely on call order to convey information (Engesser & Townsend
386 2019), we proposed to extend the Urgency Principle to other known encoding
387 mechanisms that are relevant to these species. This extended Urgency Principle states
388 that encoding mechanisms that convey urgent information should take place before
389 those that do not, regardless of the mechanism. Our hypothesis was that, if the extended
390 Urgency Principle reflected the sequential organization of the titi monkeys' alarm call
391 sequences, mechanisms encoding information about predator type and location should
392 appear early in the sequences.

393

394 Two main information types were encoded in the sequences. First, information
395 about the predatory situation (mainly, the nature and location of the predator) was
396 encoded since the very beginning of the sequence (Fig. 1), using eight mechanisms that
397 occurred throughout the whole sequence, and the last call which mostly took place at
398 the beginning of the sequence (Fig. 2). Second, social information (mainly the number
399 of individuals and the number of juvenile females) was sporadically encoded later (Fig.
400 1), using one mechanism that was salient throughout the whole sequence (proportion of
401 3-gram AAA, which also encoded information about the predatory situation), one
402 mechanism that mostly occurred at the beginning of the sequence (last call, which also
403 encoded for predator type, species and height), and two mechanisms (the proportion of
404 3-grams BAB and BBA) that appeared later in the sequence (Fig. 2). Overall,
405 mechanisms encoding for urgent information took place since the beginning of the
406 sequence, while mechanisms exclusively encoding for less-urgent information arose
later.

407

408 Our results confirm that the Urgency Principle may be applicable to animal
409 communication systems more generally. Alarm calls or sequences are designed to
410 convey rapid and reliable information to conspecifics about the presence of a nearby
411 threat. In some species, individuals react more strongly and faster to the alarm calls of
412 conspecifics than to the calls of a predator (Barrera et al. 2011) or to the presence of the
413 predator itself (McLachlan & Magrath 2020). It is not surprising that alarm sequences
414 are structured so that urgent information is conveyed at the beginning: this provides an
415 effective warning to conspecifics, especially those that are naive to the presence of the
416 threat (Griesser 2013). Similarly to titi monkeys, New Holland honeyeaters encode
417 urgent information (there, the urgency of the threat) in the very first call of their alarm
sequences (McLachlan & Magrath 2020).

418 While information about the nature of the predator was encoded throughout the
419 sequence, information about its location was mostly present at the start of the sequence.
420 Two hypotheses can explain this difference. First, it is possible that information about
421 predator location is of lesser importance than information about predator species or
422 type. While information about the predator's nature is crucial to adopt an adaptive
423 reaction (e.g., mobbing, specific escape strategy) and may need to be redundantly sent
424 to ensure reception by conspecifics (McLachlan & Magrath 2020) and effective
425 coordination of the group, information about a predator location may only be needed at
426 the beginning to make sure that all members have correctly spotted the predator. The
427 second hypothesis is that mechanisms encoding predator location are related to
428 identification mistakes. Even if tayra and oncillas are good climbers (Brosset 1968;
429 Sunquist & Sunquist 2002), predators in the canopy mostly are raptors (M. Berthet pers.
430 obs.). Raptors typically elicit sequences beginning with A-calls (Appendix I in
431 Supplemental Data). Individuals that spot something in the canopy may quickly emit A-
432 calls, even if they are not sure about the nature of the threat, in case this is a raptor
433 («better be safe than sorry» strategy, Ferrari 2009). They may later switch to B-calls if
434 determining that the threat is a terrestrial one. If so, location would be encoded as a by-
435 product of the predator identification process, while being nonetheless relevant to
436 conspecifics (Berthet et al. 2019).

437 Schlenker et al.'s (2016b) Urgency Principle was initially articulated to shed
438 light on the mechanisms underlying information transfer in putty-nosed monkeys, which
439 combined meaningful calls into meaningful sequences using an ordering rule. But
440 nonhuman animals can encode information using a large variety of encoding strategies
441 (Engesser & Townsend 2019). Here, we showed that the Urgency Principle can be
442 extended beyond single calls: in titi monkey alarm sequences, mechanisms encoding for
443 urgent information appeared earlier than those that do not. This suggests that the
444 Urgency Principle can be applied to nonhuman sequences that do not rely solely on call
445 ordination to convey information.

