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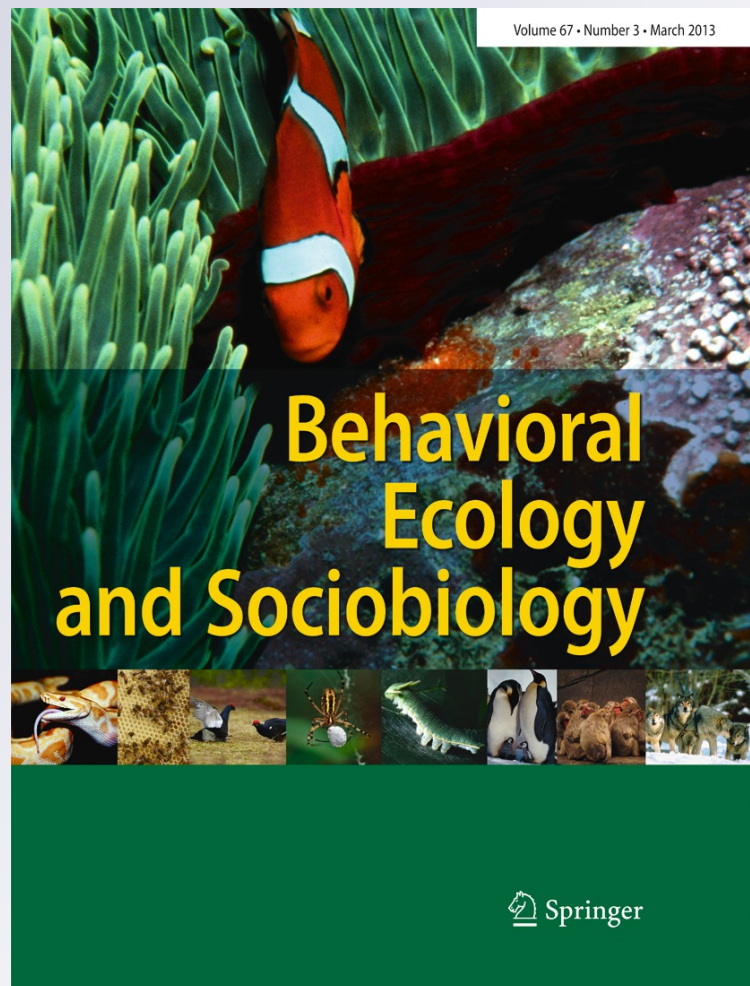
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Predator guild does not influence orangutan alarm call rates and combinations

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Abstract Monkey alarm calls have shown that in the primate clade, combinatorial rules in acoustic communication are not exclusive to humans. A recent hypothesis suggests that the number of different call combinations in monkeys increases with increased number of predator species. However, the existence of combinatorial rules in great ape alarm calls remains largely unstudied, despite its obvious relevance to ideas about the evolution of human speech. In this paper, we examine the potential use of combinatorial rules in the alarm calls of the only Asian great ape: the orangutan. Alarm calls in orangutans are composed of syllables (with either one or two distinct elements), which in turn are organized into sequences. Tigers and clouded leopards are predators for Sumatran orangutans, but in Borneo,

tigers are extinct. Thus, orangutans make a suitable great ape model to assess alarm call composition in relation to the size of the predator guild. We exposed orangutans on both islands to a tiger and control model. Response compositionality was analyzed at two levels (i.e., syllable and syllable sequences) between models and populations. Results were corroborated using information theory algorithms. We made specific, directed predictions for the variation expected if orangutans used combinatorial rules. None of these predictions were met, indicating that monkey alarm call combinatorial rules do not have direct homologues in orangutans. If these results are replicated in other great apes, this indicates that predation did not drive selection towards ever more combinatorial rules in the human lineage.

