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Vocal Repertoire of the Ucayali Bald Uakari (*Cacajao ucayalii*)

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Abstract

All primate species produce vocalizations for complex communication, conveying a wide range of information, regulating social interactions, coordinating activities, and serving as antipredator strategies. Together, these vocalizations form a species' vocal repertoire. However, despite their widespread presence and ecological significance, the vocal repertoires of less than 15% of primate taxa have been documented to date. The purpose of this study was to quantitatively characterize the vocal repertoire and behavior of a wild population of Ucayali bald or red uakaris (*Cacajao ucayalii*), a rare Amazonian platyrrhine primate. We analyzed and categorized 1,155 red uakari vocalizations using a combination of machine-learning-based random forest analyses, bioacoustic analysis, and field observations. We identified and described 12 acoustically distinct call types, two of which were not previously reported (*High-chick* and *Shriek*). The *Hic* was the most common vocalization, both in context and frequency of use. Some calls were specific to age, sex, or context, while others occurred across a range of situations. The vocal repertoire exhibited properties of both graded and discrete calls, depending on the call type and its apparent function. The uakaris' tail plays a key role in the species' acoustic-visual multimodal communication, as evidenced by the frequent combination of different call types and tail wagging, probably to draw attention from other group members and emphasize the transmission of information. The bioacoustic characterization of the Ucayali bald uakari's vocal repertoire provides a groundwork for potential acoustic monitoring of this species and the potential use of uakari monkeys as models for studying multimodal communication in primates.

Badge earned for open practices: Open Data Badge. Experiment materials and data are available in the repository at https://osf.io/78b6j/?view_only=6d0c0395f714480d800d5388a7cf070c.

Extended author information available on the last page of the article

Keywords Bioacoustic · Call · Vocalization · Multimodal communication · Random forest · Pitheciidae

Resumen

Todos los primates producen vocalizaciones para comunicar una amplia y compleja gama de información, regular interacciones sociales, coordinar actividades y como estrategia antidepredatoria. En conjunto, estas vocalizaciones conforman el repertorio vocal de una especie. Sin embargo, pese a su ocurrencia generalizada e importancia ecológica, hasta la fecha, solo se ha documentado el repertorio vocal de menos del 15% de los taxones de primates. El objetivo de este estudio fue caracterizar cuantitativamente el repertorio y comportamiento vocal de una población silvestre de huapos rojos o uakaris calvos del Ucayali (*Cacajao ucayalii*), un primate platirrino amazónico poco común. Analizamos y clasificamos 1155 vocalizaciones combinando análisis de bosques aleatorios (*random forests*) y bioacústicos, y observaciones de campo. Identificamos y describimos 12 tipos de vocalizaciones acústicamente distinguibles, dos de las cuales no estaban reportadas (*High-chick* y *Shriek*). La vocalización más común fue el *Hic*, tanto en contexto como en frecuencia de uso. Algunas vocalizaciones fueron emitidas solamente por individuos de cierta edad o sexo, o en contextos específicos, mientras que otras se emitieron en una rango variado de contextos. Registramos tanto vocalizaciones graduales como discretas, dependiendo de la aparente función de las mismas. La cola de los Uakaris parece desempeñar un papel fundamental en su comunicación multimodal acústico-visual, evidenciado por la frecuente combinación de diferentes tipos de llamadas y movimientos de la misma. Esta caracterización del repertorio vocal del huapo rojo proporciona la base para el monitoreo acústico de la especie y el uso de la misma como un modelo para el estudio de la comunicación multimodal en primates. ***The publisher did not copy edit the abstract translation**.