446 Interestingly, information related to the predatory event is predominant in the
447 sequences, while social information (mainly, the number of individuals and the number
448 of juvenile females) occurs sporadically. Information about group composition is not
449 crucial in a predatory context, and encoding mechanisms specifically allocated to this
450 information pertain to disruptions of the sequence pattern (proportion of 3-grams BAB
451 and BBA), which could suggest that social encoding is a by-product of the group's call
452 emission. Titi monkeys live in groups composed of one breeding pair and their
453 offspring (Bicca-Marques & Heymann 2013). The group often remains in close physical
454 proximity, which makes it impossible to isolate each individual's vocal contribution
455 from the chorus. As a result, our study investigated the vocal reactions of the groups,
456 comprising between two and seven individuals. The first hypothesis is that each
457 individual's vocal utterance may disrupt others' utterances. Cäsar et al. (2013) showed
458 that individual sequences encoded predator type and location through disruption
459 patterns (e.g., a sequence composed of B-calls indicated a terrestrial predator on the

497

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501

502

DISCLOSURE STATEMENT

503

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504

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517

ETHICAL STANDARD

518

519 The research reported in this article was conducted in compliance with all
520 relevant local and international laws. The 2008-2010 data collection was approved by
521 the University of St Andrews Psychology Ethics Board, the 2014-2016 data collection
was approved by the ethical committee CEUA/UNIFAL (number 665/2015).

522

AUTHOR CONTRIBUTION

523

524 L. Narbona Sabaté: conceptualization, data curation, data analysis, writing
original draft, editing and revision; G. Mesbahi: conceptualization, data analysis, editing
525 and revision; G. Dezechache: redaction of the original draft, editing and revision; C.
526 Cäsar: data collection, data curation, editing and revision; K. Zuberbühler: funding
527 acquisition, editing and revision; M. Berthet: conceptualization, data collection, data
528 curation, data analysis, writing original draft, editing and revision, supervision.

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535 DATA ACCESSIBILITY

536 The full dataset and the associated statistical scripts are available on a Figshare
537 depository

538 (https://figshare.com/projects/Animal_linguistics_inthe_making_The_Urgency_Principles_and_titi_monkeys_alarm_system/121914).

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690

691

SUPPLEMENTAL DATA

692

Appendix I.

693

694

695

696

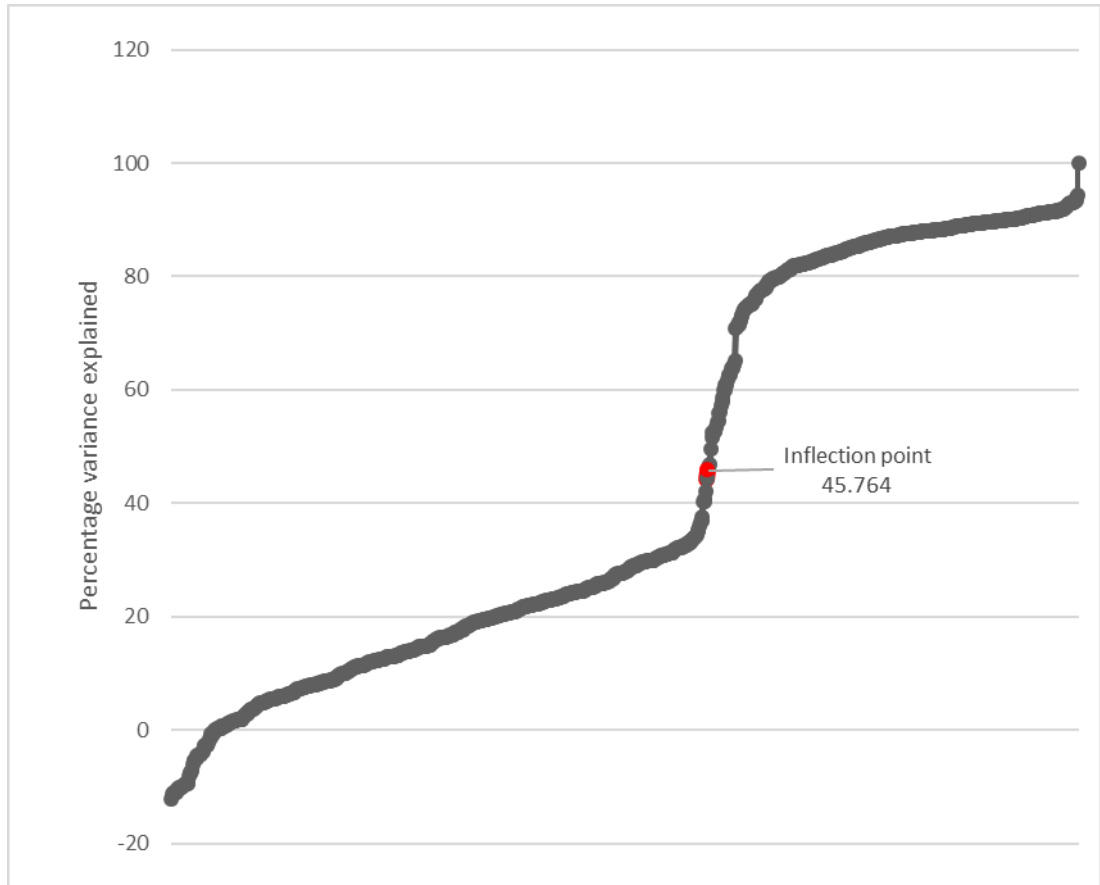
697

Alarm sequences given by six groups of titi monkeys in response to experimental presentations of predator models. One line represents one sequence (up to 50 first calls), with each A representing an A-call, each B, a B-call, each O, an 'other' call (either another call type, or an undetermined call type), and blanks, sequences of less than 50 calls.

