

# Animal linguistics in the making: the Urgency Principle and titi monkeys' alarm system

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1 2	Animal linguistics in the making: The Urgency Principle and titi monkeys' alarm system
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13	Switzerland
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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56 Running head: Animal linguistics: Urgency Principle and titi monkeys

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 the notion of functionally referential communication (e.g., Wheeler & Fischer 2012; 62 63 Townsend & Manser 2013) or the debates around the specificity of animal calls (Fichtel 64 & Kappeler 2002; Schlenker et al. 2016b; Dezecache & Berthet 2018). Debates surrounding the concept of meaning in animals come from practical and 65

theoretical difficulties encountered when investigating animal semantics. First, methods 66 commonly used in animal communication to reveal linguistic-like capacities in 67 nonhuman animals sometimes fail to reveal these capacities even in humans (Prat 68 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 linguistics, which applies methods from linguistics to animal communication. This is 78 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. 2019). Second, formal linguistics provides tools to investigate the combination rules 86 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, 2016c, 2017) proposed to (1) investigate the literal meaning of calls based on the 89 circumstances of their emission (a concept otherwise redefined in Dezecache & Berthet 90 2018), (2) identify the pragmatic inferences that enrich their meanings, and (3) establish 91 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 can infer that the more informative call is not applicable (otherwise, the emitter would 96

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.

The Informativity Principle and the Urgency Principle have demonstrated their
heuristic value for the alarm calling behaviours of several nonhuman primate species.
Specifically, they propose principles based on competition among meaningful
vocalizations to help understand why one call is emitted rather than another.
Nevertheless, it remains unclear whether the framework proposed by Schlenker et al.
(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 reflects the organisation of the alarm sequence of a nonhuman primate, the titi monkey, 156 157 using methods borrowed from computational linguistics. Titi monkeys (Callicebus 158 nigrifrons) are an ideal candidate species for this exercise. Their alarm vocal system has been well investigated by biologists and linguists (Cäsar et al. 2012a, 2012b, 2013; 159 160 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 10- and 30-alarm sequences are mostly composed of two alarm soft calls, A- and B-169 170 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.

To investigate whether the extended Urgency Principle reflects the organizationof 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. Second, these sequences can be reliably analysed, for few callers are involved in the 186 187 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 call sequences, mechanisms encoding urgent information (i.e., information about the 189 190 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.

Experiments were conducted from August 2008 to July 2010 on five groups (A, D, M, P and R groups), and replicated from May 2015 to August 2016 on the same five groups plus the S group. Group composition varied between study periods, due to births, dispersals and deaths (see details in Berthet et al. 2021). For full experimental 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 individual to call and the predator, (9) number of individuals composing the group, and 215 (10-18) demographic features of the group, namely the number of infants, of female and 216 217 male juveniles, of female and male subadults, of female and male adults, of paired adults and of non-paired adults. We considered individuals as adults from the age of 30 218

- months, sub-adults between 18 and 30 months, juveniles between six and 18 months,
  and infants if less than 6 months old (Cäsar 2011).
- The final dataset comprised 58 sequences: 23 sequences were collected during the first field period (August 2008–July 2010), and 35 sequences collected during the second field period (May 2015–August 2016).
- 224 Sequence coding

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

- L. Narbona Sabaté extracted the first calls up to 50, and labelled each of them as A-, B-call, or 'other' (undetermined call or other call type), based on listening and visual inspection of the spectrograms. L. Narbona Sabaté also measured each inter-call silence interval. Labelling and measurements were conducted using the PRAAT acoustic analysis software (version 6.1, Boersma & Weenink 2009).
- The final dataset comprised 58 sequences. Fifty-two sequences were 50-call long. Five sequences were shorter than 50 calls, because monkeys stopped calling before the emission of 50 calls (four sequences were one-call long and one was 43-call 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*

This study aimed to investigate how semantic information unfolds within titi monkey alarm sequences. The first step of this analysis was to unroll the sequence, and describe how its organization and structure changed with the emission of new calls. To do so, each sequence was cut into subsequences, so that a sequence of x calls was decomposed into x subsequences starting with the first call of the sequence and ranging from one to x calls long. Our final dataset was thus composed of 58 sequences, 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 = standard deviation/mean of inter-call silence durations, (3-4) the proportion of254 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 slopes (here, 2-gram and 3-gram slopes), to test whether a N-gram is more present in the 258 259 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 al. 1999) and extracted a coefficient of regression: a negative slope indicated an 265 266 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).

