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Lara Narbona Sabaté, Geoffrey Mesbahi, Guillaume Dezecache, Cristiane Cäsar, Klaus Zuberbühler, et al.. Animal linguistics in the making: the Urgency Principle and titi monkeys' alarm system. Ethology Ecology and Evolution, 2022, pp.1-17. 10.1080/03949370.2021.2015452 . hal-03518874

HAL Id: hal-03518874
https://hal.inrae.fr/hal-03518874v1

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

LARA NARBONA SABATÉ[1,*], GEOFFREY MESBAHI[2], GUILLAUME DEZECACHE[3], CRISTIANE CÄSAR[4], KLAUS ZUBERBÜHLER[5,6] and MÉLISSA BERTHET[1]

[1]*Institut Jean Nicod, Département d'Études Cognitives, ENS, EHESS, CNRS, PSL Research University, 75005 Paris, France*

[2]*INRAE, UE FERLUS, 86600 Lusignan, France*

[3]*Université Clermont Auvergne, LAPSCO CNRS, 63000 Clermont-Ferrand, France*

[4]*Vale S.A., Nova Lima, MG, Brazil*

[5]*School of Psychology & Neurosciences, University of St Andrews, Scotland, United Kingdom*

[6]*Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, 2000 Neuchâtel, Switzerland*

HIGHLIGHTS

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

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

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

* Corresponding author: Lara Narbona Sabaté, Institut Jean Nicod, 29 Rue d’Ulm, 75005 Paris, France (E-mail: lara.narbona@gmail.com).

INTRODUCTION

The investigation of meaning (or ‘semantics’) in nonhuman animal vocalizations has played a central role in the field of animal communication since the foundational work on vervet monkey alarm calls (Seyfarth et al. 1980a, 1980b). The question and 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; Townsend & Manser 2013) or the debates around the specificity of animal calls (Fichtel & Kappeler 2002; Schlenker et al. 2016b; Dezecache & Berthet 2018).

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

One attempt to overcome these difficulties is the emerging field of animal linguistics, which applies methods from linguistics to animal communication. This is based on the vision that an interdisciplinary collaboration between biologists and linguists can result in a shared terminology and methodology, and that this will foster a more thorough investigation of the communicative capacities of nonhuman animals. Two main linguistic domains are of particular relevance. First, computational linguistics offers mathematical tools that can help to detect underlying structures in complex vocal sequences (see Kershenbaum et al. 2014). Such methods have been successfully applied to several communication systems (Kershenbaum 2014; Alger et al. 2016; Berthet et al. 2019). Second, formal linguistics provides tools to investigate the combination rules linked to the meaning of individual calls, in order to determine the semantics of the 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 circumstances of their emission (a concept otherwise redefined in Dezecache & Berthet 2018), (2) identify the pragmatic inferences that enrich their meanings, and (3) establish the rules that structure the sequences and contribute to their semantics. Following this approach, Schlenker et al. (2016b) proposed the ‘Informativity Principle’, which states that if one call conveys more information than another call, then the most informative 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 have uttered it). A concrete example comes from the alarm system of male blue monkeys (Cercopithecus mitis). They emit ‘pyow’ calls in a wide variety of alerting situations, such as the presence of a terrestrial predator or during agonistic interactions. The literal meaning of pyow is thus ‘alert’. However, when a raptor is present, pyows are typically not emitted (even though the presence of a raptor is an alerting situation). Rather, male blue monkeys emit ‘ka’ calls. Thus, these calls are specific to the presence of aerial predators. ‘Ka’ calls are more informative than ‘pyow’ calls: while ‘pyow’ refers to a large set of alerts, the emission of ‘ka’ is linked to a much-restricted set of circumstances (namely, the presence of a raptor). The Informativity Principle states that, since individuals tend to be as informative as possible when communicating, the least informative call (‘pyow’) is only emitted when its most informative counterpart (‘ka’) is not applicable. As such, the enriched meaning of ‘pyow’ is ‘alert but not raptor-related’ (otherwise, the ‘ka’ call would have been emitted).

