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COMBINATION CALLS IN OLIVE COLOBUS MONKEYS (*PROCOLOBUS VERUS*) IN TAÏ NATIONAL PARK, CÔTE D'IVOIRE

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ABSTRACT

*In many primate species, individuals produce a finite number of acoustically distinct calls as part of a species-specific vocal repertoire. The calls usually have context-specific functions, such as defending a home range, avoiding predators, or alerting conspecifics to a food source, etc. In some primates, call systems are structurally more complex because calls are assembled into higher-order level of sequences that sometimes carry specific meanings. Here, we describe a specific vocal acoustical structure which revealed a high level of combination of finite vocal unit in sequences. We conducted focal animal samples method in three habituated groups of Olive colobus monkeys (*Procolobus verus*). Three call combination types in sequence were found composed from two to five call units. Some of these call combinations were linked to specific contexts. Our study thus provides further evidence that the propensity to combine acoustic units into higher order sequences is not an exclusively human trait but a behavioural feature that may be widespread in the primate communication.*

Key Words: Primates, Olive colobus, Taï national park, Combination call, Call context

INTRODUCTION

Among the axes explored to understand the origin and evolution of language, one research line consist to use a comparison between non-human primate and human language. Primate alarm calls have attracted considerable attention, particularly because in some cases different types of predators elicit acoustically distinct alarm calls. Vervet monkeys are the classic example, but other

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species such as Diana monkeys, Campbell's monkeys, and putty-nosed monkeys have demonstrated similar capacities (Struhsaker 1967; Seyfarth *et al.* 1980; Zuberbühler *et al.* 1997; Zuberbühler 2000d, Bene et al. 2007; Bene & Zuberbuehler 2009; Ouattara 2009a,b). In Most cases, Primate alarm signals generally consist of structurally unique and discrete call types that can be distinguished by ear.

More recently, there have been a number of cases in which it has been demonstrated that non-human primates can go beyond this simple semanticity in which one call type belongs to one discrete predator context. The Campbell's monkey call system may be the most complex example of 'proto-syntax' in animal communication known to date. Indeed, adult males produced six different loud call types, which they combine into various sequences in highly context-specific ways (Ouattara et al., 2009b). Before this relevant finding, it has been demonstrated in Nigerian that putty-nosed monkeys, for instance, produce two call types in response to predators, the *hacks* and *pyows*. Individual calls do not denote a particular predator type; however, instead, calls are given as part of longer structurally distinct sequences that are given in context-specific ways (Arnold & Zuberbühler 2006a). In black-and-white colobus monkeys species (Colobus guereza), callers often introduce their powerful *roars* with a brief *snort*. Marler (1972) argued that the *snorts* emitted alone act as alarm calls, while they function as group spacing calls if combined with the *roars*.

Whether or not these combinatorial differences are perceptually meaningful to recipients has never been tested. A third study, finally, conducted with West African Campbell's monkeys (Cercopithecus campbelli) in Taï National Park has provided some evidence that call combinations can indeed carry semantic content independent of the composite elements (Zuberbühler 2002). Campbell's males give acoustically different alarm calls to leopard and eagles. Diana monkeys who live sympatrically with Campbell's monkey respond to these calls with their own corresponding alarm calls. To some disturbances, Campbell's male also emit a pair of low resounding "*boom*" calls that always precede their alarm calls. Playback experiments have shown that Diana monkeys no longer respond to the leopard or eagle alarm calls of Campbell's monkeys if preceded by "*booms*". The monkeys' behaviour indicates that the "*boom*" calls devaluate the semantic meaning of the alarm calls by turning predator-specific eagle or leopard alarm calls into ordinary alert calls with little referential specificity. Importantly, if combined with other vocalisations, such as the Diana monkeys' own alarm calls, the *booms* have no effect, demonstrating that *booms* can only exert their semantic force on the Campbell's own alarm calls.