When calculating proportions of 2- and 3-grams, we ignored calls that were coded as 'other': since this label refers to a large set of cases (non-identifiable calls, calls given by naïve individuals in the background, or non-alarm calls), we remained conservative and removed them from the analysis. Concretely, the computation of 2and 3-grams stopped before the 'other' call and re-started from null right after. For each occurrence of one of these calls, two less 2-grams and three less 3-grams were 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 proportion i = (yi + yi)alpha)/(total number of events + k \* alpha), with yi the number of events i before 281 282 Bayesian correction, k, the number of possible events, and  $\alpha$ , the prior distribution. We 283 chose  $\alpha$  = total number of events/(k \* 100) as prior distribution, so that we simulated 284 that each subsequence comprised 1% more events i. For example, to calculate the 285 proportion of A-calls in a subsequence of 10 calls, yi is the number of A-calls in the 286 sequence, the 'total number of events' is the number of calls in the sequence (here, 10) 287 and k is the number of possible call types (here, two: A and B-calls). More details about 288 the method can be found in Alger et al. (2016), Berthet et al. (2019), and in the online 289 scripts.

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

## 292 Statistical analysis

In order to investigate semantic information as the sequence unrolls, we analysed how the structure of the sequence (its metrics) varied with the number of calls already emitted and the contextual information. To this end, we investigated what contextual parameters (if any) influenced the metrics' values of each subsequence using random forests algorithms. Random forests are machine learning algorithms that predict
the value of a variable to explain (here, each metric) based on explanatory variables
(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.

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

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

The analyses were conducted using R version 3.6.1 (R Core Team 2020), the tidyverse package version 1.3.0 (Wickham et al. 2019), the VSURF package version 1.1.0. (Genuer et al. 2015), the randomForest package version 4.6-14 (Liaw & Wiener 2002), and the inflection package version 1.3.5 (Christopoulos 2019). The full dataset and the associated statistical scripts are available on a Figshare depository (https://figshare.com/projects/Animal\_linguistics\_inthe\_making\_The\_Urgency\_Principl e\_and\_titi\_monkeys\_alarm\_system/121914).

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

RESULTS

- 336 was the case for 398 out of 1,197 random forests. While random forests were built with
- a total of 24 metrics as variables to explain, only 11 metrics were present in the retained
- 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
- retained random forest included  $1.11 \pm 0.36$  (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 only for subsequences of one to three calls long), the number of juvenile females 350 351 (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 and the predator, the height of the first caller, the group identity, the number of unmated 354 355 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 transition probability from B- to B-calls, the proposition of 2-grams BB, and the 360 361 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 proportion of 3-grams AAA (relevant for 45 subsequences). Finally, the last call was 364 365 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 was encoded by a metric that also coded for predator type and species: the proportion of 371 372 3-grams AAA (Table 1).

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.

			Inform	nation about	the predate	ory event				Social infor	mation		
		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
	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										
M e	Transition probability from B to B	16	33	2									
t													
r	Proportion of 2-grams AA	18	19										
ו ר	Proportion of 2-grams BB	15	34	2									
s	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

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

407 Our results confirm that the Urgency Principle may be applicable to animal 408 communication systems more generally. Alarm calls or sequences are designed to 409 convey rapid and reliable information to conspecifics about the presence of a nearby 410 threat. In some species, individuals react more strongly and faster to the alarm calls of 411 conspecifics than to the calls of a predator (Barrera et al. 2011) or to the presence of the 412 predator itself (McLachlan & Magrath 2020). It is not surprising that alarm sequences 413 are structured so that urgent information is conveyed at the beginning: this provides an 414 effective warning to conspecifics, especially those that are naive to the presence of the 415 threat (Griesser 2013). Similarly to titi monkeys, New Holland honeyeaters encode 416 urgent information (there, the urgency of the threat) in the very first call of their alarm 417 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 light on the mechanisms underlying information transfer in putty-nosed monkeys, which 438 439 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 and BBA), which could suggest that social encoding is a by-product of the group's call 451 452 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