Another principle proposed by Schlenker et al. (2016b) is the ‘Urgency Principle’. The principle postulates that, in a threatening situation, urgent information (e.g., nature or location of the threat) should be communicated as soon as possible. As a consequence, calls conveying urgent information should come before those conveying non-urgent information in the call sequence (Schlenker et al. 2016b, 2016c). One concrete example is the male putty-nosed monkey alarm system (Cercopithecus nictitans). Male putty-nosed monkeys emit ‘hack’ calls when confronted with an aerial threat (typically, a raptor), while ‘pyow’ is emitted to unspecific, general alerts. They also emit ‘pyow-hack’ sequences to elicit group movements (Arnold & Zuberbühler 2006a, 2006b). The rules of combination of these “pyow-hack” sequences are puzzling. The system does not seem to be idiomatic, since the sequences are slowly emitted and not stereotyped. However, it is not compositional either, since the conjunction of a raptor-related call (‘hack’) and a general alert call (‘pyow’) in no obvious way refers to a group movement. Schlenker et al. (2016a, 2016b) argued that this combination might be ruled by the Urgency Principle. According to this principle, if a raptor was present, calls conveying urgent information about the threat (here, ‘hack’) should come before calls that do not (here, ‘pyow’). On the contrary, ‘pyow-hack’ sequences can only be emitted when group movement is required, but no raptor is present (otherwise ‘hack’ would have been emitted before ‘pyow’). The Urgency Principle is useful here to determine that the meaning of ‘hack’ is not ‘raptor’, as could be expected from the context of emission of individual calls, but rather ‘non-ground movement related alert’: when a ‘hack’ is uttered first, it refers to the most urgent non-ground movement related 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 testing it with further data. Second, the understanding of cognitive mechanisms underlying call production and comprehension, which could support the authors' hypotheses, is lacking. Third, the Urgency Principle is currently tailored to species whose sequence structure relies solely on call ordering. However, an increasing amount of evidence suggests that call sequences can convey reliable information through a large set of other encoding mechanisms, such as call intervals, repetition of elements, or probabilities (see review in Engesser & Townsend 2019). For the Urgency Principle to be more largely applicable to animal systems, it needs to be refined to integrate any sort of encoding mechanisms. Finally, these theoretical principles are post-hoc speculations, which provide an interpretation of the sequences of calls once they have been produced. It remains to be tested whether they are relevant to the studied species and whether they account for the mechanisms underlying call production.

Here, we test the hypothesis that the Urgency Principle can be applied to nonhuman animal communication more generally. First, we propose an extended version of the Principle stating that encoding mechanisms (hereafter, 'mechanisms') conveying urgent information should take place before those that do not in the 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, using methods borrowed from computational linguistics. Titi monkeys (Callicebus 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; Schlenker et al. 2017; Berthet et al. 2018, 2019; Commier & Berthet 2019).

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

To investigate whether the extended Urgency Principle reflects the organization of titi monkey alarm sequences, we propose to investigate how information about the context of emission of the call unfolds with the emission of a sequence. To this end, we investigate how contextual parameters (predatory and social situation) influence specific features of the sequence as it unfolds, using random forests algorithms. Importantly, we extend the analysis window to up to 50 calls (mean ± SD = 54.84 sec ± 52.14). This choice is two-fold. First, it allows us to ensure that, in case it is strictly encoded after 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 chorus at this stage and calls do not extensively overlap. We hypothesized that, if the extended Urgency Principle reflected the sequential organization of titi monkeys' alarm call sequences, mechanisms encoding urgent information (i.e., information about the predatory situation) should appear before mechanisms that do not.

