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Olive colobus (*Procolobus verus*) call combinations and ecological parameters in Taï National Park, Côte d'Ivoire

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Abstract

Animal communication is any transfer of information on the part of one or more animals that has an effect on the current or future behavior of another animal. The ability to communicate effectively with other individuals plays a critical role in the lives of all animals and uses several signals. Acoustic communication is exceedingly abundant in nature, likely because sound can be adapted to a wide variety of environmental conditions and behavioral situations. Olive colobus monkeys produce a finite number of acoustically distinct calls as part of a species-specific vocal repertoire. The call system of Olive colobus is structurally more complex because calls are assembled into higher-order level of sequences that carry specific meanings. Focal animal studies and Ad Libitum conducted in three groups of Olive colobus monkeys in Taï National Park indicate that some environmental and social parameters significantly affect the emission of different call combination types of this monkey species.

Keywords: Olive colobus, call combination, social parameter, environment parameter.

1. Introduction

Animal communication is any transfer of information on the part of one or more animals that has an effect on the current or future behavior of another animal. Close-range visual signals are used to send a variety of messages and sound signals carry over considerable distances and give information immediately. In any cases, animals communicate with their own kind or other species to coordinate the search for food, attract mates, bring up young, or escape from danger. In this process, various species send signals using sight, sounds, body language, touch, scent, complex chemicals, or a combination of all of these. The communication through vocalization is essential for many tasks including mating rituals, warning calls, conveying location of food sources, and social learning. For example, male mating calls are used to signal the female and to beat competitors in species such as hammer-headed bats, red deer, humpback whales and elephant seals. In whale species, whale song has been found to have different dialects based on location. Other instances of communication include the alarm calls of the Campbell monkey, the territorial calls of gibbons and the use of frequency in greater spear-nosed bats to distinguish between groups^[1].

The ability to communicate effectively with other individuals plays a critical role in the live of all animals and communication involves a sender and a listener. Whether we are examining how moths attract a mate, ground squirrels convey information about nearby predators, or chimpanzees maintain positions in a dominance hierarchy, communication systems are involved^[2]. Many often, both the sender and receiver benefit from exchanging information^[3]. Animals use a variety of sensory channels, or signal modalities, for communication. Visual signals are very effective for animals that are active during the day. Even if some visual signals are permanent advertisement, some are actively produced by an individual only under appropriate conditions^[4]. Acoustic communication is also exceedingly abundant in nature, likely because sound can be adapted to a wide variety of environmental conditions and behavioral situations. Thus, the field of vocal communication has been and continues to be investigated in the animal kingdom by researchers.

The study of vocal behavior in Primates has shown similarities between this group acts and vocalizations and Human language.

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Particularly, Primates alarm calls have attracted considerable attention, because in some cases different types of predators elicit acoustically distinct alarm calls. Vervet monkey, Diana monkeys, Campbell's monkeys, and Putty-nosed monkeys have demonstrated similar capacities^[5-11]. The Campbell's monkey call system may be the most complex. Adult males produce six different loud call types, which they combine into various sequences in highly context-specific ways^[12]. Previously, study conducted in this monkey species by^[13] has provided some evidence that call combinations can indeed carry semantic content independent of the composite elements. Campbell's males give acoustically different alarm calls to leopard and eagles. When these alarm calls are emitted, Diana monkeys respond to these calls with their own corresponding alarm calls. The study has shown that Diana monkeys no longer respond to the leopard or eagle alarm calls of Campbell's monkeys if preceded by "booms". The monkeys' behavior indicates that the "boom" calls change the semantic meaning of the alarm calls by turning predator-specific eagle or leopard alarm calls into ordinary alert calls with little referential specificity, because the "boom" always preceded disturbance events alarm call. Importantly, if combined with the Diana monkeys' own alarm calls, the booms have no effect, demonstrating that booms can only exert their semantic force on the Campbell's alarm calls.

More recently, it has been demonstrated that Olive colobus (*Procolobus verus*) in the same forest, has a vocal repertoire consists of eight types of unit calls characteristic of some social contexts^[9, 14]. Some of these unit calls are used in different ways depending on the sex of the individuals^[10]. Moreover, they were influenced by social and environmental parameters such as the day-time, the illumination of the environment, vegetation density and group activity^[15]. Three of these unit calls are regularly combined in different complex sequences depending on the context^[11]. For example, during intergroup encounters, Olive colobus emits call sequences consisted of the core "cbab". Ground predator elicits "ab" call sequences while aerial predator is signaled by a complex sequence of "cbab".