460 ground while a single A-call at the beginning of the B-sequence indicated a terrestrial 461 predator in the canopy). Several individuals spotting the predator at different times may 462 produce asynchronous alarm sequences that disrupt others' sequence. The second 463 hypothesis pertains to communication development. While call production (i.e., the 464 emission of well-formed acoustic structures) seems to be largely innate in nonhuman primates (Gultekin et al. 2021; e.g., Snowdon 2009; but see Watson et al. 2015), call 465 466 usage (i.e., the production of calls in the right situation) is socially learnt (Seyfarth & 467 Cheney 1986; Snowdon 2009): young individuals gradually learn to produce calls in the right context. The larger the titi monkey group, the more immature individuals 468 469 (including juvenile females), which may increase the chances of emission of 470 inappropriate calls and therefore, create disruption patterns. Further work is needed to 471 test the effect of additional factors such as the variation of distance between individuals 472 or the latency of each individual's call emission, and conclude on the underlying 473 mechanisms.

474 In this article, we were able to confirm that methods from computational 475 linguistics can be successfully applied to animal communication to process large 476 datasets, highlight underlying structure and unroll information transfer processes. We have also shown that one of the key principles from the animal formal semantics 477 478 framework (namely, the Urgency Principle) is an encoding strategy that is found in at 479 least one species of nonhuman primates. Further verifications are needed to confirm that 480 these methodologies are entirely reliable, such as testing whether the Informativity 481 Principle is also relevant to nonhuman animals, and extending these investigations to 482 other taxa. Overall, our work provides further evidence that the emerging field of 483 animal linguistics offers promising methods and theories that can help unveil the 484 linguistic properties of nonhuman communication systems.



485

487 sequence. Coloured cells represent the information type encoded at each point of the 488 sequence: green cells represent information about the predatory event and yellow cells, 480 acciel information. N is the number of accuracy that were used in the analysis at each

489 social information. N is the number of sequences that were used in the analysis, at each

<sup>490</sup> point of the sequence.

N	58	54		53	 	 	52	
Last call						7 0		
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								

491

Fig. 2. — Encoding mechanisms from the first to the 50th call of the alarm

492 sequence. Blue cells represent encoding mechanisms that are salient at a given point of

493 the sequence. Black cells represent encoding mechanisms that are not possible at

494 specific points of the sequence, because not enough calls are emitted yet. N is the

495 number of sequences that were used in the analysis, at each point of the sequence.

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521	was approved by the ethical committee CEUA/UNIFAL (number 665/2015).
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523	L. Narbona Sabaté: conceptualization, data curation, data analysis, writing
524	original draft, editing and revision; G. Mesbahi: conceptualization, data analysis, editing
525	and revision; G. Dezecache: redaction of the original draft, editing and revision; C.
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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_Principl
539	e_and_titi_monkeys_alarm_system/121914).
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691	SUPPLEMENTAL DATA
692	Appendix I.
693	Alarm sequences given by six groups of titi monkeys in response to
694	experimental presentations of predator models. One line represents one sequence (up to
695	50 first calls), with each A representing an A-call, each B, a B-call, each O, an 'other'
696	call (either another call type, or an undetermined call type), and blanks, sequences of
697	less than 50 calls.



# Appendix II.





Appendix III.