In this study, we were interested in the vocal acoustical structure of the olive colobus monkeys. In the Taï forest, Cote d'Ivoire, this species lives sympatrically with seven other monkey species including two other colobines (western red colobus, Procolobus badius badius and western black-and-white colobus, Colobus polykomos). The olive colobus is the smallest of the three colobines (Oates *et al.* 1994). The species have been studied before both on Tiwai Island (Sierra Leone) and in the Taï National Park, but their vocal behaviour has never been thoroughly investigated (Booth 1957; Oates 1984; 1988, Oates & Whitesides 1987, 1990, Whitesides 1989, McGraw 1996; 1998, Höner *et al*. 1997, Davies *et al*. 1999, Korstjens and Noé, 2004). Their social behaviour is most remarkable. Individuals form almost-permanent associations with one particular Diana monkey group, even in habitats where predation pressure is relatively low (Oates 1984, Noë & Bshary 1997). Although average group size is very small, both adult males and females migrate between groups, resulting in a remarkably fluid social system with a wide array of grouping patterns, including pairs, one-male/multi-female and multi-male/multi-female groups (Korstjens and Noé, 2004). The vocal repertoire of olive colobus monkeys consists of eight different call types (Bene *et al*. 2007). Our pilot study suggested that olive colobus monkeys combine calls into longer sequences depending on social contexts. These call combined concerned three calls types produced frequently. Also, the aim of this study was to describe the structure of these call sequences and determine the contextual rules underlying the production of these call combinations.

METHODS

Study site and subjects

The Taï National Park, located between 6°20N to 5°10N and 4°20W to 6°50W, is classified as a tropical evergreen seasonal lowland forest with an average annual rainfall of 1,940 mm and an average temperature of 21°C. Data were collected in a study area of about 1.5km x 1.5km delineated by a grid-system marked at 100m intervals, about one kilometre east of the 'Centre de Recherches en Ecologie' station (5°50 N and 7°21 W).

Twelve primate species live in the park: three nocturnal prosimians, three Colobine species, four guenons, one mangabey, and one chimpanzee species. The main predators of the monkeys are the chimpanzees, crowned eagles, leopards, and human poachers (Boesch & Boesch 1989, Shultz 2001, Refisch & Koné 2001, Zuberbühler & Jenny 2002). The olive colobus is the most cryptic of all Taï monkeys (Korstjens and Noé, 2004). Data were collected on three groups, whose members were known individually and fully habituated to the presence of human observers. The three groups consisted of three adult males, nine adult females, two juveniles and six infants in total.

Data collection and analyses

Data collection was performed on two habituated groups of olive colobus from June 2001 to February 2002 as part of our PhD field survey. For this purpose, a focal animal sampling (Altmann, 1974) was conducted by the observer (JCKB) and monitored during 15 minutes period between 07:00 and 17:00 GMT. Then, natural calling events were recorded from adult individuals. During each period, all vocalizations produced by an individual as behaviour and eventual event immediately preceding a vocalization were recorded. No individual was sampled twice in a row.

The vocal repertoire of olive colobus monkeys consists of eight different call types; three were more frequently used: **A**: “Zih”, **B**: “Hoo”, **C** “Zuk”, and five less produced: **D**: “Tr”, **E**: “ZZ”, **F**: “Whi”, **G**: “Ha” and **H**: “Thio” (Bene *et al*. 2007). Our pilot study showed that the three first calls (**A**, **B**, **C**) were typically produced as part of longer call sequences. Calls were not produced randomly, but were given as part of various combinations. Also, we performed measurements of these calls while determining age and sex, class of caller and identify their social context. Then, we used the acoustic software CoolEdit 2000 and RAVEN 1.3 to generate spectrograms.

RESULTS

Sequence composition of call types

We recorded 548 call sequences. In 338 of them (61.7%) we could assign to one of four distinct contexts (intergroup, intragroup, alarm calls, falling wood). Analyses revealed that although the three calls (**A, B, C)** were produced in several contexts, they were combined in different and context-specific ways (table 1).

Table-1. Relative distribution (%) of the three main call types in calling sequences

	call combined sequences				
Context	A, B, C	A, B	A, C	B, C	**N**
Intergroup encounter	**69.9**	17.5	0.0	12.6	103
Intragroup communication	16.0	14.7	0.0	**69.3**	75
Response to alarm calls from other monkeys	**46.5**	28.9	0.0	24.6	114
Response to falling of tree/branch	39.5	**51.2**	0.0	9.3	43

N=3 ‘other contexts’ excluded from analysis

Our result showed that three call types could composed the sequence in several disturbances, (1) mainly in inter-group encounters context. However, that sequence occurred, at somewhat lower rates, in response (2) to alarm calls from other monkey species, (3) to the thundering noise of falling trees or large branches, a common source of disturbance in the forest although. This last context leads mostly the sequence composed by A and B calls (Table 1). In peaceful situation, olive colobus callers typically produced a sequences composed by B and C calls in response to intense social calls of Diana monkeys and/or red colobus.