The purpose of this study is to determine the ecological parameters under which these calls of complex compounds are issued and the parameters that influence their emissions.

2. Methods

2.1 Study site

The rainforest of Taï National Park provided the framework of our study. With about 457 000 ha size, the TNP is the largest bloc of continuous, protected forest in West Africa. Vegetation is largely dense evergreen rainforest of Guinean type with a continuous canopy of between 25 and 45 m and emergent trees up to 60 m. The Taï forest is located at the south-western Côte d'Ivoire between 5°08 and 6°07 latitudes north and 6°47 and 7°25 longitudes west. The rainfall pattern is bimodal with two rainy seasons and two dry seasons or less rainfall. The average annual rainfall is 1,940 mm and the average temperature is 21 °C. This forest hosts about 140 mammals' species including 12 primate species.

2.2 Sampling

Focal animal and ad libitum observation were performed on three habituated groups of Olive colobus as part of our field survey from June 2001 to February 2002. Adults are defined as individuals whose secondary sexual characters are developed and clearly visible. Juveniles are those whose secondary sexual characters are not visible and infants are individuals that continue to suck.

2.2.1 Focal animal observation

All individuals of the three groups are clearly identified and known to make sure that the same individual is not collected twice in the period. Each individual is followed within 15 min, and several times alternately. Observations generally begin at 07:00 AM and end at 5: 30 PM. The first individual is chosen at random, then, we observe a break of 15 minutes to allow us to have enough time to seek for another individual. Then we collect information about the behavior of the focal individual and environmental parameters according to table 1.

Table 1: Description of Ecological parameters considered in the study

Variables	Modalities	Description
Individual	Adult male Adult Female Juvenile	Male sexually mature Female sexually mature Young that has not reached sexual maturity
Calls	Call combination	Call type emitted by combining unit call types
General illumination	Dark Medium Clear	No shadow on the ground, sky heavily overcast No shadows on ground, sky moderately overcast Direct sunlight
Vegetation density	Close Medium Open	Thick undergrowth, upper canopy not visible Moderate or little undergrowth Some tree crowns visible
Location in home range	Border Centre	Outer most or overlapping grid cells Inner grid cells not bordering on or visited by a neighboring group
Neighboring groups	Mixed Close Distant	Groups are together Separate groups of approximately 50m Separate groups of at least 100m
Polyspecific associations	Mixed Close Distant	Groups are together Separate groups of approximately 50m Separate groups of at least 100m
Key behaviors	Locomotion Game Foraging Sitting Grooming Sleep	Move action, locomotion Action to play alone or with others Action to feed To be sited Action to scratch, scratch or be scratched Action to sleep

2.2.2 Ad libitum observation

During the 15-minutes break between two focal samples, all calls emitted by Olive colobus are recorded using the same ecological variables mentioned in table 1. This enabled us, in addition to the calls recorded during the focal observations, to identify all the calls emitted by the group during the day and the ecological parameters under which these calls are emitted.

2.3 Data analysis

Data analysis consisted to calculate the frequencies of different combination call types emitted under the ecological parameters. Consequently, the test of Pearson Chi-square was conducted to determine whether the differences observed in the transmission frequencies of these calls were significant or not.

3. Results

3.1 Effects of environmental parameters on the call combinations

3.1.1 Day-time and call combinations

The frequencies of the call combination types emitted in morning time is $N_{\text{morning}} = 238$ (49.17%) while in evening $N_{\text{evening}} = 246$ (50.83%). Certain call types are dominant in the morning with ab 63.85%, bab 56.14% and cb 55.49%. By cons, acb with 62.50%, babcb with 75%, bacb 100%, cbab with 59.10%, bcbabcb with 81.82%, bcbacb with 75% and bcbab with 57.70% are more emitted in the evening time (table 2). Within each period, we have dominance of cbab 26.47% in the morning, while ab with 22.27% and cb with 18.49%. In the evening time we have: cbab with 36.99%, cb with 14.22%, ab with 12.19% and bcb with 10.97% (Table 3).

Chi-square test of Pearson notes a significant difference between the frequencies of the combination call types issued depending on the day-time (Chi-square = 23873, df = 11 and p = 0.013).