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Introduction

Several nonprimate mammal and nonhuman primate species use sophisticated combinatorial capacities in their call systems to influence conspecifics and/or predators (Blumstein 1999; Zuberbühler 2002; Clarke et al. 2006; Arnold and Zuberbühler 2008; Ouattara et al. 2009a, b; Schel et al. 2010; Candiotti et al. 2012; Kershenbaum et al. 2012; ten Cate and Okanoya 2012). Animals can generate, generalize, and categorize call strings or sequences; learn about the co-occurrence of elements within call sequences; and learn combinatorial rules such as attending to phonetic similarity between elements, co-occurrence of elements, and duplication of elements, although the animal capacity for learning abstract rules needs substantial more independent research (ten Cate and Okanoya 2012). Within the primate clade, such combinatorial rules have been mainly described in monkeys and lesser apes. Similar primate rules are only known to exist in humans. This is relevant to the debate on the emergence of recursion (the capacity to generate an infinite range of expressions from a finite set of elements), which is suggested to represent a uniquely human component of language (Hauser et al. 2002). Remarkably, however, the call systems of great apes have seldom been studied for the potential occurrence of call combinations (cf. Crockford and Boesch 2005; Clay and Zuberbühler 2011). In nonprimate mammals and nonhuman primates, such evidence has mostly been demonstrated in alarm call systems (Zuberbühler 2002; Clarke et al. 2006; Arnold and Zuberbühler 2008; Ouattara et al. 2009a, b; Schel et al. 2010; Candiotti et al. 2012; Kershenbaum et al. 2012). A relevant question is, thus, whether predation constituted an important ecological effect for the emergence and evolution of combinatorial rules in the primate lineage. Such possibility would be in agreement with several observations indicating that nonhuman primates exert some flexibility over their antipredator (acoustic) responses, such as variation of alarm calls according to predator guild (Kavanagh 1980; Fichtel and Van Schaik 2006; Fichtel and Kappeler 2011) and adjustment of antipredator responses to newly introduced predators or local predator guild (Gil-da-Costa et al. 2003; Rainey et al. 2004; Yorzinski and Ziegler 2007; Schel and Zuberbühler 2009).

A recent study has presented evidence supporting the hypothesis that increased predation pressure (i.e., number of predator species) increases the number of ways monkeys combine alarm call elements, that is compositionality (Stephan and Zuberbühler 2008). This hypothesis suggests an ecological/evolutionary scenario with predation operating

as selective pressure towards more call combinatorial rules in our early ancestors and conceivably towards the emergence of acoustic recursion in the hominin lineage. The predation pressure hypothesis (Stephan and Zuberbühler 2008) implies that predator species with different physiognomic/behavioral features elicit different call responses by primate prey; thus, a larger number of predator species will elicit a larger number of different call responses by the primate prey. There are potentially two ways to communicate about new predators. The first is to invent or learn novel call types. This, however, requires fine voluntary motor control over call production, which is limited in nonhuman primates (Cheney and Seyfarth 2005; cf. Owren et al. 2010). The second possibility is thus to assemble the same call types differently into novel sequences generating a larger number of different call responses using combinatorial rules (e.g., Zuberbühler 2002; Candiotti et al. 2012). Although it is highly likely that hominins experienced some periods of increased predation pressure (e.g., big cats, canids) in the course of evolution (Hart and Sussman 2008), for instance, during range expansions or migrations, the generality of the predation pressure hypothesis for increased compositionality in human evolutionary lineage has not yet been assessed in great apes.

Orangutans offer a useful great ape model to examine these two major questions on (1) the possibility of combinatorial rules in great ape alarm calls and (2) the possibility of predation effects on the compositionality of great ape alarm calls. On both islands where orangutans occur, Sumatra and Borneo, alarm calls towards potential predators comprise four different single calls—kiss squeak (KSQ), grumph (GR), gorkum (GK), and complex call (CXC)—and three combined calls—KSQ + GR, KSQ + GK, and KSQ + CXC (Hardus et al. 2009a), thus producing seven possible syllables. Each of these seven syllables has been well described and is distinguishable audibly and/or by visual inspection of spectrograms (Hardus et al. 2009a) (see aim.uzh.ch/orangutannetwork). Orangutan alarm call responses towards potential predators typically last several minutes and can continue for more than an hour, creating sequences of syllables with varying length and with silence gaps between sequences of varying length. Therefore, the orangutan alarm call system allows the analysis of compositionality at two levels: single and combined calls within syllables and syllables within sequences. Other antipredator behavioral responses by orangutans include shaking branches and throwing branches at the predator (Hardus et al. 2009b), but here, focus is only given to alarm calls.

The predators preying on orangutans differ between Sumatra and Borneo. While clouded leopards (*Neofelis diardi*) and pythons (*Python* spp.) constitute potential arboreal predators on both Borneo and Sumatra (Rijksen 1978), tigers (*Panthera tigris sumatrae*), which are largely terrestrial but

prey upon orangutans (Rijksen 1978), are only present in Sumatra. In Borneo, the presence of tigers has been suggested at two locations for the Late Pleistocene and Early Holocene (circa 10–12 ka (Piper et al. 2007) or 400–480 orangutan generations ago (Wich et al. 2009b)), but there is no evidence that their distribution extended beyond these regions and tigers have become extinct since then. Although the exact timing of this extinction is not known, there are no historical records of tigers in Borneo after this period. Hence, the geographic distribution of orangutan natural predators allows investigating the predation pressure hypothesis on the alarm calls of great apes. In the absence of a predator, a reduction of the number of different combinations is expected in Borneo, as the predator's specific call sequence would become obsolete and there would be no advantages for learning this sequence by individuals in the population. In monkeys, this process is observed over a period of 30 years (Stephan and Zuberbühler 2008); thus, one would expect, at least, similar effects in orangutans.