Calls order in sequence according to the context

Further analyses revealed that within call sequences individual calls were not given in random order, but they were assembled into a small number of call combinations that were highly context-specific (table2).

Table-2. The relative frequencies of the nine most frequent call combination given in four different contexts.

Context	Call types										N
	A, B, C			A, B		A, C	B, C				
	BABCB	**CBAB**	**BCBAB**	**AB**	**BAB**		**CB**	**BCB**	**CBB**	**BCBB**	total
Intergroup	0.1	**63.1**	5.8	7.8	9.7	0.0	5.8	4.9	0.9	0.9	103
Intragroup	0.0	13.3	2.7	2.7	12.0	0.0	**50.7**	18.7	0.0	0.0	75
Alarm calls	1.8	**40.4**	4.4	**15.8**	13.2	0.0	18.4	0.9	0.9	4.4	114
Falling of tree or branch	2.3	30.2	7.0	**39.5**	11.6	0.0	0.0	4.7	0.0	4.7	43

The vast majority of call combinations during inter-group encounters consisted of **CBAB** (figure 1) sequence type (63.1%). This call sequence leads two groups of olive colobus to avoid contact. Although we witnessed encounters between neighbouring olive colobus groups on several occasions, no contact was observed. Neighbouring individuals could answer to this sequence by producing also **CBAB** sequences. These combination calls were mainly given by adult males. Females rarely call in this context, while juveniles typically produce **E** calls.

Figure-1. Spectrographic representation of combination calls of olive colobus during intergroup encounter.

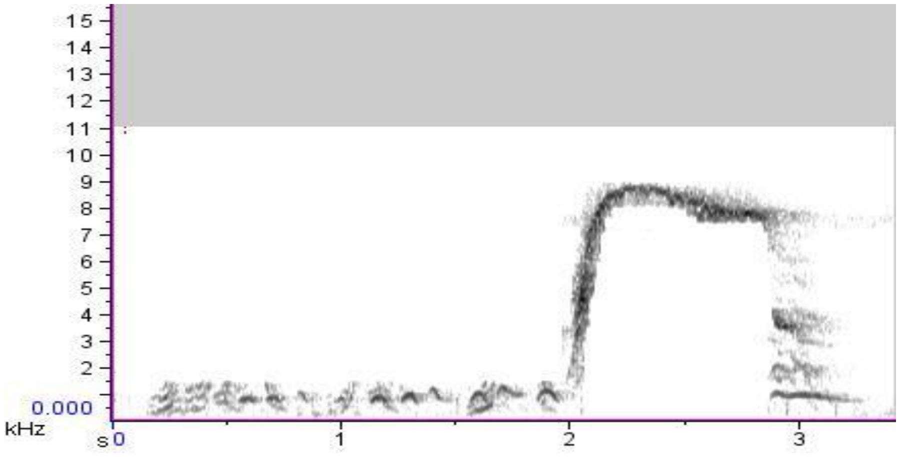


Figure-1a. Spectrographic representation of BCBAB call from female olive colobus during intergroup encounter