MATERIAL AND METHODS

Dataset

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

For each recording, we collected 18 contextual parameters: (1) group identity, (2) predator type (aerial or terrestrial), (3) predator species (caracara, tayra, or oncilla), (4) predator location (canopy or ground), (5) predator height (i.e., its distance from the ground), (6) identity of the first individual to call at the predator, (7) height of the first 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 (10-18) demographic features of the group, namely the number of infants, of female and 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 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).

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 recorded due to logistic issues (Appendix I in Supplemental Data).

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.

We characterized each subsequence by a set of 24 quantitative variables (henceforth, 'metrics'), following the procedure used in Berthet et al. (2019). Metrics comprised: (1) the mean call interval, defined as the mean of the inter-call silence durations in the subsequence, (2) the coefficient of variation of call interval, defined as CV = standard deviation/mean of inter-call silence durations, (3–4) the proportion of each A-call and B-call in the subsequence, (5-8) the proportion of each possible two consecutive calls, or 2-grams (AA, AB, BA, BB) in the subsequence, (9-16) the proportion of each possible combination of three consecutive calls, or 3-grams (AAA, 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 subsequence than the others. To compute this metric, we drew a graphic representation of the probability of each N-gram (either 2- or 3-gram) sorted by decreasing probability, and we extracted the coefficient of regression: if it was different from 0, then one N-gram was more represented in the sequence, (19) the slope of entropy, calculated using Shannon entropy, to measure the organizational complexity of a subsequence. To 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 important sequential organization and high communication capacities, while a null slope indicated a random organization, with low communicative capacities, (20-23) the probability of transitions between each call types (A to A, A to B, B to A, B to B), (24) the last call emitted as a proxy of call order. More details can be found in Berthet et al. (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 2- and 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.

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

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

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.

We split the dataset into 50 subsets, one for each subsequence length. For each subset, we conducted the following analysis: first, for each metric, the explanatory variables that accounted for most of the metric's variance, if any, were extracted. To this end, we used a Variable Selection Using Random Forest (VSURF) method: for each metric, we ran 50 random forests, each composed of 2,000 decision trees built using six randomly selected contextual parameters as explanatory variables. We then used a three-step variable selection procedure to eliminate contextual variables that were redundant and/or irrelevant to the metric (Genuer et al. 2015). Remaining contextual variables were the most likely to impact the metric for this subsequence length. In other terms, these contextual parameters were likely to be encoded by the 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_Principle_and_titi_monkeys_alarm_system/121914).

RESULTS

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 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 composed the retained random forest, out of the 18 contextual variables proposed. Each retained random forest included 1.11 ± 0.36 (mean ± SD) contextual variables (a schematic summary can be found in Appendix IV in Supplemental Data).

What information is conveyed, and when

Twelve main contextual variables were retained. Two contextual variables (namely the type of predator and the predator species) were predominantly encoded throughout the sequence: they were relevant for subsequences of all lengths and accounted for most of the variance of 148 and 246 of the retained random forests, respectively (Fig. 1, Table 1). Three other contextual variables were of lesser importance in the sequences: they accounted for most of the variance of eight to 11 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 (relevant for subsequences of eight to 18 calls long), and the number of individuals (relevant for some subsequences from eight calls long) (Fig. 1). Finally, other 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 adults, the number of juveniles and the number of subadult males, were sporadically present along the later sequence (from eight to 50 calls long, Fig. 1, Table 1).

How information is conveyed

Eleven metrics were selected by the statistical analysis (Fig. 2). Five of these 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 proportion of 3-grams BBB. Three other metrics were relevant for more than 70% of subsequences lengths: the transition probabilities from A- to A-calls (relevant for 39 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 relevant for 27 subsequences mostly comprised within the first 20 calls, and the proportions of 3-gram BAB and BBA were only relevant for two subsequences each (nine to 10 and eight to nine, respectively). Interestingly, predator's type, species and height were encoded by all metrics except the proportions of 3-grams BAB and BBA. These two metrics exclusively coded for social information and were relevant for 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 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.