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

										LE	NGT	H OF	THE	SEQ	UEN	CE									
	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
Last call	*	***	**	***	**	**	*	*	*	*	***	-	*	*	-	-	*	**	**	-	*	-	-	-	-
Proportion of A-calls	*	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
Proportion of B-calls	*	***	**	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
○ Transition probability from A to A	х	***	***	***	***	***	***	***	***	***	***	***	-	-	-	-	-	***	***	***	***	***	***	***	***
- Transition probability from B to B	х	*	**	**	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
	х	***	***	***	***	***	***	***	***	***	***	***	-	-	-	-	-	-	***	***	***	***	***	***	***
Proportion of 2-grams BB	х	*	**	**	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
Proportion of 3-grams AAA	х	X	**	***	***	**	**	***	***	***	***	**	**	**	***	**	**	**	-	***	**	**	**	**	**
<b>Z</b> Proportion of 3-grams BAB	x	x	-	-	-	-	-	-	*	**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Proportion of 3-grams BBA	X	X	-	-	-	-	-	**	*	-	-	-	-	-	-	-	-	-	-	_	_	-	-	-	-
Proportion of 3-grams BBB	x	X	*	**	**	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
										LE	NGT	н оғ	THE	SEQ	UEN	CE									
	26	27	28	29	30	31	32	33	34	LE 35	NGT 36	H OF 37	THE 38	SEQ 39	UEN 40	CE 41	42	43	44	45	46	47	48	49	50
Last call	26	27 *	28 *	29	30	31	32 *	33	34 *	LE 35 *	NGT 36 *	H OF 37 -	THE 38	39	UEN 40	CE 41 *	42	43	<b>44</b> -	45 *	46	47	48 *	<b>49</b> -	50 *
Last call Proportion of A-calls	<b>26</b> - ***	27 * ***	28 * ***	<b>29</b> - ***	<b>3</b> 0 - ***	<b>31</b> - ***	32 * ***	<b>33</b> - ***	34 *	LE 35 *	NGT 36 *	H OF 37 - ***	THE 38 - ***	SEQ 39 - ***	UEN 40 - ***	CE 41 *	<b>42</b> ***	<b>43</b> - **	44 - **	45 * **	<b>46</b> - **	47 - **	48 * **	49 - **	50 * **
Last call Proportion of A-calls ∽ Proportion of B-calls	26 - ***	27 * ***	28 * ***	<b>29</b> - ***	<b>3</b> 0 - ***	<b>31</b> - ***	32 * ***	33 - ***	34 * ***	LE 35 * ***	NGT 36 * ***	H OF 37 - ***	THE 38 - ***	SEQ 39 - *** ***	UEN 40 - *** ***	CE 41 * ***	<b>42</b> - *** ***	43 - **	44 - **	45 * **	46 - **	47 - ** ***	48 * **	49 - **	50 * **
Last call Proportion of A-calls ∽ Proportion of B-calls ∵ Transition probability from A to A	26  *** ***	27 * *** ***	28 * *** ***	29  *** ***	<b>30</b>  *** ***	31 - *** ***	32 * *** ***	33 - *** ***	34 * *** ***	LE 35 * *** ***	NGT 36 * *** ***	H OF 37 - *** ***	THE 38 - *** ***	SEQ 39 - *** ***	UEN 40 - *** ***	CE 41 * *** ***	42 - *** ***	43 - ** ***	44 - ** ***	45 * ** ***	<b>46</b> - **	47 - ** **	48 * ** **	49 - ** ***	50 * ** **
Last call Proportion of A-calls ∽ Proportion of B-calls ℃ Transition probability from A to A ∽ Transition probability from B to B	26 	27 * *** *** ***	28 * *** *** ***	29 - *** *** ***	<b>3</b> 0  *** ***	31 *** *** **	32 * *** *** **	33 - *** *** **	34 * *** *** **	LE 35 * *** *** **	NGT 36 * *** *** **	H OF 37 - *** *** **	THE 38 *** *** **	SEQ 39 - *** *** **	UEN 40 - *** ** **	CE 41 * *** *** ***	42 - *** - ***	43 - ** ***	44 - ** *** **	45 * ** *** **	46 - ** ***	47 - ** ***	48 * ** ***	49 - ** ** **	50 * ** ** **