In this study, we exposed female orangutans to a predator model (i.e., tiger model) and to a control model (i.e., white model of the same shape) at two sites, one on each island, Ketambe (Sumatra) and Tuanan (Borneo). Only at Ketambe are orangutans familiar with tigers. We first assessed the possibility of combinatorial rules and the effect of predation at the syllable level (i.e., single and combined calls). When orangutans use combinatorial rules at the syllable level, we expect syllable frequencies to vary between models at Ketambe (because one model is familiar and the other unfamiliar), but not at Tuanan (because both models are unfamiliar). When predator presence affects orangutan use of syllables, we expect that syllable frequencies will differ between populations when presented with the tiger model (because the model is familiar in one population but unfamiliar in the other), but not when presented with the white model (because the model is unfamiliar in both populations).

Secondly, we assessed the possibility of combinatorial rules and effects of predation at the level of syllable sequences. When orangutans use combinatorial rules at the level of syllable sequences, we expect that the rate of performing (at least) two- and three-syllable sequences will differ between predator and control model at Ketambe, but not at Tuanan. When predation affects orangutan syllable sequences, we expect that the rate of (at least) two- and three-syllable sequences will differ between Ketambe and Tuanan towards the tiger model, but not towards the white model. If orangutans use syllable sequences with a larger number of syllables, this will be detectable in the use of two- and three-syllable sequences. Moreover, at each level of compositionality (syllables and syllable sequences), we condense our data and replicate the analyses by categorizing syllable and syllable sequences as (composed by) single or combined

calls, irrespective of the exact type of call(s). For instance, for KSQ, KSQ + GR, and KSQ + GK, we consider instead one single call and two combined calls, respectively. In addition, we analyzed the data using information theory algorithms (Kershenbaum et al. 2012) to validate the results obtained.

Methods

Site and data collection

Data were collected at Tuanan (2°09' S, 114°26' E), Central Kalimantan, Borneo, and Indonesia, between December 2004 and August 2005 and at Ketambe (3°41' N, 97°39' E), Aceh, Sumatra, and Indonesia, between December 2010 and May 2011, following the same protocol. Six females were tested at Ketambe and five females at Tuanan. These individuals constituted the most habituated adult females resident in the central part of each study site. Orangutans live in dispersed fission–fusion communities, where females spend the majority of their time alone with the exception of their own single offspring (Delgado and van Schaik 2000). Other females could not be experimentally tested due to extremely low encounter rates by human observers. All females tested were parous with dependent offspring, except one female (i.e., nulliparous) at each population. The predator model consisted of a realistic tiger-patterned sheet draped over a human demonstrator who is walking on fours (Fig. 1). A similar model, but covered with a white sheet, exposed to the same orangutan females, served as an experimental control, in order to isolate the effect of familiarity with tigers. When a focal female was between 12- and 20-m height in the forest, feeding, resting, or slowly moving, the model moved past in front of the focal. The model halted for approximately 2 min when the focal viewed it and then continued moving until out of sight. Model movements relative to the subject orangutan were coordinated by an

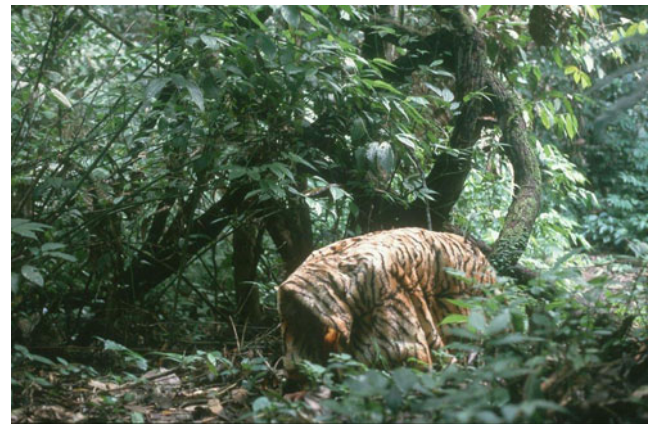


Fig. 1 Tiger model in experimental setting

additional human observer collecting behavioral and acoustic data continuously from the appearance of the model until 30 min after disappearance. Experiments were never conducted in the same location in the forest. Each individual was exposed only once to each model, and the two different models were presented to the same individual at least 5 days apart to avoid habituation. Presentation order of the models within population was pseudo-randomized according to the females whose location was known.

The use of a clouded leopard model as control in both populations was not conducted for several reasons. First, the presentation of the clouded leopard model on the ground (to preserve experimental settings consistent across models) could be perceived by orangutans as an encounter presenting little underlying danger, as clouded leopards characteristically hunt through the canopy. Second, the presentation of the model on the canopy would require a different presentation scheme since it would be impossible for a human demonstrator to walk on fours through the canopy. Third, because orangutans are fundamentally arboreal, the presentation of a model on the canopy, instead of on the ground, could be perceived differently by orangutans. For instance, a wild orangutan highly habituated to humans and followed for more than three decades may respond intensively when encountering human in the canopy (ARL and MEH, personal observation). Fourth, responses towards a model in the canopy could invoke responses due to proximity to the model, creating biases between models.