Introduction

Vocal repertoires are the collection of distinct vocal signals produced in various contexts that a species uses for communication. They can vary significantly in complexity and are essential for understanding animal communication systems. Phylogenetic relatedness (Hasiniaina *et al.*, 2020; Meyer *et al.*, 2012), geographic range (Wich *et al.*, 2008), habitat density (Brown & Waser, 2017; Marten & Marler, 1977), predation risk (Stephan & Zuberbühler, 2008), social structure (McComb & Semple, 2005), body size (Bowling *et al.*, 2017; Garcia *et al.*, 2017), and arousal level (Hauser, 1993; Morton, 1977) are just a few of the many variables that affect the bioacoustic features of primate vocalizations. The first step to understanding the role of these variables in the evolution of primate vocal communication is to characterize and classify the acoustic signals that form a species' vocal repertoire. Hence, careful descriptions of vocal repertoires are essential to understanding the proximate mechanisms underlying the meaning and function of calls. These descriptions are also pivotal for elucidating the ultimate mechanisms

involved in the coevolution of social behavior and communication systems in primates (Dunbar, 2003; Smith & Harper, 2003). Studying primate vocal repertoires and their role in multimodal communication also allows broader comparative research on primate communication systems and their evolution and may help to clarify the primate roots of human language (Fedurek & Slocombe, 2011; Slocombe *et al.*, 2011).

Primate vocalizations were first recorded in captivity more than 130 years ago (Radick, 2005). However, the development of quantitative methods to objectively identify and characterize acoustic patterns of primate calls has advanced significantly in recent decades (Fischer *et al.*, 2013; Hammerschmidt & Fischer 2019; Slocombe & Zuberbühler 2010; Tchernichovski *et al.*, 2000). Nevertheless, we have only established vocal repertoires for ca. 10% of platyrrhine taxa (Cäsar *et al.*, 2017). This knowledge gap undermines our understanding of the communication of a major clade of the primate lineage.

The subfamily Pitheciinae (i.e., genera *Cacajao*, *Chiropotes*, and *Pithecia*) includes some of the least-known platyrrhine primates (Veiga *et al.*, 2013). Of these, the *Cacajao* monkeys, commonly known as uakaris, are endemic to the Amazon rainforest and comprise three black-headed uakari species and five bald or red uakari species (Silva *et al.*, 2024); the latter are notable for their distinctive bald heads and vibrant red faces (Mayor *et al.*, 2015). Bald uakaris form larger groups and exhibit more flexibility in their social organization than other platyrrhines. Their social organization involves high fission-fusion dynamics and multilevel societies of at least three levels. The largest level consists of troops of 50 to >200 individuals, which are made of groups of 25–50 individuals that occasionally come together. These groups split into smaller units of up to ten individuals, which comprise multiple females and one or more males (Aquino, 1998; Bowler *et al.*, 2012; Bowler & Bodmer, 2009; Heyman, 1992). In this context, we expect that bald uakaris, like other primate species with fluid social dynamics that inhabit dense rainforests, rely heavily on their vocal communication to maintain group cohesion and pair bonds, coordinate activities, and defend their food, mate, and territorial resources (Batist *et al.*, 2023; Ceccarelli *et al.*, 2021; De Gregorio *et al.*, 2024; Dolotovskaya & Heymann, 2022).

Vocal communication is almost entirely uninvestigated in uakaris, with the exception of goldenbacked uakaris, *Cacajao melanocephalus* (Bezerra *et al.*, 2010a, b, c, 2012, 2013). A qualitative description of calls emitted by captive bald uakaris (*Cacajao ucayalii*) of uncertain geographical origin and taxonomic classification reported 12 calls with brief descriptions of the behavioral context and demographics of vocal behavior (Fontaine, 1981). The most common call was the *Hic* call, which uakaris produced in a variety of contexts (Fontaine, 1981). A subsequent study described an additional "barking call" that did not resemble any of the previously described vocalizations (Heymann, 1990). A field study reported a high production of contact calls just before dawn, probably to locate other group members sleeping in nearby trees, and that uakaris emitted contact calls when foraging or resting and "high-pitched sounds" when travelling (Ayres, 1986). A further study stated that aroused uakaris interleaved 'hic,' 'chick,' and 'chyook' calls (Ward & Chism, 2003). Beyond these descriptions,

however, communication in wild bald uakaris has not been studied in detail, and their vocal repertoire has not been quantitatively described and classified.