3.1.2 Illumination and call combinations

The effect of luminosity of the environment on the issue of different types of call combination is very remarkable with $N_{\text{clear}} = 250$ (51.65% of the overall calls), $N_{\text{medium}} = 169$ (34.91% of the overall calls) and $N_{\text{dark}} = 65$ (13.43% of the overall calls). Our results reveal that few calls: ab, acb, bab, bacb, bcbacb are usually issued when the illumination of the environment is not total. While others combinations of calls (cbab, cb and bcbab) are issued mainly in time of total illumination. Put out the calls babcb and bcbabcb, all the other calls are emitted in the dark period but in lower proportions than in the other two types of lighting (table 2). Within each type of lighting differences appear in call combinations. Indeed for *clear-illumination*, the highest frequencies of call combinations are 33.60% for cbab, 18.80% for cb, 16% for bcb and 12% for ab. In *medium-illumination*, call combinations are dominated by cbab (28.97%), ab (20.70%), bab (14.80%) and cb (13.60%). In *dark illumination*, we have again domination of the cbab (32.31%), ab (27.69%) and bab (15.40%) (Table 3). Call combinations are highly tied to the illumination of the environment (Chi-square = 68.048, df = 33, and p < 0.001).

3.1.3 Vegetation density and call combinations

Calls occurred mostly in dense vegetation $N_{\text{dense}} = 325$ (67.15%) than medium vegetation $N_{\text{medium}} = 116$ (23.96%) and opened vegetation $N_{\text{open}} = 43$ (8.88%) for. Apart from call acb which was more issued in medium vegetation (62.50%), all other call combinations were emitted in dense vegetation (Table 2). Within covered vegetation, we have domination of cbab (35.07%), cb (16.31%) and ab (13.54%). While in opened vegetation, cbab is more emitted (37.21%) than cb (16.28%) and bab (16.28%). With regard to medium covered vegetation, the domination order of call combination types is ab (28.45%), cbab (20.70%) and cb (16.40%) (Table 3).

Table 2: Frequency of call combination types based on environmental parameters considered in our study

Parameters	Variable	Combination call cores										
		ab	acb	bab	babcb	bacb	bcb	cbab	bcbabcb	bcbacb	cb	bcbab
Illumination	Clear	36.14	37.50	38.59	50.00	0.00	72.72	54.55	72.72	0.00	59.49	53.84
	Medium	42.16	50.00	43.86	50.00	66.66	25.45	31.82	27.28	75.00	29.11	34.61
	Dark	21.68	12.50	17.54	0.00	33.34	1.82	13.63	0.00	25.00	11.39	11.54
Day time	Morning	63.85	37.50	56.14	25.00	0.00	50.90	40.90	18.18	25.00	55.69	42.30
	Afternoon	36.15	62.50	43.86	75.00	100	49.10	59.10	81.82	75.00	44.31	57.70
Home range	Border	65.06	100	64.91	25.00	0.00	69.09	65.58	81.82	25	65.82	88.46
	Centre	34.94	0.00	35.09	75.00	100	30.91	34.42	18.18	75.00	34.18	11.54
Stratum	Strate0	0.00	0.00	0.00	0.00	0.00	0.00	0.64	0.00	0.00	0.00	0.00
	Strate1	28.91	0.00	0.00	0.00	0.00	25.45	23.37	18.18	50.00	15.19	7.69
	Strate2	62.65	8.75	0.00	100	100	67.28	52.60	54.54	50.00	62.02	61.53
	Strate3	6.02	12.50	0.00	0.00	0.00	7.27	20.13	18.18	0.00	16.45	26.92
	Strate4	2.40	0.00	0.00	0.00	0.00	0.00	3.24	9.10	0.00	5.06	3.84
Vegetation	Strate5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.26	0.00
	Dense	53.01	12.50	64.91	75.00	100	72.72	74.02	81.82	75.00	67.08	69.23
	Medium	39.76	62.50	22.80	25.00	0.00	23.63	15.60	9.09	25.00	24.05	23.08
	Open	7.23	25.00	2.28	0.00	0.00	3.64	10.38	9.09	0.00	8.86	7.70

3.1.4 Location in the home range and call combinations

Our results showed that call combinations is much influenced by the position in the home range (Chi-square = 64.172, df = 11, p < 0.0001). We have a very clear difference between the border and the centre with $N_{\text{border}} = 324$ (66.94%) against $N_{\text{centre}} = 160$ (33.06%). Moreover, we note that all calls *acb* (N = 8) were issued alongside the home range while *bacb* (N = 3) is emitted in the centre of this living space. Eight of the call combination types

recorded are more issued when the monkeys visits the border of the home range. These calls are: ab, acb, bab, bcb, cbab, bcbabcb, cb and bcbab. In opposite babcb, bacb and bcbacb have been more encountered in the centre of the home range (Table 2). Both at the border and centre of the home range, the call combinations most emitted by Olive colobus are cbab (31.17%), ab (16.67%), cb 16.04% for border; for the centre we have cbab (33.13%), ab (18.13%) and cb (16.88%) (Table 3).