Data analyses

For syllable analyses, single- and combined-call syllable rates were considered during the first 10 min of the alarm call response towards either model, since in an encounter with a potential predator, this will be the most critical period in prey response. That is, during this period, we measured the number of occurrences of each of the seven syllables comprising orangutan alarm call repertoire (see above).

For syllable sequence analyses, firstly we identified the optimum duration of silence that would indicate a break between syllable sequences. This was necessary because silence gaps between orangutan syllables have varying durations, and the choice of intersequence gap affects the number and length of sequences. For instance, a 5-s silence gap between potential syllables sequences yields a smaller number of sequences than a 30-s silence gaps for the same data set. We calculated the duration of silence gaps at which the increase of the number of sequences with respect to gap duration decelerated (i.e., when the increase rate became less than 1). We considered this to be the optimum point because of the trade-off between simplicity/speed and versatile/informative communication in alarm calls (cf. Kemp

and Regier 2012). For this calculation, we used the first 10 min of alarm call response towards the tiger model by all six females at Ketambe, as these responses were expected to be the most syllable dense from all predator model experiments. We determined the number of two- and three-syllable sequences when considering 5-, 10-, 15-, 20-, 25-, and 30-s gaps between syllable sequences for these responses. We fitted a logarithmic curve through the average number of syllable sequences, averaged across the six females. The nonnegative numerator of the second derivative of this logarithmic curve indicates the length of the silence gaps above which the increase rate of the number of sequences becomes less than 1. This value is equal to the coefficient of $\ln(x)$ in the fitted logarithmic curve (Lyons 1995).

Secondly, we identified all two- and three-syllable sequences emitted by all females in both populations towards both models. When orangutans use syllable sequence rules, one expects that these will be frequently used and conventionalized between the individuals of the population. Accordingly, only those two- and three-syllable sequences that were used by at least two individuals of one population at one type experiment *and* that were produced at least five times by one of the two individuals were considered for statistical testing. A syllable comprised by a combined call (e.g., KSQ + GR) differed unequivocally from a syllable sequence composed by the same calls (e.g., KSQ – GR), in that calls follow each other immediately within a combined-call syllable (i.e., less than 500 ms) while they are separated by more than 3 or 4 s within a sequence.

Finally, to examine the presence of combinatorial rules by means of an alternative method, we used a technique taken from information theory to examine the data content of the different call sequences. We generated Markov transition tables separately for each individual, indicating the transition probabilities between common sequences, where each element $T_{a,b}$ of the transition matrix represents the probability that sequence a will be followed by sequence b . We then calculated the entropy of the transition table $H = -\frac{1}{N^2} \sum_a \sum_b T_{a,b} \ln[T_{a,b}]$, where N is the number of distinct sequences. Transition table entropy is a measure of the deviation from random sequences (Cover and Thomas 2006) and hence an indication of the extent to which combinatorial rules are being used. Entropy measures have been used to analyze animal acoustic communication sequences in various taxa, including hyraxes (Kershenbaum et al. 2012) and humpback whales (Suzuki et al. 2006). We used two-way ANOVA to test for differences in Markov entropy between populations and between models, using as our null hypothesis that neither population location (Sumatra vs. Borneo) nor model type (tiger vs. white) affects the combinatorial complexity of call sequences.

Apparatus

All calls were recorded during the experiments with a Marantz Recorder PMD-660 with a Rode NTG2 Microphone (at Ketambe), with a Marantz Recorder PMD222 with a Sennheiser Microphone ME 64, and with a Sony Recorder TCD-D100 with a Sony Microphone ECM-M907 (at Tuanan). Statistical tests were conducted using IBM SPSS 19 (2010, SPSS, Inc.), with significance level set at $P < 0.05$.

Results

Syllable analyses

Total emission rate of syllables did not differ between populations for both models (Mann–Whitney U : tiger model— $N_{Ketambe}=6, N_{Tuanan}=5$, exact $P=0.20$; white model— $N_{Ketambe}=6, N_{Tuanan}=5$, exact $P=0.18$). Median syllable rates (25 and 75 % percentiles) were 6.2 min^{-1} (2.7, 7.225) and 8.4 min^{-1} (5.75, 12.1) at Ketambe and Tuanan, respectively, towards the tiger model, and 0 min^{-1} (0, 3.1) and 4.3 min^{-1} (0.2, 8.35) towards the white model.