We quantitatively described the vocal repertoire of wild Ucayali bald uakaris by recording their behavioral patterns and calls. In doing so, we aimed to 1) comprehensively characterize the acoustic structure and behavioral context of Ucayali bald uakari vocalizations; 2) define the species' vocal repertoire by objectively categorizing these calls using statistical classification and clustering methods; and 3) relate the species' vocal repertoire to its behaviors and other communication modes.

Methods

Study Site and Subjects

We conducted fieldwork in a continuous lowland forest in the Lago Preto Conservation Concession (4°27.5'S, 71°45.9'W), a 9,926 ha public–private reserve on the Peruvian side of the Yavari River, 175 km southeast of Iquitos, Peru. The study area has a total area of 2,200 ha, which includes *terra firme* forest, white-water *várzea* forest, and *aguajal* palm swamps dominated by moriche palms (*Mauritia flexuosa*) (Bowler *et al.*, 2012; Bowler & Bodmer, 2011). There are 13 primate species in the study area. We collected data from individuals from one troop of free-ranging Ucayali bald uakaris of at least 200 individuals, who occasionally travelled together. Groups of ca. 100 uakaris sometimes foraged together for several days, but the most common formations were groups of 20–50 individuals, which comprised various smaller units that displayed frequent fission-fusion events through the day (Bowler & Bodmer, 2009). Because of the fission-fusion dynamics of the species, we followed some individuals more than others, resulting in varying degrees of habituation. As a result, after the first few weeks of sampling, most individuals tolerated the presence of researchers at ~10–15 m, whereas others required 1 to 3 days of continuous following before becoming habituated to researchers, and very few continued to react to researchers throughout the study. Whenever possible, we aged (infant, juvenile, subadult, and adult) and sexed (male and female) subjects, following Fontaine (1981) and Bowler (2007). Infants were frequently carried by their mothers and had less saturated facial coloration, ranging from grey to pink. Juveniles were larger than infants but smaller than subadults, had thick grey scalp hair, and had pink to red facial coloration that was less intense than that of older individuals. We could not determine sex in infants and juveniles. Subadults had little scalp hair, lacked bulging cranial muscles, and were completely independent of their mother; males were larger than females. Adult males differed from adult females in their larger body size, more conspicuous pelage, and intense scarlet facial coloration. Genitalia (labia and scrotum) were usually visible and distinguishable from the subadult age onward.

Data Collection

We collected data in two sampling periods. During the first, between March 2003 and June 2005 (945 hr of contact time), we collected data on vocal behavior and

usage by recording vocalizations and their context with *ad libitum* recordings (Altmann, 1974). We recorded calls in Sony.dvf format with an 8 kHz sampling rate, using a Sony ICD-P28 digital recorder with a Sony ECM-Z60 Microphone. To calculate call rates for the most common uakari calls and investigate whether caller activity affected call rate, we recorded and counted all vocalizations of all call types given by the unit or group every 10 min for 1 min for 30 days in August 2003, resulting in 340 x 1-min samples. We used recordings during these samples to verify counts recorded in the field and to classify calls. We discarded samples where the center of the group was more than 60 m from researchers, because in such cases part of the group was out of earshot for the quieter calls.

During the second sampling period, from June to July 2015 (56 hr of contact time), we collected recordings for bioacoustic analyses and data on vocal behavior and the relative frequency of occurrence of each type of call per age-sex class. We made recordings at ≤25 m from the subjects (7.43 hr of recordings from 213 audio files) and recorded the caller's behavioral context and age-sex class, and the number and age-sex classes of visible audience members, whenever possible. We recorded all sound files as.wav files with a 44.1 kHz sampling rate and a 16-bit amplitude resolution, using a Marantz PMD 661 MKII digital recorder and a ME 67 Sennheiser directional microphone. When we observed individual monkeys giving visual and tactile signals while vocalizing, we recorded the communication modes, the behavior, and the age-sex classes of the givers and receivers of the signal. We calculated the relative frequency of occurrence of each call type across age-sex classes using all vocalizations in the sound files for which we knew the callers' age-sex class.