		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
Metrics	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

DISCUSSION

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

Two main information types were encoded in the sequences. First, information 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 occurred throughout the whole sequence, and the last call which mostly took place at the beginning of the sequence (Fig. 2). Second, social information (mainly the number of individuals and the number of juvenile females) was sporadically encoded later (Fig. 1), using one mechanism that was salient throughout the whole sequence (proportion of 3-gram AAA, which also encoded information about the predatory situation), one mechanism that mostly occurred at the beginning of the sequence (last call, which also encoded for predator type, species and height), and two mechanisms (the proportion of 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 sequence, while mechanisms exclusively encoding for less-urgent information arose later.

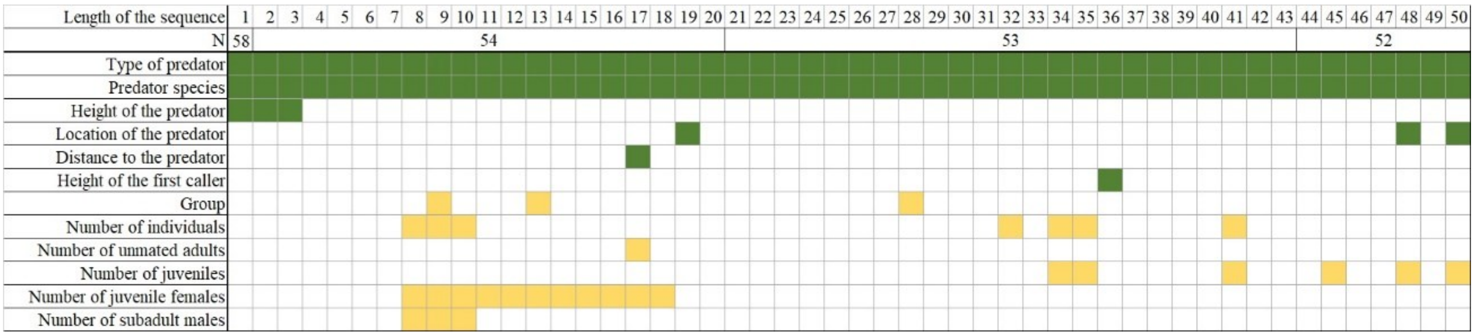
Our results confirm that the Urgency Principle may be applicable to animal communication systems more generally. Alarm calls or sequences are designed to convey rapid and reliable information to conspecifics about the presence of a nearby threat. In some species, individuals react more strongly and faster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

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

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

Interestingly, information related to the predatory event is predominant in the sequences, while social information (mainly, the number of individuals and the number of juvenile females) occurs sporadically. Information about group composition is not crucial in a predatory context, and encoding mechanisms specifically allocated to this 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 emission. Titi monkeys live in groups composed of one breeding pair and their offspring (Bicca-Marques & Heymann 2013). The group often remains in close physical proximity, which makes it impossible to isolate each individual's vocal contribution from the chorus. As a result, our study investigated the vocal reactions of the groups, comprising between two and seven individuals. The first hypothesis is that each individual's vocal utterance may disrupt others' utterances. Cäsar et al. (2013) showed that individual sequences encoded predator type and location through disruption patterns (e.g., a sequence composed of B-calls indicated a terrestrial predator on the ground while a single A-call at the beginning of the B-sequence indicated a terrestrial predator in the canopy). Several individuals spotting the predator at different times may produce asynchronous alarm sequences that disrupt others' sequence. The second hypothesis pertains to communication development. While call production (i.e., the 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 usage (i.e., the production of calls in the right situation) is socially learnt (Seyfarth & 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 (including juvenile females), which may increase the chances of emission of inappropriate calls and therefore, create disruption patterns. Further work is needed to test the effect of additional factors such as the variation of distance between individuals or the latency of each individual's call emission, and conclude on the underlying mechanisms.