The emission rate of only one syllable (KSQ) was higher towards the tiger model than the white model at both sites Ketambe and Tuanan (A in Table 1 and Table S1). None of the syllable rates differed between populations for each model (B in Table 1 and Table S1). When condensing the data, and considering syllables solely either as single- or combined-call syllables (S or C), the emission rate of single-call syllables differed between models only at Tuanan, with higher emission rates towards the tiger (A in Table 1). Moreover, the emission rate of single-call syllables towards the tiger model was higher at Tuanan than at Ketambe (B in Table 1). To verify whether these results were solely an effect of high KSQ emission rates, we conducted the analyses once again but excluding KSQs. Emission rates of single calls differed no longer between models at Tuanan (Mann–Whitney test, $N=5, Z=-0.904, P=0.366$) or

between populations towards the tiger model (Mann–Whitney test, $N_{Ketambe}=6, N_{Tuanan}=5, Z=-1.354, P=0.176$).

Syllable sequence analyses

The number of two- and three-syllable sequences per minute increased when a longer duration of silence gaps between syllable sequences was permitted (Fig. 2). The average number of sequences plotted against the duration of silence gaps fitted a logarithmic curve ($R^2=0.957, y=17.514 \times \ln(x)+0.307$; Fig. 2). Accordingly, the logarithmic coefficient 17.514 indicates the optimum duration of silence gaps (see “Methods”). Since we assessed the number of syllables sequences at 5-s intervals, we considered the value of 15 s for the duration of silence gaps between syllables for subsequent analyses.

From a total of 49 (i.e., 7^2) possible two-syllable sequences, 33 different sequences were recorded at Ketambe towards the tiger model and 11 towards the white model, whereas 11 and 15 different sequences were recorded at Tuanan. The two populations did not differ in the total emission rate of two-syllable sequences to either of the models (Mann–Whitney U : tiger model— $N_{Ketambe}=6, N_{Tuanan}=5$, exact $P=0.2$; white model— $N_{Ketambe}=6, N_{Tuanan}=5$, exact $P=0.135$). Median two-syllable sequence rates (25 and 75 % percentiles) were 5.5 min^{-1} (1.725, 6.3) and 7.4 min^{-1} (4.65, 11.35) at Ketambe and Tuanan, respectively, towards the tiger model, and 0 min^{-1} (0, 2.725) and 3.0 min^{-1} (0.1, 7.5) towards the white model.

We determined whether the use of particular two-syllable sequences seemed habitual. Overall, eight two-syllable sequences were used by at least two individuals in a single population in response to the same model and were used at least five times by at least one of these individuals (Table S2). Within populations, the rate at which these two-syllable rates were given to the two models did not differ significantly (A in Table 2). However, two (out of eight) sequences given towards the tiger model (i.e., KSQ – KSQ and KSQ + GR – GR) were given at significantly higher rates, concerning one sequence at each population (B in Table 2).

Table 1 Exact P values of statistical comparison per syllable (A) between models within populations and (B) between populations for each models

		KSQ	GR	GK	CXC	KSQ + GR	KSQ + GK	KSQ + CXC	S	C
A	Ketambe	<i>0.041</i> (T)	0.655	0.715	0.109	0.102	0.144	0.066	0.225	0.141
	Tuanan	<i>0.043</i> (T)	1	0.655	0.317	0.461	0.345	1	<i>0.043</i> (T)	0.223
B	Tiger	0.056	0.361	1	1	0.203	0.134	0.104	<i>0.022</i> (Tu)	0.853
	White	0.056	0.361	1	1	0.203	0.134	0.104	0.251	0.91

Significance of italicized values at $p < 0.05$. S single call, C combined call

Letters in parentheses indicate model or population with significantly higher syllable emission rate: for A: T=tiger model and for B: Ke=Ketambe, Tu=Tuanan