Acoustical Analysis

First, we screened sound files and extracted recordings of sufficient quality (e.g., low signal-to-noise ratio, no clipping and no signal overlap) for further analyses, using spectrograms with a Hamming window of 1024 FFT, 75% overlap, and 22.05 kHz sampling frequency produced in Audacity 3.7.0 (Audacity Team, 2020). We obtained 1,155 vocalizations for further analysis. We categorized these vocalizations into 13 possible call types: 11 call types described by Fontaine (1981) and Heymann (1990), and two previously unreported call types (Table I). Then, to characterize the vocalizations, we manually extracted 27 spectral, temporal, and entropy-based acoustic parameters from the first harmonic of each call (Table S1 provides a description of all parameters). We chose these parameters, because they collectively capture the features of sounds, while avoiding subjectivity (contrary to amplitude-based measures), and provide a multidimensional acoustic space for signal classification. When analyzing calls given in series (i.e., *Hics*), we measured the first, middle, and last vocalizations of the series. We extracted all acoustic parameters manually from spectrograms by using a Hamming window of 1024 FFT, 75% overlap and 22.05 kHz sampling with Raven 1.6.5 software (Center for Conservation Bioacoustics, 2014). Finally, to improve normality in the extracted data, we applied a Box-Cox transformation and scaled and centered all

Table I Confusion matrix illustrating the classification of call types by the random forest clustering analysis for Ucayali bald uakari at Lago Preto Conservation Concession, Peru, March 2003 to June 2005, and June to July 2015.

	Predicted call type membership													
Call type (n)	Chick	Hic	Purr	Bark	High chick	Chyook	Wa	Kreek	Wee-ook	Rhä	Shriek	Kik	Rhork	Classification error
Chick (61)	**60**	0	0	0	0	0	0	0	1	0	0	0	0	0.0164
Hic (621)	0	**607**	0	8	0	4	0	0	0	1	0	1	0	0.0225
Purr (9)	0	0	**8**	0	0	0	0	0	0	1	0	0	0	0.1111
Bark (114)	0	9	0	**98**	0	3	0	0	0	2	0	2	0	0.1404
High chick (44)	0	0	0	0	**35**	0	0	0	3	0	6	0	0	0.2045
Chyook (58)	1	8	0	4	0	**45**	0	0	0	0	0	0	0	0.2241
Wa (43)	0	1	0	0	0	0	**32**	2	0	2	4	2	0	0.2558
Kreek (41)	0	0	0	1	0	0	6	**25**	0	4	3	0	2	0.3902
Wee-ook (27)	0	0	0	4	0	2	1	0	**16**	2	1	1	0	0.4074
Rhä (41)	0	2	0	7	0	0	2	5	1	**22**	1	0	1	0.4634
Shriek (43)	0	0	0	1	6	0	6	5	4	4	**17**	0	0	0.6047
Kik (26)	0	4	0	4	0	3	1	0	2	1	2	**8**	1	0.6923
Rhork (23)	0	2	0	6	0	2	1	2	1	8	0	1	**0**	1

feature values (Keen *et al.*, 2021). We used the resulting dataset to evaluate the robustness of call classification.

Call Classification and Statistical Analyses

We used a supervised machine learning approach to classify acoustic signals following Keen *et al.* (2021). Specifically, we conducted a supervised random forest analysis by using 1,000 decision trees and five randomly selected acoustic parameters at each split with the randomForest R package (Liaw & Wiener, 2002). We decided to use random forest as a classification method, because it is more effective at detecting small differences between groups, provides more accuracy, and performs more consistently than other classification methods (i.e., discriminant function analysis, neural networks, and support vector machines) in datasets of different sample sizes (Wierucka *et al.*, 2025). Unfortunately, and despite our considerable sample size, our dataset was not large enough to implement unsupervised machine learning approaches.

We then employed the criteria used by Wegdell *et al.* (2025) to assess the validity of a call type. We defined a call type as valid if the number of vocalizations categorized by the random forest as the "initial call type" was the highest. We coupled unreliable call types with the valid call type with which they were misclassified in most cases. To determine the overall significance of the classification, we used a two-tailed binomial test with a level of chance equal to the number of call types to be classified (i.e., $1/13 = 0.077$).