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-gramss AA	26 **** **** ****	27 * *** *** ***	28 * *** *** ***	29  *** *** ***	<b>30</b> *** *** ***	31 	32 * *** *** ** **	33 - *** *** ** **	34 * *** *** **	LE 35 * *** *** *** ***	NGT 36 * *** *** *** ***	H OF 37 - *** *** *** ***	THF 38 - *** *** *** ***	SEQ 39 *** *** ** **	UEN 40 - *** *** *** ***	CE 41 *** *** ***	42 	43  ***  ***	44 ** *** ***	45 * *** *** ***	46  ***  ***	47 - ** *** ***	48 ** *** - ***	49  *** *** *** ***	50 * ** ** ** **
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	26 - *** *** ***	27 * *** *** *** ***	28 * *** *** *** ***	29 *** *** *** ***	30 	31 *** *** ** **	32 * *** *** *** ***	33  *** *** *** *** ***	34 *** *** *** ***	LE 35 *** *** *** *** ***	NGT 36 *** *** *** ***	H OF 37 - *** *** *** *** ***	THF 38 - *** *** *** ***	SEQ 39 - *** ** ** ** **	UEN 40 	CE 41 *** *** *** ***	42 - *** - *** - ***	43 - *** - *** - ***	44 - *** *** *** - ***	45 * *** *** ***	46  ***  ***	47 - *** - *** ***	48 ** *** *** ***	49 - ** *** *** ***	50 * ** ** ** **
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	26 **** *** *** ***	27 * *** *** *** *** ***	28 **** *** *** *** ***	29 *** *** *** *** ***	30 *** *** *** ***	31 *** *** *** *** ***	32 * *** *** *** *** ***	33  *** *** *** *** ***	34 **** *** *** *** ***	LE2 35 **** *** *** *** *** ***	NGT 36 * *** *** *** *** *** ***	H OF 37 - *** *** *** *** *** ***	THF 38 *** *** *** *** ***	SEQ 39 *** *** *** *** *** ***	UEN 40 - *** *** *** *** *** ***	CE 41 *** *** *** *** *** ***	42 	43 	44  *** *** ***  ***	45 * *** *** *** - ***	46  ***  ***  ***	47  ***  *** *** ***	48 ** *** *** *** ***	49 *** *** *** *** ***	50 * ** ** ** ** **
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-gramss AA ← Proportion of 2-grams BB ≃ Proportion of 3-grams BAB	26 **** **** **** ***	27 * *** *** *** *** ***	28 * *** *** *** *** ***	29 *** *** *** *** ***	30  *** *** *** ***	31 *** *** *** *** ***	32 **** *** *** *** *** ***	33 *** *** *** *** ***	34 *** *** *** *** ***	LE2 35 * *** *** *** *** *** ***	NGT 36 * *** *** *** *** *** ***	H OF 37 - *** *** *** *** *** *** ***	THE 38 *** *** *** *** *** ***	E SEQ 39  *** *** *** *** *** *** ***	UEN 40 - *** *** *** *** *** ***	CE 41 *** *** *** *** *** ***	42 	43  ***  *** *** ***	44  *** *** ***  ***	45 * *** *** *** ***	46  ***  *** *** ***	47  *** *** *** *** ***	48 *** **** **** *** ***	49  *** *** *** *** ***	50 * ** ** ** ** *** ***
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-gramss AA ⊢ Proportion of 2-grams BB ≃ Proportion of 3-grams BAB Proportion of 3-grams BAB Proportion of 3-grams BBA	26 	27 * *** *** *** *** *** ***	28 *** *** *** *** *** ***	29 *** *** *** *** ***	30 *** *** *** *** ***	31 *** *** *** *** ***	32 * *** *** *** *** *** ***	33 	34 * *** *** *** *** ***	LE2 35 **** *** *** *** *** ***	NGT 36 * *** *** *** *** *** *** ***	H OF 37 - *** *** ** ** ** ** **	THE 38 *** *** *** *** *** ***	SEQ 39  *** *** *** *** *** *** ***	UEN 40 - *** *** *** *** *** ***	CE 41 * *** *** *** *** *** *** ***	42 	43  ***  *** ***  	44  *** *** *** *** ***	45 * *** *** *** *** ***	46  *** - *** *** ***	47  *** *** *** ***	48 * *** *** *** ***	49  *** *** *** *** ***	50 * ** ** ** ** ** **

### Appendix IV.

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