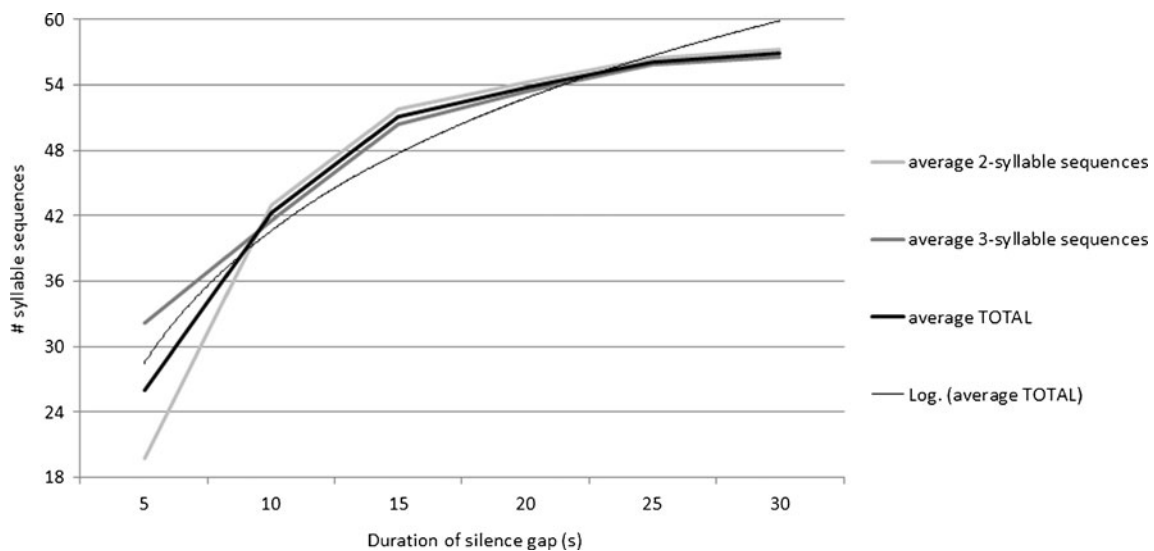


Fig. 2 Number of two- and three-syllable sequences vs. duration of silence gaps considered between these sequences

When condensing our data, none of the four possible two-syllable sequences (SS, SC, CC and CS) differed between the models at both sites (A in Table 3). However, the rate of one two-syllable sequence (i.e., single call–single call) towards the tiger model was higher at Tuanan than at Ketambe (B in Table 3).

Based on the same silence criterion, we also distinguished three-syllable sequences. From a total of 343 (i.e., 7^3) possible three-syllable sequences, 63 and 20 different sequences were recorded at Ketambe towards the tiger and the white model, respectively, and 23 and 27 different sequences were recorded at Tuanan, respectively. The rate of three-syllable sequences did not differ between populations for both models (Mann–Whitney *U*: tiger model— $N_{Ketambe}=6$, $N_{Tuanan}=5$, exact $P=0.17$; white model— $N_{Ketambe}=6$, $N_{Tuanan}=5$, exact $P=0.135$). Median three-syllable sequence rates (25 and 75 % percentiles) were 5.35 min^{-1} (1.5, 6.225) and 7.3 min^{-1} (4.9, 11.1) at Ketambe and Tuanan, respectively, towards the tiger model, and 0 min^{-1} (0, 0.27) and 2.6 min^{-1} (0.05, 7.35) towards the white model.

Overall, six three-syllable sequences were used by at least two individuals in a single population in response to

the same model and were used at least five times by the same individual (Table S3). One three-syllable sequence rate differed between models (i.e., KSQ – KSQ – KSQ) at Tuanan, with higher rates emitted towards the tiger model (A in Table 4). Two sequences (out of six) differed between populations (i.e., KSQ – KSQ – KSQ and KSQ + GR – KSQ – KSQ) towards the tiger model, with higher rates emitted at Tuanan (B in Table 4).

When condensing our data pertaining to three-syllable sequences, one of the possible eight (i.e., 2^3) three-syllable sequences differed between models (i.e., single call–single call) at Tuanan, with higher rates emitted towards the tiger model (A in Table 5). The same three-syllable sequence towards the tiger model also differed between populations, with higher rates at Tuanan (B in Table 5).

Information theory analysis

Markov entropy (and hence combinatorial complexity) was slightly higher at Ketambe ($N=7$, mean 1.34 ± 0.19 standard error (SE)) than Tuanan ($N=9$, mean 1.11 ± 0.11 SE). At

Table 2 Exact *P* values of statistical comparison of two-syllable sequences (A) between models within populations and (B) between populations for each model

		GR – GR	KSQ + GR – KSQ + GR	KSQ – KSQ	GR – KSQ + GR	KSQ + GR – GR	KSQ + CXC – KSQ + GR	KSQ + GR – KSQ	KSQ – KSQ + GR
A	Ketambe	0.715	0.144	0.18	0.715	0.715	0.18	1	0.593
	Tuanan	1	0.273	0.08	1	0.317	0.854	0.416	0.273
B	Tiger	0.082	0.712	0.015(Tu)	0.073	0.034(Ke)	0.833	0.109	0.222
	White	0.361	0.29	0.91	1	1	0.104	0.59	0.351

A Wilcoxon signed-rank test, B Mann–Whitney test

Letters in parentheses indicate model or population with significantly higher syllable emission rate

Table 3 Exact *P* values of statistical comparison of two-syllable sequences (A) between models within populations and (B) between populations for each models, considering single- and combined-call syllables irrespective of call type(s)

		SS	SC	CC	CS
A	Ketambe	0.345	0.465	0.109	0.465
	Tuanan	0.08	0.336	0.279	0.5
B	Tiger	0.044(Tu)	0.926	0.926	1
	White	0.205	0.29	0.09	0.134

S single call, *C* combined call, *A* Wilcoxon signed-rank test, *B* Mann–Whitney test

Ketambe, animals presented with the tiger model gave slightly more complex calls than when presented with the white model ($N=5$, mean 1.48 ± 0.49 SE vs. $N=2$, mean 1.00 ± 0.52 SE). In contrast, at Tuanan, the entropy was lower on presentation of the tiger model than the white model ($N=5$, mean 1.00 ± 0.33 SE vs. $N=4$, mean 1.25 ± 0.28 SE). However, the results of a two-way ANOVA test showed no significant effect for population ($P=0.601$), model ($P=0.590$), or population–model interaction ($P=0.115$). Sample sizes differed between information theory analysis and previous analysis because only individuals who produced alarm calls could be included in the information theory analyses.