3.1.5 Occupation of stratum and call combinations

Strate2 records the highest frequency of call combinations, $N_{strate2} = 286$ (59.09%) followed respectively by strate1, $N_{strate1} = 111$ (22.93%), strate3 $N_{strate3} = 71$ (14.67%) and strate4 $N_{strate4} = 14$ (2.89%). When considering the overall stratum, cbab is dominant

in all of them followed by ab in strata 1 (21.62%) and 2 (18.18%); then by cb in strata 3 (18.31%) and 4 (28.57%) (Table 3).

However, there is no significant difference between the observed frequencies in call combinations emission and the position of Olive colobus in vertical stratification of the forest (Chi-square = 49.307, $df = 55$ and $p = 0.691$).

Table 3: Frequency of call combination types inside each environmental parameter considered in our study

Calls	Environmental parameters															
	Illumination		Day time			Home range		Stratum					Vegetation			
	Clear	Medium	Dark	Morning	Afternoon	Border	Centre	Strate 0	Strate1	Strate2	Strate3	Strate4	Strate5	Dense	Medium	Open
ab	12,00	20,70	27,69	22,27	12,20	16,67	18,13	0,00	21,62	18,18	7,04	14,30	0,00	13,54	28,45	13,95
acb	1,20	2,40	1,54	1,26	2,03	2,50	0,00	0,00	0,00	2,45	1,41	0,00	0,00	0,31	4,31	4,65
bab	8,80	14,80	15,40	13,45	10,16	11,41	12,50	0,00	17,12	10,14	11,27	7,14	0,00	11,40	11,20	16,28
babcb	0,80	1,17	0,00	0,42	1,22	0,31	1,87	0,00	0,00	1,40	0,00	0,00	0,00	0,92	0,84	0,00
bacb	0,00	1,20	1,54	0,00	1,22	0,00	1,87	0,00	0,00	1,05	0,00	0,00	0,00	0,92	0,00	0,00
bc	16,00	8,30	1,54	11,76	11,00	11,73	10,63	0,00	12,61	12,94	5,63	0,00	0,00	12,30	11,21	4,65
cbab	33,60	28,97	32,31	26,47	36,99	31,17	33,13	100,00	32,42	28,32	43,66	35,71	0,00	35,07	20,70	37,21
bcbabcb	3,20	1,77	0,00	0,84	3,66	2,78	1,25	0,00	1,80	2,10	2,82	7,14	0,00	2,77	0,86	2,33
bcbacb	0,00	1,77	1,54	0,42	1,22	0,30	1,87	0,00	1,80	0,70	0,00	0,00	0,00	0,91	0,86	0,00
cb	18,80	13,60	13,82	18,49	14,22	16,04	16,88	0,00	10,81	17,13	18,31	28,57	100,00	16,31	16,40	16,28
bcbab	5,60	5,32	4,62	4,62	6,08	7,09	1,87	0,00	1,82	5,59	9,86	7,14	0,00	5,55	5,17	4,65
Total	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00

3.2 Effects of social parameters on call combinations

3.2.1 Group activity and call combinations

The analysis of three of the most performed activities showed that the highest call combinations occurred when sitting, $N = 393$ (81.19%) than foraging, $N = 47$ (9.71%) and locomotion, $N = 44$ (9.09%). The majority of the call combinations was issued when the monkey was sat. In addition, some call combinations were recorded during foraging (*acb* 35.50%, *bcbab* 26.92%, *cb* 15.19% and *ab* 13.25%) and during locomotion (*bcbabcb* 18.18%, *ab*, *acb* 12.05% each, and at lower frequencies *bc*, *cbab*, *cb* and *bcbab*) (table 4). Within sitting activity the frequency of call combinations differ from one to another. When sitting, *cbab* is more emitted (34.09%) than *ab* (15.78%) and *cb* (14.78%). During forage, *cb* is the most combined call emitted (25.53%) compare to *ab* (23.40%) and *cbab* (14.90%) whereas during locomotion, *cbab* was more emitted (29.55%) than *ab* (22.73%) and *cb* (20.45%) (Table 5).