699

Appendix II.

700 Value of the variance explained for each computed random forest (N=1,197),
701 sorted by increasing values.



702

703

704

Appendix III.

705
706

Robustness of the random forests. Stars indicate the percentage of variance explained per metric per subset of length. *>46%, **>64%, ***>83%. “x”: encoding mechanisms that are not possible at specific lengths of the sequence, because not enough calls were already emitted

		LENGTH OF THE SEQUENCE																									
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
S C I R T M	Last call	*	***	**	***	**	**	*	*	*	*	***	-	*	*	-	-	*	**	**	-	*	-	-	-	-	
	Proportion of A-calls	*	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
	Proportion of B-calls	*	***	**	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
	Transition probability from A to A	x	***	***	***	***	***	***	***	***	***	***	***	-	-	-	-	-	***	***	***	***	***	***	***	***	***
	Transition probability from B to B	x	*	**	**	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
	Proportion of 2-grams AA	x	***	***	***	***	***	***	***	***	***	***	***	-	-	-	-	-	-	-	***	***	***	***	***	***	***
	Proportion of 2-grams BB	x	*	**	**	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
	Proportion of 3-grams AAA	x	x	**	***	***	**	**	***	***	***	***	***	**	**	**	***	**	**	**	-	***	**	**	**	**	**
	Proportion of 3-grams BAB	x	x	-	-	-	-	-	-	*	**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Proportion of 3-grams BBA	x	x	-	-	-	-	-	**	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Proportion of 3-grams BBB	x	x	*	**	**	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	

		LENGTH OF THE SEQUENCE																												
		26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50				
S C I R T M	Last call	-	*	*	-	-	-	*	-	*	*	*	-	-	-	-	*	-	-	-	*	-	-	*	-	*				
	Proportion of A-calls	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***			
	Proportion of B-calls	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***			
	Transition probability from A to A	***	***	***	***	***	**	**	**	**	**	**	**	**	**	**	**	-	-	**	**	-	-	-	**	**				
	Transition probability from B to B	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***			
	Proportion of 2-grams AA	***	***	***	***	***	**	**	**	**	**	**	**	**	**	**	-	-	-	-	-	-	**	**	**	**				
	Proportion of 2-grams BB	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***			
	Proportion of 3-grams AAA	**	**	-	**	-	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**			
	Proportion of 3-grams BAB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
	Proportion of 3-grams BBA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
Proportion of 3-grams BBB	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***				

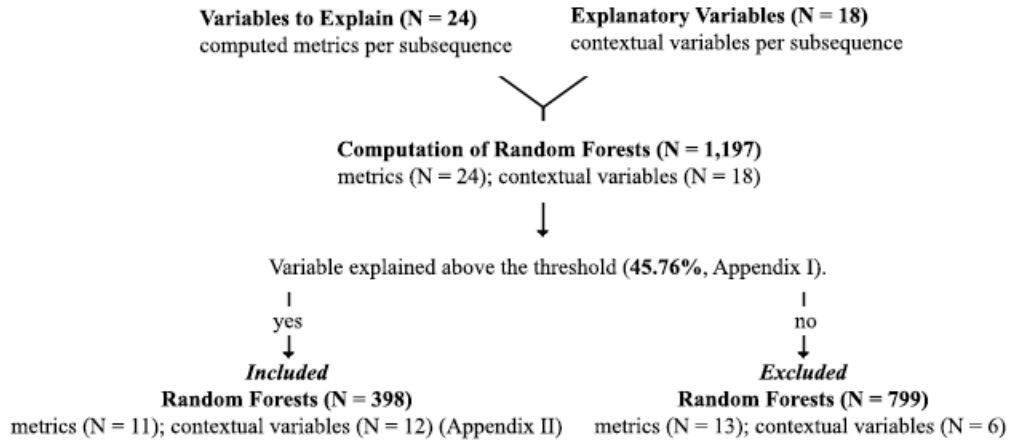
707

Appendix IV.

708

Summary of the random forest's analysis. Random forests were retained in the analysis if their variance explained was greater than the threshold (see Appendix II).

709



710