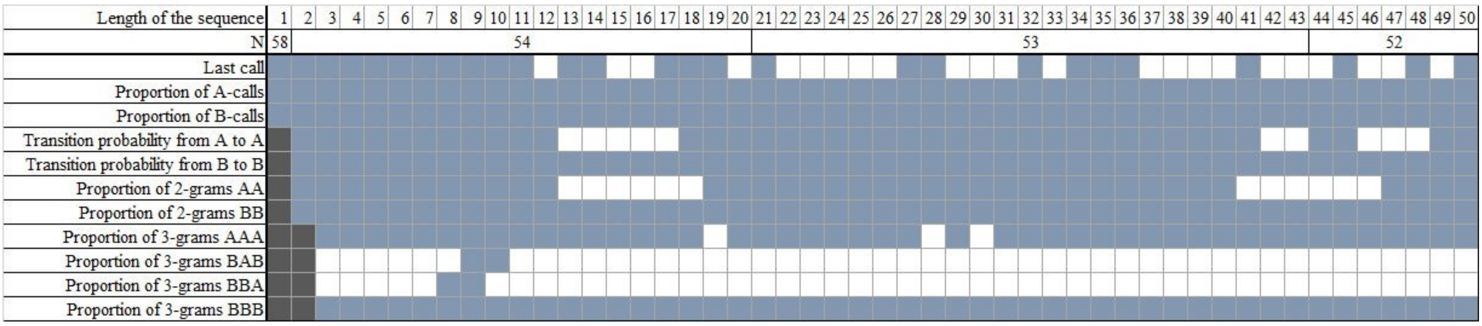
In this article, we were able to confirm that methods from computational linguistics can be successfully applied to animal communication to process large datasets, highlight underlying structure and unroll information transfer processes. We have also shown that one of the key principles from the animal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



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
N	58	54																			53				
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 juvenile females								🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨	🟨							
Number of subadult males								🟨	🟨	🟨															

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
N																			52						
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 juvenile females																									
Number of subadult males																									

Fig. 1. — Information encoded from the first to the 50th call of the alarm sequence. Coloured cells represent the information type encoded at each point of the sequence: green cells represent information about the predatory event and yellow cells, social information. N is the number of sequences that were used in the analysis, at each point of the sequence.



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	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
N	58	54																			53																							52						
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	⬛	⬛	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦

Fig. 2. — Encoding mechanisms from the first to the 50th call of the alarm sequence. Blue cells represent encoding mechanisms that are salient at a given point of the sequence. Black cells represent encoding mechanisms that are not possible at specific points of the sequence, because not enough calls are emitted yet. N is the number of sequences that were used in the analysis, at each point of the sequence.

ACKNOWLEDGEMENTS

The authors thank Philippe Schlenker and Emmanuel Chemla for helpful discussions, the many field assistants and master students who took part into data collection, and the Santuário do Caraça for their logistic support.

DISCLOSURE STATEMENT

The authors declare that they have no conflict of interest.

FUNDING

This work received funding from the European Research Council under the European Union's Seventh Framework Programme (FP7/2007–2013)/ERC grant agreement no. 283871 (PI: K. Zuberbühler), the Swiss National Science Foundation and the University of Neuchâtel, the European Research Council (ERC) under the European Union's Seventh Framework Programme (FP/2007-2013)/ERC Grant Agreement N°324115–FRONTSEM (PI: P. Schlenker), the European Union's Horizon 2020 research and innovation programme (grant agreement No. 788077, Orisem, PI: P. Schlenker), from the Fyssen Foundation (post-doc grant) and from the Institut d'Etudes Cognitives, Ecole Normale Supérieure − PSL Research University supported by grants ANR-10-IDEX-0001-02 and FrontCog ANR-17-EURE-0017. We acknowledge the support received from the Agence Nationale de la Recherche of the French government through the program ''Investissements d'Avenir'' (16-IDEX-0001 CAP 20-25).