The emission of these calls frequencies present a highly significant difference with Chi-square = 142.726, $df = 55$ and $p < 0.001$.

3.2.2 Dispersion of the group and call combinations

Call combination types dominated when Olive colobus individuals are together $N_{together} = 469$ (96.90%) than spread $N_{dispersed} = 15$ (3.10%). Four types of call combinations (*cbab*, *abcb*, *bab* and *ab*) were issued when the individuals are dispersed. When the monkeys are together they emit all types of handsets calls but with a dominance of *cbab* $N = 149$ (31.76%), *ab* $N = 81$ (17.27%), *cb* $N = 79$ (16.84%), *bcb* $N = 55$ (11.72%) and *bab* $N = 54$ (11.51%) (Table 4). When considering each grouping category, *cbab* and *bcbab* are the most emitted when monkeys are dispersed. However *cbab*, *ab* and *cb* are the most call combinations issued when Olive colobus individuals are together (table 5).

The differences observed between call combinations and the dispersion of the group were significant (Chi-square = 23.323, $df = 11$ and $p = 0.016$).

3.2.3 Individual age class and call combinations

All the combination call cores recorded during the study were the vocalization of adult, males or female (table 4). When considering the different call combination types, the most issued are *cbab* $N = 154$, (31.82%), *ab* $N = 83$ (17.15%), *cb* $N = 79$ (16.32%), *bab* $N = 57$ (11.78%) and *bcb* $N = 55$ (11.40%). The others call types appear

in low rate (table 5).

Chi-square test shows a highly significant difference between these combinations issued by adults (Chi-square = 57.247, $df = 22$, $p < 0.001$).

3.2.4 Sex of the individual and call combinations: None call combination regarding individuals of indeterminate sex including juvenile and infant was recorded. The maximum combination calls is emitted by adult males, $N = 432$ (89.25%) versus adult females, $N = 52$ (10.75%). Most of call combinations were recorded within the males, while three of them were registered within the females (*bacb*, *bcbabcb* and *bcbacb*) (table 4). In each sex class, females emit more *ab* (42.31%), *cb* (19.23%) and *acb* (11.54%) while males emit more *cbab* (34.49%), *cb* (15.97%) and *ab* (14.12%) (Table 5).

These differences in the emission of combinations call types based on the sex of the individual are highly significant (Chi-square = 776.970, $df = 22$, $p < 0.001$).

3.2.5 Presence of neighbor and call combination

In general, the number of call combinations emitted decreases with the increase of the individual target neighbor except the number of neighbor = 1. We were unable to determine the number of neighbors in 52 cases. Olive colobus monkeys emit more call combinations when there is no individual within five meters of them with 34.45% of cases versus 27.52% for two neighbors, 18.57% for one neighbor, 15.66 % for three neighbors, 2.46% for four neighbors and 1.34 % for five neighbors. No call combinations was heard when there were six neighbors, a single call (*cbab*) was issued in the presence of 5 neighbors and 5 call combinations in the presence of four neighbors (*bab*, *bcb*, *cbab*, *bcbabcb* and *cb*). In the presence of one neighbor the calls most often issued are *cbab*, *cb* and *ab*. The *babcb* calls have been heard in the presence of one or two neighbors within five meters of the transmitter. However, *bcbacb* were issued three times by individuals with no neighbors (table 4). When considering the different types of call combinations issued in accordance with a group of neighbors, we note that in all cases the most dominant are *cbab*, *ab* and *cb* (Table 5)

According to the Chi-square test of Pearson these differences are highly significant (Chi-square = 1633.022, $df = 77$ and $p < 0.001$).