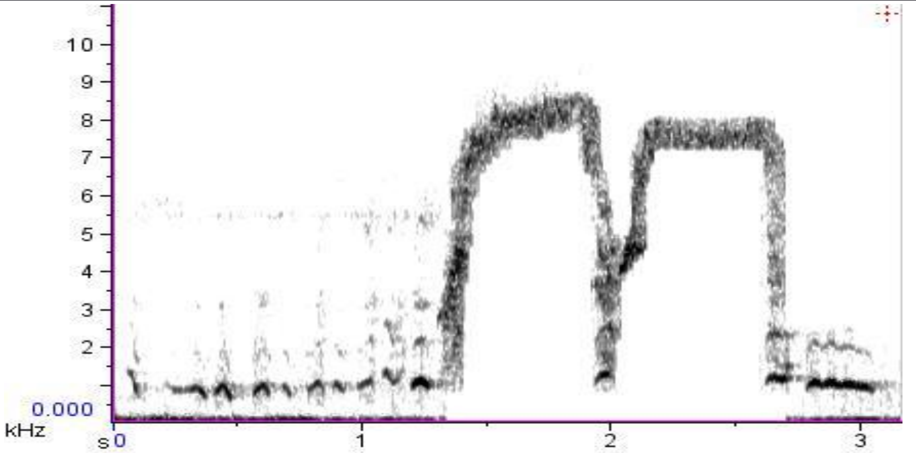
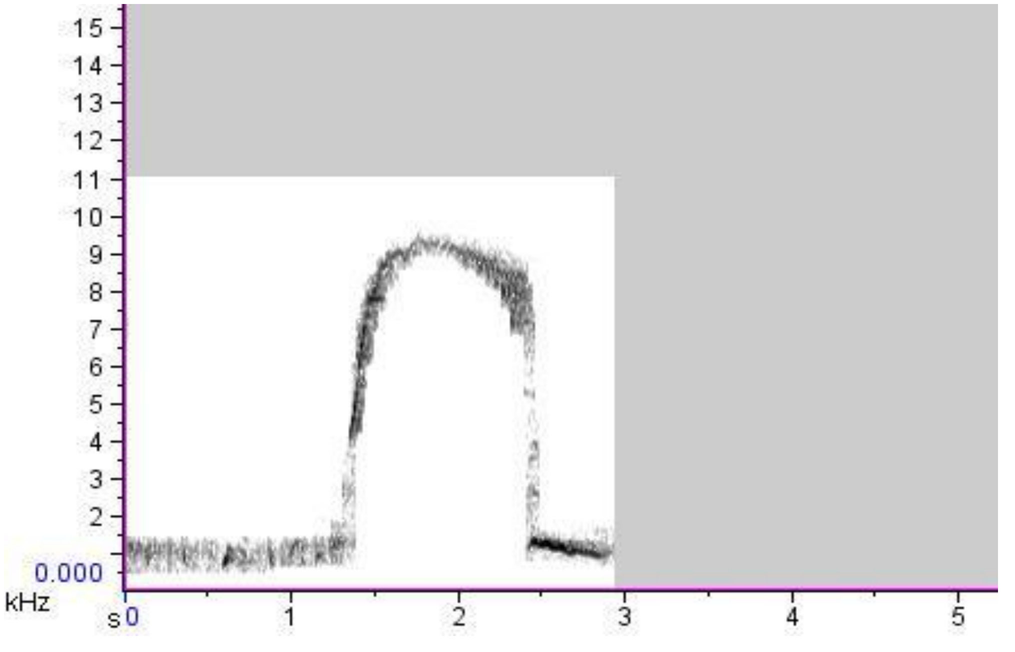


Figure-1b. Spectrographic representation of CBABAB call from male olive colobus during intergroup encounter

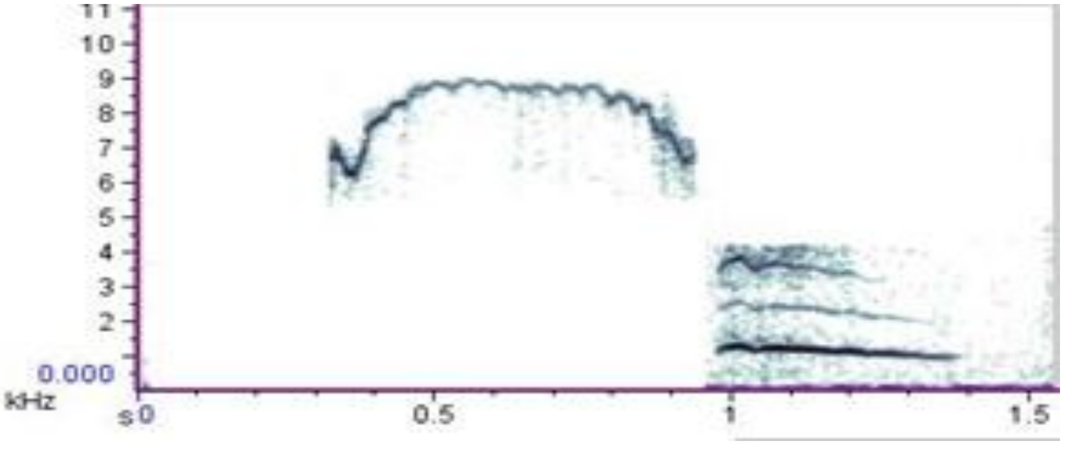
Vocal responses of olive colobus, to the alarm calls of other monkey species were similar which produced in intergroup context, **CBAB** sequences (40.4%) (figure 2), but there was considerable variability within this context. Several other combinations were performed in this alarming context. Also, this colobus monkey produced **CB** combinations only (18.4%), but other common combinations were **AB** (15.8%) and **BAB** (13.2%).