Discussion

The results of this study show few differences between orangutan alarm call responses towards different models and between different populations. Foremost, the only difference between models at both populations concerned the emission rate of KSQs, where individuals of both populations emitted significantly more KSQs per unit of time towards the tiger model than the white model (Table 2). This suggests that both populations perceived a tiger-patterned sheet as being potentially more dangerous than a white sheet. This indicates that, as predicted by the multi-predator hypothesis (Blumstein 2006), pattern recognition at

Tuanan, where tigers are absent, may have persisted after potentially up to 480 generations due to the presence of other cat predators with a patterned fur, such as the clouded leopard. Nonetheless, it seems unlikely that orangutans in both populations could have mistakenly identified the tiger model as a clouded leopard (which is present in both populations), since the size and hunting techniques differ between the two cats and their fur pattern is distinct; in Sumatran tiger’s fur, the black outline is comprised by narrow and vertical stripes on a largely orange background with pronounced white parts, while in Sunda clouded leopard’s fur, the black outline is comprised by round forms, with both dense black and spotted sections and with thin orange gaps between black forms, without any pronounced white parts.

At Tuanan, a significantly higher emission rate of single calls was detected towards the tiger model than the white model (Table 2). However, this was verified to be an effect of the high emission rates of single KSQs. The fact that individuals at Tuanan emitted significantly higher rates of single-call syllables towards the tiger model than individuals at Ketambe seems also to be due to the high emission rates of single KSQs. At the level of syllable sequences, some two- and three-syllable sequences differed between models at Tuanan and between populations towards the tiger model. However, all these sequences included KSQs as one or two syllable(s). Hence, these results may therefore be an effect of considerably high emission rates of single KSQs. For instance, emission rates of KSQ + GR – GR towards the tiger model were significantly higher at Ketambe than Tuanan, but this sequence was not used significantly more at Ketambe towards the tiger model than the white model; thus, this population difference was unlikely meaningful.

Altogether we did not find evidence to support our predictions related to either the use of combinatorial rules or an effect due to predation guild size on combinatorial rules of orangutan alarm calls. We expected that different syllable or syllable types (i.e., S and C) would be used to indicate different models in the population experiencing tiger predation (i.e., Ketambe) while predicting these differences on

Table 4 Exact *P* values of statistical comparison of three-syllable sequences between models within populations and between populations for each model

		KSQ + GR – KSQ + GR – KSQ + GR	KSQ – KSQ – KSQ	KSQ – KSQ + GR – KSQ + GR	KSQ + GR – KSQ – KSQ	KSQ + GR – KSQ – KSQ + GR	KSQ + GR – KSQ + GR – KSQ
A	Ketambe	0.068	0.180	0.655	0.317	1	1
	Tuanan	0.273	0.043(T)	0.414	0.705	0.465	0.593
B	Tiger	0.664	0.015(Tu)	0.421	0.037(Tu)	0.246	0.146
	White	0.562	0.091	0.351	0.351	0.294	0.139

A Wilcoxon signed-rank test, *B* Mann–Whitney test

Table 5 Exact *P* values of statistical comparison of three-syllable sequences (A) between models within populations and (B) between populations for each model, considering single- and combined-call syllables irrespective of call type(s)

		SSS	SSC	SCS	SCC	CCC	CCS	CSC	CSS
A	Ketambe	0.345	0.715	0.593	0.715	0.068	0.715	1	0.715
	Tuanan	0.043(T)	1	0.273	0.465	0.273	0.715	0.498	1
B	Tiger	0.017(Tu)	0.925	0.773	0.711	0.644	0.711	0.562	0.848
	White	0.205	0.484	0.562	0.562	0.416	0.134	0.29	0.662

S single call, *C* combined call, *A* Wilcoxon signed-rank test, *B* Mann–Whitney test

Letters in parentheses indicate model or population with significantly higher syllable emission rate

syllable use to be absent in the population lacking this predator (i.e., Tuanan). However, this was not found. Syllables were not used differently by individuals of the two populations nor used differently against the two models. In addition, the analysis of two- or three-syllable sequences also did not uncover any patterns. Moreover, the information theory analysis did not reveal any difference in entropy. Therefore, we do not have evidence for the use of combinatorial rules in orangutans to signify predators.