Table 4: Frequency of call combination types based on social parameters considered in our study

Parameter	Variable	call Combination cores										
		<i>ab</i>	<i>acb</i>	<i>bab</i>	<i>babcb</i>	<i>bacbc</i>	<i>bc</i>	<i>cbab</i>	<i>bcbabcb</i>	<i>bcbacb</i>	<i>cb</i>	<i>bcbab</i>
Activity	Sit	74,70	50,00	0,00	100,00	100,00	87,27	87,01	81,82	100,00	73,41	69,23
	Forage	13,25	37,50	0,00	0,00	0,00	7,28	4,55	0,00	0,00	15,19	26,92
	Locomotion	12,05	12,50	0,00	0,00	0,00	5,45	8,44	18,18	0,00	11,39	3,84
	Play	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
	Sleep	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Age	Adult	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00	100,00
	Juvenile	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
	Infant	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Dispersion	Dispersed	2,40	0,00	5,26	0,00	0,00	0,00	3,24	0,00	0,00	0,00	19,23
Sex	Together	97,60	100,00	94,73	100,00	100,00	100,00	96,75	100,00	100,00	100,00	80,77
	Female	26,50	25,00	10,53	25,00	0,00	7,27	3,25	0,00	0,00	12,66	7,70
	Male	73,50	75,00	89,47	75,00	100,00	92,73	96,75	100,00	100,00	87,34	92,30
Neighbor	0	34,94	37,50	36,84	0,00	33,33	34,54	26,62	18,18	25,00	34,17	38,48
	1	16,86	0,00	12,30	50,00	33,33	21,81	16,88	27,27	0,00	20,25	3,84
	2	25,30	12,50	19,29	50,00	0,00	18,18	25,97	36,36	0,00	32,91	23,07
	3	9,63	12,50	12,28	0,00	33,33	18,18	16,88	18,18	75,00	7,59	15,38
	4	0,00	0,00	3,50	0,00	0,00	1,81	1,29	18,18	0,00	1,26	0,00
	5	0,00	0,00	0,00	0,00	0,00	0,00	0,65	0,00	0,00	0,00	0,00
	6	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
	Not seen	13,25	37,50	15,78	0,00	0,00	5,45	11,68	0,00	0,00	3,79	19,23

Table 5: Frequency of call combination types inside each social parameter considered in our study

	Activity			Age	Dispersion		Sex		Neighbor					
	Seat	Feed	Locomotion	Adult	Dispersed	Together	Femelle	Male	Neig0	Neig1	Neig2	Neig3	Neig4	Neig5
<i>ab</i>	15,78	23,40	22,73	17,15	13,34	17,27	42,31	14,12	18,83	17,07	17,35	11,94	0,00	0,00
<i>acb</i>	1,02	6,38	2,27	1,65	0,00	1,70	3,85	1,39	1,95	0,00	0,83	1,49	0,00	0,00
<i>bab</i>	12,47	6,38	11,36	11,78	20,00	11,50	11,54	11,81	13,64	8,54	9,10	10,45	28,57	0,00
<i>babcb</i>	1,02	0,00	0,00	0,82	0,00	0,85	1,92	0,69	0,00	2,44	1,65	0,00	0,00	0,00
<i>bacbc</i>	0,75	0,00	0,00	0,62	0,00	0,64	0,00	0,69	0,65	1,22	0,00	1,49	0,00	0,00
<i>bc</i>	12,21	8,51	6,82	11,40	0,00	11,73	7,69	11,81	12,34	14,63	8,26	14,92	14,28	0,00
<i>cbab</i>	34,09	14,90	29,55	31,82	33,33	31,77	9,62	34,49	26,62	31,71	33,06	38,81	28,59	100,00
<i>bcbabcb</i>	2,28	0,00	4,55	2,27	0,00	2,35	0,00	2,55	1,30	3,66	3,31	1,49	14,28	0,00
<i>bcbacb</i>	1,02	0,00	0,00	0,82	0,00	0,85	0,00	0,92	0,65	0,00	0,00	4,48	0,00	0,00
<i>cb</i>	14,78	25,53	20,45	16,32	0,00	16,84	19,23	15,97	17,53	19,51	21,48	8,96	14,28	0,00
<i>bcbab</i>	4,58	14,90	2,27	5,35	33,33	4,50	3,84	5,56	6,49	1,22	4,96	5,97	0,00	0,00

Table 6: Frequency of combination call types based on polyspecific associations during our study