ETHICAL STANDARD

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

AUTHOR CONTRIBUTION

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

ORCID

Lara Narbona Sabaté: https://orcid.org/0000-0002-5115-5614

Geoffrey Mesbahi: https://orcid.org/0000-0003-0276-3901

Guillaume Dezecache: https://orcid.org/0000-0002-9366-6287

Klaus Zuberbühler: https://orcid.org/0000-0001-8378-088X

Mélissa Berthet: https://orcid.org/0000-0002-3170-1315

DATA ACCESSIBILITY

The full dataset and the associated statistical scripts are available on a Figshare depository (https://figshare.com/projects/Animal_linguistics_inthe_making_The_Urgency_Principle_and_titi_monkeys_alarm_system/121914).

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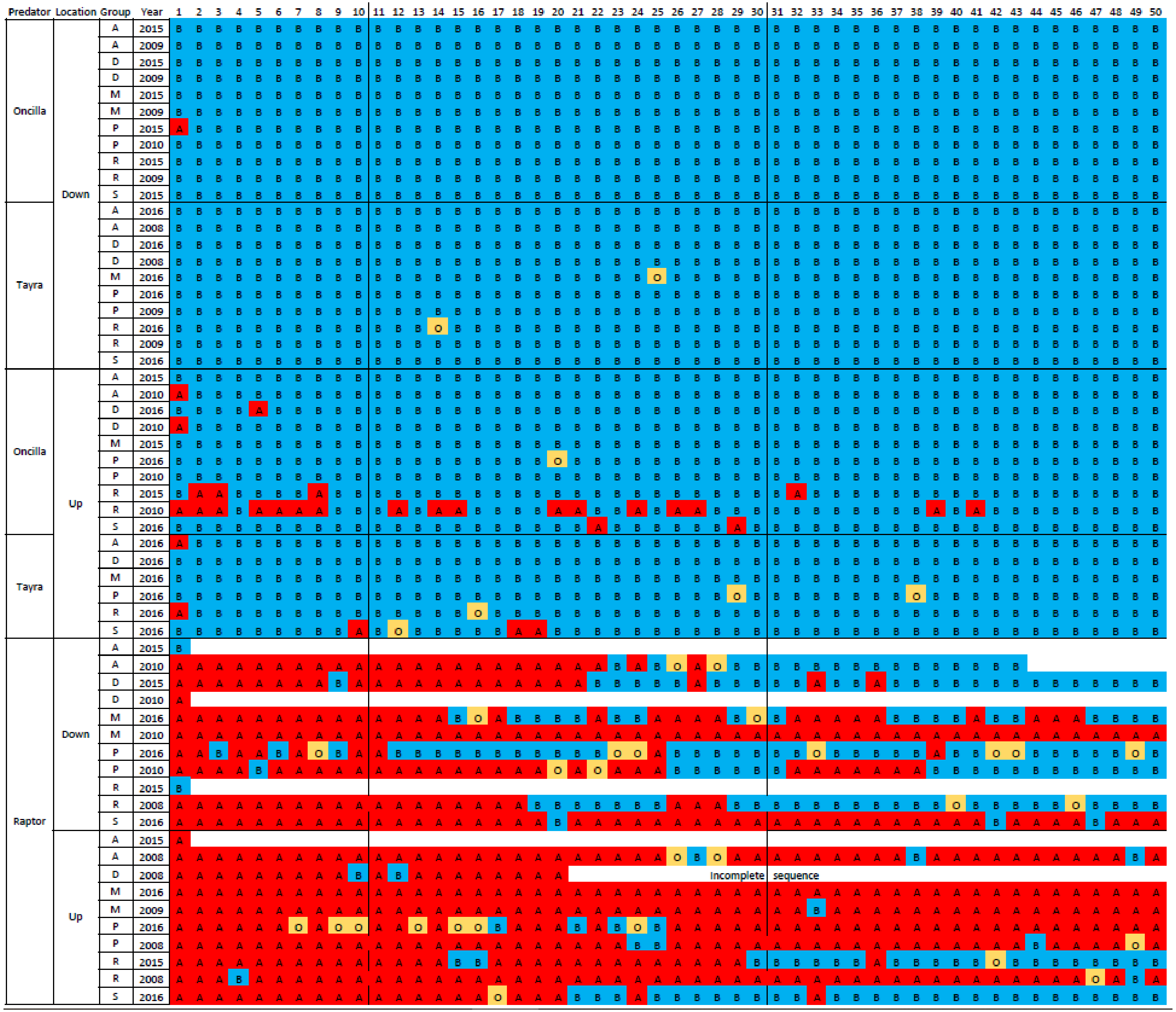
SUPPLEMENTAL DATA