The lack of significant effects may be due to the relatively low statistical power of analyses with small number of females comprising local populations. However, we sampled all possible females at each population, and extending the number of individuals would lead to heterogeneous samples. However, the few obtained significant results were opposite to the predictions built at the start of the study. Moreover, information theory analyses corroborated the results. Thus, conclusions can be drawn with relative confidence.

Interestingly, orangutans within populations showed considerable variability in their alarm call responses. These differences suggest that orangutan alarm call system may not be strictly hardwired and affect-based (sensu Owren and Rendall 2001), as commonly assumed. Indeed, orangutans are suggested to socially acquire some aspects of their alarm call system related to the production of KSQs (e.g., use of instrumental tools during KSQ production, van Schaik et al. 2003, 2009; Hardus et al. 2009b). This may also be the case with other types of alarm calls. Moreover, these considerable differences within populations exclude the possibility that habitat differences (e.g., canopy height above 12–20 m available for escape) affected our results in any crucial manner. These intrapopulation differences, in combination with relatively low numbers of individuals in the sample, limited our ability to interpret in detail the obtained results and to detect biologically meaningful differences in orangutan alarm calls towards different predators, specially so at the site where tigers were familiar. In addition to significant differences in the use of KSQs, other components of orangutan's antipredator behavioral responses showed differences

between the tiger and the white model. For instance, mean and maximum number of branches thrown at the models was 1 magnitude order higher towards the tiger than the white model (ARL, MEH, and SAW, unpublished data). While these latter data are preliminary and lay outside the direct scope of this article, they confirm to some extent that orangutans perceived the models differently and suggest that, as it occurs in monkey species (Kavanagh 1980; Fichtel and Van Schaik 2006; Fichtel and Kappeler 2011), alarm call usage may be flexible and dependent on multiple factors.

The results suggest that the combinatorial rules known to organize monkey alarm calls (Zuberbühler 2002; Arnold and Zuberbühler 2008; Ouattara et al. 2009a, b; Schel et al. 2010) do not apply in a straightforward way to orangutan alarm calls. Moreover, the absence of an island difference in orangutans' response suggests no effect of the size of predator guild on alarm call complexity in this genus, suggesting that the selective pressure due to predation on behavioral and alarm call responses is much stronger in monkeys than in orangutans. This may be a result of the relative larger body size of orangutans compared to monkeys, which reduces the number of predator species as, for instance, raptors do not prey on orangutans and a healthy adult may only be successfully hunted by the largest cat species. If this negative proportional rule between prey body size and predators' number is accurate, one may then expect smaller nonhuman primates (and perhaps smaller nonprimate mammals as well) to present a richer repertoire in terms of combinations' number relatively to bigger species (of the same taxon) when their alarm call system is based on call combinations. This may be addressed by future research.

Future work should also investigate whether the effect of predator guild applies to other great apes, which are on average more terrestrial. If it is confirmed, this suggests that predation may have remained a relatively relaxed selective pressure for ground-dwelling hominins, facilitated by the acquisition of effective material culture (e.g., van Schaik et al. 2003) and subsequent fire control (e.g., Wrangham and Books 2010), even though they must have encountered new

predator species both before and after migrations out of the region of origin, including new species of felids, canids, and ursids (Hart and Sussman 2008).

Overall, our results are consistent with the view that, within the primate clade, the emergence and use of combinatorial rules may be dependent on the number of critical events in the environment about which the individuals communicate, modulated by the species' ability to learn new calls. Thus, combinatorial rules are positively selected when the number of the species' single alarm calls is lower than the number of predators. This is the case in some monkey species, as mentioned above. On the other hand, because great apes may be able of extending their alarm call repertoire with new calls (Hopkins et al. 2007; Hardus et al. 2009b; Wich et al. 2009a, 2012) and because they are preyed upon by fewer species, the threshold for the emergence and use of combinatorial rules is not reached. In other monkey species other than Diana monkeys (*Cercopithecus diana*), such as vervets (*Chlorocebus pygerythrus*), selective pressures seem to operate differently, where each predator species is assigned a distinct single alarm call (Cheney and Seyfarth 1992), instead of a combined call or call sequence. Further studies are needed to examine the conditions that favor the evolution of such a system rather than the combined call-based alarm system of Diana monkeys. Moreover, the work by Stephan and Zuberbühler (2008) should be replicated with other monkey and nonprimate mammals species using combined calls to assess the general validity of the predation pressure hypothesis within such type of alarm systems and the putative indirect role of body size (as a determinant of predators' number). Only such a comparative database on the presence of combinatorial rules in multiple primate and nonprimate mammal species and the conditions favoring such rules will provide an evolutionary framework for understanding the evolution of speech combinatorial communication.

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