Species	State	Combination core										
		<i>ab</i>	<i>acb</i>	<i>bab</i>	<i>babcb</i>	<i>bacbc</i>	<i>bc</i>	<i>cbab</i>	<i>bcbabcb</i>	<i>bcbacb</i>	<i>cb</i>	<i>bcbab</i>
Atys	Absent	78,31	100,00	73,37	100,00	100,00	54,54	59,10	81,82	100,00	63,29	69,23
	Mix	18,07	0,00	15,79	0,00	0,00	32,72	29,87	18,18	0,00	24,05	19,23
	Close	3,61	0,00	10,52	0,00	0,00	12,73	11,04	0,00	0,00	12,66	11,54
Badius	Absent	42,17	12,50	42,10	25,00	33,33	27,27	37,70	45,45	25,00	29,11	50,00
	Mix	50,60	87,50	43,86	50,00	66,67	50,91	48,70	18,18	50,00	53,16	46,15
	Close	7,23	0,00	14,03	25,00	0,00	21,82	13,64	36,36	25,00	17,72	3,85
Campbell	Absent	60,24	87,50	45,61	25,00	0,00	30,91	20,78	45,45	0,00	36,71	63,38
	Mix	39,76	12,50	50,87	75,00	100,00	61,82	74,67	54,54	100,00	58,23	34,61
	Close	0,00	0,00	3,51	0,00	0,00	7,27	4,55	0,00	0,00	5,06	0,00
Diana	Absent	97,59	100,00	94,73	100,00	100,00	76,36	74,02	72,73	100,00	86,07	76,92
	Mix	2,41	0,00	1,75	0,00	0,00	0,00	3,90	0,00	0,00	0,00	23,08
	Close	0,00	0,00	3,51	0,00	0,00	23,64	22,07	27,27	0,00	13,92	0,00
Petaurista	Absent	49,40	37,50	40,35	25,00	0,00	49,10	45,45	54,54	25,00	39,24	23,08
	Mix	49,40	62,50	47,37	75,00	100,00	40,00	43,50	45,45	75,00	48,10	76,92
	Close	1,20	0,00	12,28	0,00	0,00	10,91	11,04	0,00	0,00	12,66	0,00
Polykomos	Absent	77,11	62,50	78,95	100,00	100,00	76,36	68,83	81,82	100,00	64,56	69,28
	Mix	20,48	37,50	21,05	0,00	0,00	21,82	28,57	18,18	0,00	34,18	30,77
	Close	2,41	0,00	0,00	0,00	0,00	1,82	2,60	0,00	0,00	1,27	0,00
Verus	Absent	97,59	100,00	94,73	100,00	100,00	76,36	74,02	72,73	100,00	86,07	76,92
	Mix	2,41	0,00	1,75	0,00	0,00	0,00	3,90	0,00	0,00	0,00	23,08
	Close	0,00	0,00	3,51	0,00	0,00	23,64	22,07	27,27	0,00	13,92	0,00

3.2.6 Polyspecific association and call combinations

We recorded the maximum call combinations when Olive colobus was associated with Red colobus, than Campbell's monkeys and the Lesser spot-nosed monkeys. Very few calls are recorded in the

presence of Diana guenon (neighbor), the Black-and-white colobus and Sooty mangabey. Call combinations formed by *acb*, *babcb*, *bacbc* and *bcbacb* were not issued by Olive colobus in association with the Sooty mangabey while all the call combinations recorded

during the study were heard at least once during associations with Red colobus monkeys, Campbell's monkeys and Lesser spot-nosed monkeys. The call combinations compound by *babcb*, *bacb* and *bcacb* have not been heard when Olive colobus was associated with the Black-and-white colobus. During intergroup encounters, combination calls issued, at least once, by Olive monkeys were composed of: *ab*, *bab*, *bc*, *cbab*, *bcbabcb*, *cb* and *bcbab* (Table 6).

4. Discussion

Animal communication is classically defined as occurring when "...the action of or cue given by one organism (the sender) is perceived by and thus alters the probability pattern of behavior in another organism (the receiver) in a fashion adaptive to either one both of the participants"^[4]. The ability to communicate effectively with other individuals plays a critical role in the lives of all animals and uses several signals. Tactile signals, in which physical contact occurs between the sender and the receiver, can only be transmitted over very short distances. Tactile communication is often very important in building and maintaining relationship among social animals^[16]. Acoustic communication is also exceptionally abundant in nature, likely because sound can be adapted to a wide variety of environmental conditions and behavioral situations. Sounds can vary substantially in amplitude, duration, and frequency structure, all of which impact how far the sound will travel in the environment and how easily the receiver can localize the position of the sender^[4].

Whether tactile, visual, chemical, acoustic (vocal or non-vocal), or any other types, communication signals are used to transmit information to individuals of the same species (intraspecific communication) or different species (interspecific communication). A number of functions of communication have been studied in particular detail. They include agonistic interactions (everything to do with contests and aggression between individuals), mating rituals (signals made by members of one sex to attract or maintain the attention of potential mate, or to cement a pair bond), ownership/territorial (signals used to claim or defend a territory, food, or a mate), food-related signals ("food calls" that attract a mate, or offspring, or members of a social group generally to a food source), alarm calls (signals made in the presence of a threat from a predator, allowing all members of a social group and often members of other species to run for cover, become immobile, or gather into a group to reduce the risk of attack) etc.^[17-18].