Appendix I.

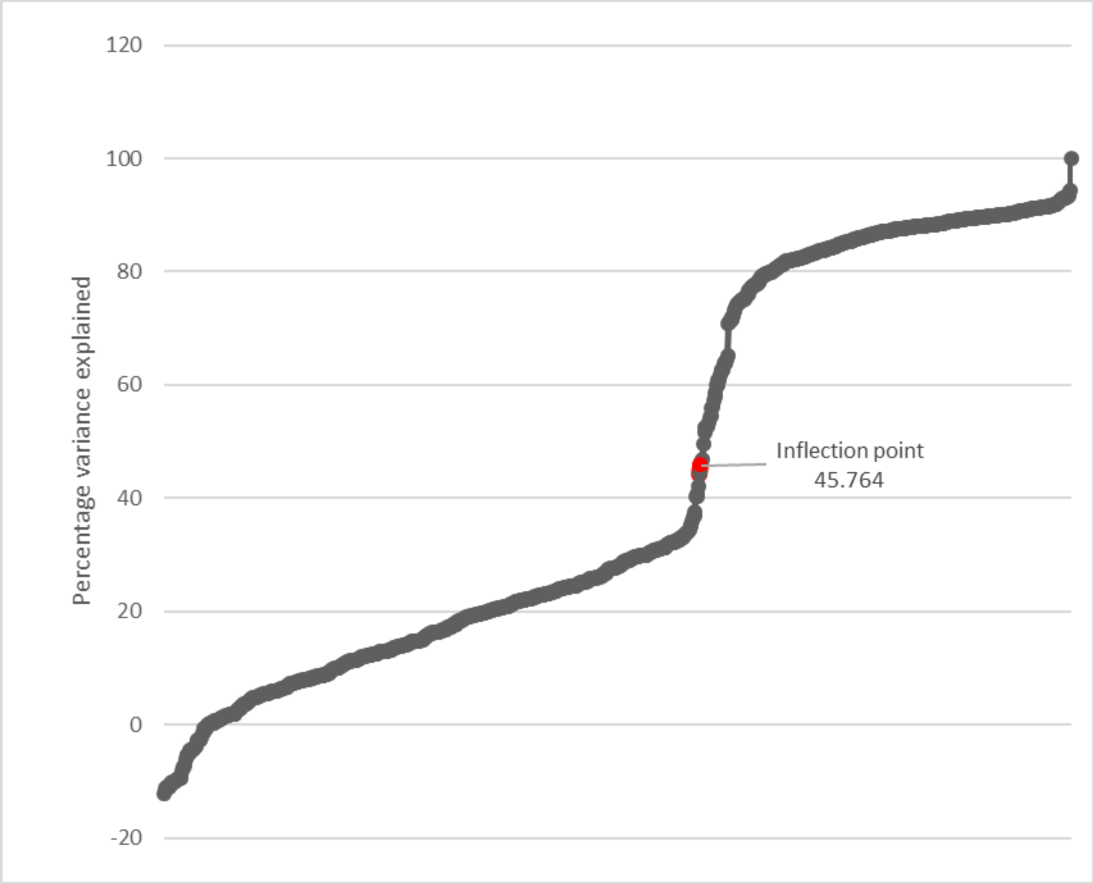
Alarm sequences given by six groups of titi monkeys in response to experimental presentations of predator models. One line represents one sequence (up to 50 first calls), with each A representing an A-call, each B, a B-call, each O, an ‘other’ call (either another call type, or an undetermined call type),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