Figure-2. Spectrographic representation of CBAB combination calls of male olive colobus in response to alarm call from other monkey.



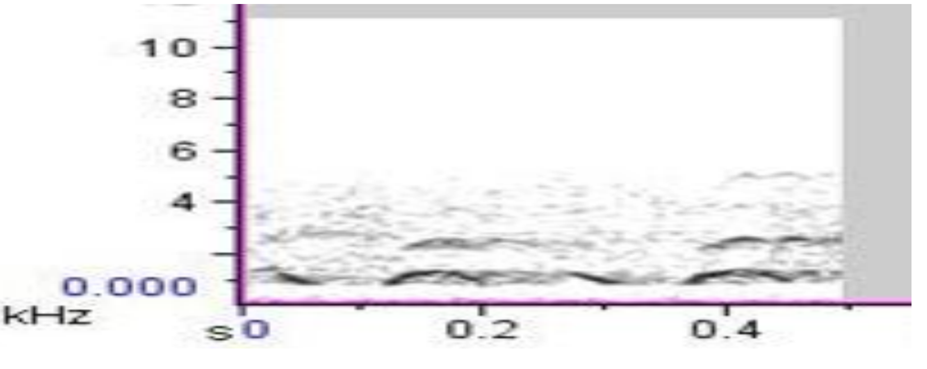
Some pilot observations suggested that in response to leopard models, olive colobus monkeys respond with **AB** combinations, sometimes doubled as **ABAB** combinations (figure 3). During this study period, olive colobus were attacked five times by chimpanzees during which no vocal behaviour was recorded. When the chimpanzees were detected, often, an individual of Diana monkey produced an alarm call that induce that monkey ran away silently and develop cryptic behaviour during long period according to the presence of chimpanzee around their area. Once we observed an attack by a crowned eagle and on this occasion the olive colobus gave a call combination consisting of **CBAB** as part of a longer sequence consisting of **CCCBBB-CBCBAB.** When trees or branches were falling down, male produced sequences consisting of, mainly **CBAB** sequence (30.2%), and **AB** combinations (39.5%).

Figure-3. Spectrographic representations of AB call from male olive colobus in presence of ground predator



When hearing the contact calls of associated Diana monkeys, both males and female olive colobus monkeys typically responded with call sequences consisting of **B** and **C** calls, mainly **CB** combinations (50.7%) and sometimes **BCB** combinations (18.7%) (figure 4). The same responses sometimes occurred in response to **B** or **E** calls from other group members, suggesting that these two combinations served functions in intra-group communication.

Figure-4. Spectrographic representations of CB call from female olive colobus in peaceful context



Sex differences in the production of call combinations

In a previous study, we have reported substantial sex differences in call use by adult male and female of olive colobus monkeys. A number of sex differences are also visible when looking at call combinations (table 3).

Table-3. Combination calls emission and sex/age class

	Combination calls									
Sex/age class	**AB**	**BAB**	**BABCB**	**BCB**	**CBAB**	**BCBB**	**CB**	**BCBAB**	**CBB**	N
Adult male	**10.6**	11.9	1.3	6.1	**42.9**	2.3	19.7	4.5	0.6	310
Adult female	**48.0**	8.0	0.0	12.0	**4.0**	4.0	16.0	8.0	0.0	25

Context “other” excluded from analysis; N=3

Both males and females combined the three basic call types (A, B, C) into different call sequences depending on social context. However, as indicated in table 3, males produced mostly call combinations (92.5%) while females only contributed very little (7.5%) despite comparable sampling efforts.