Most primates spend their lives in complex, tightly woven societies and need to frequently communicate with each other. Like other animals, primates communicate to satisfy their biological and social needs, such as avoiding predators, interacting with other group members, or maintaining cohesion during travel. To this end, they use a range of different signals^[19]. For many primates, vocalizations are the main channel of communication. Non-human Primates vocal repertoires shown that these animals can use unit or combination call types to communicate^[14, 11]. This ability to combine unit call types into sequences more complexes has been demonstrated in some species like vervet^[5], Diana monkeys^[13], Campbell's monkey^[20] and Olive colobus monkeys^[14].

In addition, some environmental and behavioral parameters have significant influence on the emission of unit call types of Olive colobus monkeys^[15], and also on its combination call types. In this monkey species, the ability to combine calls is exclusive to adults with a very important part for males. Regarding females, they show low complexity sequences involving mainly two types of unit calls (a, b or b, c). However, the same authors reported that some

combination calls integrate three unit calls a, b and c^[11]. These calls are emitted with no preference of day-time. These calls serve both to intragroup and intergroup communication, and also to warn of the presence of predators or disturbances. The stimuli of these events are not necessarily related to a period in the day. Indeed, a predator attack can occur at any time of the day although some predators prefer to hunt when the lightning is low and in dense vegetation^[7, 21]. Therefore, these conditions under which hunting seems to be favored are likely to explain the dominance of combination calls in dense vegetation, medium and low lightness.

Monkeys avoid some predators by hiding themselves and being silent in the foliage. The stratum 2 is supposed to be the place of camouflage for Olive colobus to escape from predators. The other mean to fight against predation is polyspecific association^[22, 23]. According to these authors, the other species and especially Red colobus initiate the association with Diana guenon. During these associations more calls are issued in the presence of Red colobus, Campbell's monkeys and lesser spot-nosed monkeys^[14]. In addition, calls emitted in the presence of other groups of Diana monkeys, therefore Olive colobus, were a lot when the groups were closer. During polyspecific associations, in addition to intraspecific communication, animals also benefit from interspecific communication. Some animals even develop special provisions allowing them to make optimal the use of this communication type. Indeed, one study suggested that the Madagascan spiny-tailed iguanas have well-developed ears despite the fact that they don't communicate vocally. So they can hear the warning calls of the Madagascan paradise flycatcher. The two species have nothing in common except for the fact that they share a general habitat and raptors like to snack on them. So when an iguana hears a bird raise the alarm among other birds, it likely knows to be on alert for incoming predators, too^[24].

Communication signals also play an important role in conflict resolution, including territory defense^[18]. Olive colobus monkeys visit all its home range which is also the territory of the associated Diana guenon group. The edges of the home range constitute area where the chances to meet other groups of monkeys of the same species increase, the monkey perform combination call types working like spacing-call^[5, 25-26]. During intergroup encounter it was noted that individuals were closer to each other and issue contact calls that decrease with increasing the number of neighbors within a radius of five meters^[11]. According to^[5], contact calls maintain social cohesion. In this sense, monkey feel directly related to the individual of the same group that is not seen because of the dense vegetation of the TNP. It is therefore clear that the issuance of these call types decreases, as we observed in our study, where visual communication is used with individuals very close to each other. In contrast to the Diana guenon which the male does not emit contact calls^[27], male Olive colobus often involves in production of this call type^[9, 11]. In addition to primate species, contact calls are used by a wide variety of birds and mammals^[1].

5. Conclusion

The vocal behavior of Olive colobus monkeys is significantly influenced by some environmental and social parameters. Indeed, this monkey visits its home range without any preference party (border or centre) in the quest for food and mostly, Olive colobus uses the lower strata (5-15 meters). However, individuals reduce the distance between them when they visit the border of their home range. In all cases Olive colobus individuals are interconnected by vocal communication with unit or call combination emitted in

different social contexts. Thus, the illumination of the environment, vegetation density, the position in the home range, the number of neighbors within a radius of 5 meters and polyspecific association affect the emission frequency of call combinations of this monkey in Taï National Park.

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