Predator	Location	Group	Year	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	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
Oncilla	Down	A	2015	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		A	2009	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		D	2015	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		D	2009	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		M	2015	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		M	2009	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		P	2015	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		P	2010	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		R	2015	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		R	2009	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		S	2015	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
Tayra		A	2016	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		A	2008	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		D	2016	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		D	2008	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		M	2016	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	O	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		P	2016	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		P	2009	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		R	2016	B	B	B	B	B	B	B	B	B	B	B	B	B	O	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		R	2009	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		S	2016	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
Oncilla	Up	A	2015	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		A	2010	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		D	2016	B	B	B	B	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		D	2010	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		M	2015	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		P	2016	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	O	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		P	2010	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		R	2015	B	A	A	B	B	B	B	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		R	2010	A	A	A	B	A	A	A	A	B	B	B	A	B	A	A	B	B	B	B	A	A	B	B	A	B	A	A	B	B	B	B	B	B	B	B	B	B	B	A	B	A	B	B	B	B	B	B	B	B	B
		S	2016	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	A	B	B	B	B	B	B	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
Tayra		A	2016	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		D	2016	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		M	2016	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		P	2016	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	O	B	B	B	B	B	B	B	B	O	B	B	B	B	B	B	B	B	B	B	B	B
		R	2016	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	O	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		S	2016	B	B	B	B	B	B	B	B	B	A	B	O	B	B	B	B	B	A	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
Raptor	Down	A	2015	B																																																	
		A	2010	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	B	O	A	O	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B							
		D	2015	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	B	B	B	B	B	A	B	B	B	B	B	A	B	B	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B
		D	2010	A																																																	
		M	2016	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	O	A	B	B	B	B	A	B	B	A	A	A	A	B	O	B	A	A	A	A	A	B	B	B	B	A	B	B	A	A	A	B	B	B	B
		M	2010	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
		P	2016	A	A	B	A	A	B	A	O	B	A	A	B	B	B	B	B	B	B	B	B	B	B	O	O	A	B	B	B	B	B	B	B	O	B	B	B	B	B	A	B	B	O	O	B	B	B	B	B	O	B
		P	2010	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	O	A	O	A	A	A	B	B	B	B	B	B	A	A	A	A	A	A	A	B	B	B	B	B	B	B	B	B	B	B	B
		R	2015	B																																																	
		R	2008	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	B	B	B	B	B	A	A	A	B	B	B	B	B	B	B	B	B	B	B	O	B	B	B	B	B	O	B	B	B	B
		S	2016	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	B	A	A	A
	Up	A	2015	A																																																	
		A	2008	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	O	B	O	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	B	A
		D	2008	A	A	A	A	A	A	A	A	A	B	A	B	A	A	A	A	A	A	A	A										Incomplete	sequence																			
		M	2016	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
		M	2009	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
		P	2016	A	A	A	A	A	A	O	A	O	O	A	A	O	A	O	O	B	A	A	A	B	A	B	O	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
		P	2008	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	O	A
		R	2015	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	B	B	B	B	A	B	B	B	B	B	O	B	B	B	B	B	B	B	B
		R	2008	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	O	A	B	A
		S	2016	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	O	A	A	A	B	B	B	A	B	B	B	B	B	B	B	B	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B

Appendix II.

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



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

		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
METRICS	**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-gramss 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
METRICS	**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 AAA	**	**	-	**	-	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**
	Proportion of 3-grams BAB	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Proportion of 3-grams BBA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Proportion of 3-grams BBB	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***

Appendix IV.

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).