According to the call sequences types produced, the most common sequences in males were **CBAB** sequence (42.9%), while in female AB sequence is predominant with 48.0%. Both males and females engaged at roughly comparable rates in peaceful intra-group calling, as evidenced by their use of **CB** and **BCB** combinations (25.8% v 28.0% respectively).

DISCUSSION

Our study shows that free-ranging olive colobus monkeys possess a unique and highly unusual calling system in which a small number of calls are assembled into larger, structurally and more complex call combinations. Hence, olive colobus do not simply produce individual calls in context-specific ways, a widespread feature of primate vocal behaviour (Arnold et al 2006, Ouattara et al, 2009b). Instead they combine three of their unit calls into structurally complex call sequences in a context-dependent way, a potentially extremely powerful communication system. Other studies show that male putty-nosed monkeys assemble individual calls into larger units, which can be part of longer sequences (Struhsaker 1970; Gautier and Gautier-Hion 1977, 1983, Arnold and Zuberbuhler, 2006b). In olive colobus repertoire, we were able to distinguish nine different calls sequences that were regularly given in four different contexts. The simplest ones consisted of only two calls (**AB** and **CB**). We also observed three combinations consisting of three calls (**BAB**, **BCB**, **and CBB**), two combinations consisting of four calls (**CBAB** and **BCBB**) and two consisting of five calls (**BABCB** and **BCBAB**). The relationship between context and these different call combinations was only probabilistic, and some of the combinations appeared in several contexts, suggesting that other still unknown variables could play additional roles as well.

Our analyses revealed a number of context-dependent effects in how callers organised their calls into sequences. Although we never witnessed a physical conflict, males of olive colobus often vocalised once a neighbouring group is closer, which typically elicited similar responses from one or more neighbouring individuals. Call sequences given in this context mainly consisted of **CBAB** combinations, perhaps functionally similar to the *roars* given by adult black-and-white colobus monkeys during between-group communication (Marler, 1970; Arcadi, 2000). In these circumstances, juveniles typically gave only **E** calls, which often elicited further responses by adult males and females. Female responses mainly consisted of **CB** or **BCB** combinations, maybe to indicate their position or to protect their infants.

We only managed to get a very limited understanding of the precise motivations and mechanisms underlying intra-group communication. In the visual density of rainforest habitats, primates heavily rely on acoustic signals for regulating their social lives and olive colobus monkeys are not an exception. Regulating spatial proximity and informing group member about ongoing events in the environment and other sorts of social information are hypothesised functions of close range calls (Uster & Zuberbühler 2001).

After disturbances including dealing with predators, alarm calls of other monkeys, and falling trees or branches, all three call types (**A, B, C**) were usually recruited to form combinations, suggesting that olive colobus monkeys did not evolve specific alarm calls but combined the same basic three call types in an order to convey information on environmental events (Zuberbühler *et al*. 1999a,b). Some of our observations suggest that in response to leopards these monkeys produced combinations consisting of **A** and **B** calls, assembled in an **AB** sequence, sometimes repeated twice or three times. In the presence of the crowned eagles, olive colobus combined all the three call types into more complex sequences that, curiously, bore some resemblance to those recorded during intergroup encounters.

During one observed case of an eagle attack we recorded a call combination of **3C3B2(CB)AB**. More observations will be needed to confirm this call type as contextual call. These calls must function as the male putty-nosed monkeys' loud calls produced in response to playbacks of predators and, as in other forest guenons (Zuberbuhler et al. 1997; Zuberbu¨hler, 2000a, 2001; Eckhardt and Zuberbühler, 2004).

In response to chimpanzees, finally, olive colobus monkeys remained silent and relied fully on the alarm call behaviour of female Diana monkeys, which usually give a few quiet alarm calls after spotting a chimpanzee (Zuberbühler *et al*. 1997). During the course of this study, chimpanzee attacks were observed on five different occasions, and the reaction has always been the same: all monkey species responded to the warning calls of the female Diana monkeys by quickly and silently fleeing into the upper canopy, whereas olive colobus monkeys typically stayed in the lower vegetation and adopted a freezing posture.

In sum, our result showed that olive colobus produce a little repertoire of call but combines them in some order to convey several information on disturbance and improve their social cohesion.

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