Finally, to examine whether call rate varied among callers' activities, we conducted a one-way ANOVA test using R version 4.0.3 (R Core Team, 2020) to compare the rate of *Hics* calls for the three most common activities uakaris performed (i.e., foraging and feeding, moving, and resting). No other calls for which we obtained call rates varied sufficiently in the context of emission or callers' activity to be analyzed in this way.

Data Visualization

We visualized the clustering of all vocalizations and updated call types using t-Distributed Stochastic Neighbor Embedding (t-SNE) to embed all extracted acoustic feature vectors into a two-dimensional acoustic space (Maaten & Hinton, 2008). To conduct the t-SNE, we used the Rtsne R package (Krijthe 2015), with a Barnes-Hut implementation and default parameters.

Ethical Statement

This research was approved by the ethics committee of the San Diego Zoo Wildlife Alliance and carried out in accordance with applicable national laws of Peru. Our research complies with the International Primatological Society's Code of Best Practices for Field Primatology. Our methods were noninvasive, and no animals were handled during the study.

Data Availability The datasets generated during and/or analyzed during the current study and the R code are available in the OSF repository, https://osf.io/78b6j/?view_only=6d0c0395f714480d800d5388a7cf070c. All additional material related to this study, including sound files, may be requested from the corresponding author.

Results

Updated Vocal Repertoire

Ucayali bald uakaris have at least 12 structurally different call types in their vocal repertoire (Figs. 1 and 2; Tables I and II; supplementary materials include audio clips of each call type). Most call types (10 of 12) had a mean duration of less than 0.5 s, ranging from 0.04 s for *Hics* to –0.9 s for *Chicks* (Table III). Similarly, mean peak frequencies fell under 2 kHz in 9 of 12 call types (range 0.88 kHz for *Hics* to –3.55 kHz for *High Chicks*), while mean delta frequencies were under 1 kHz in 10 of 12 call types (range: 0.22 kHz for *Hics* to –3.05 kHz for *Chicks*; Table III). The random forest results agreed with the initial call types on the classification of 973 of 1,151 calls (84.5%), a rate significantly exceeding the probability of a call being assigned to one of the 13 possible call types by chance (1/13*100 = 7.69%, binomial test, $p < 0.001$). However, some call types showed high (e.g., *Chicks*, *Hics*, and *Purrs*) and moderate (e.g., *Kreeks*, *Wee-ooks*, and *Rhäs*) classification accuracy, and others less so (e.g., *Shrieks* and *Kiks*) (Table I). One of the 13 possible call types, the *Rhork*, did not fulfill our criteria for a consistently acoustically discriminable call type and was combined with the *Rhä* call following our call type criteria (Table I). Moreover, t-SNE mapping indicated that some call types are discrete (*Hics*, *Chicks*, and *Purrs*), while others form highly graded groups (screams, *Kreeks*, *Shrieks,* and *Wa calls*) (Fig. 2).

Call Rates

The *Hic* call (Table I) was the most common call. Uakaris produced *Hic* calls at a mean rate of 0.24 ± SE 0.01 calls/individual/minute (1.09 ± SE 0.05 notes/individual/minute), but calling rates varied from 0 to 0.75 calls/individual/minute (5.95 notes/individual/minute). Although *Hics* appeared to occur at high rates when uakaris found fruiting trees, we found no significant difference between the rate at which uakaris produced *Hic* calls during different behaviors (ANOVA $F_{2, 172} = 0.593$, $p = 0.55$). We observed all age-sex categories giving *Hics*, but adult males appeared to use this call only rarely (Tables II and S2), and usually as a single note. We recorded *Hics* in combination with all other call types, and they were often elicited by *Chicks*, *Barks*, *Rhäs*, and screams calls or by loud noises, such as falling branches, and monkeys landing on palm fronds. Uakaris emitted *Hic* calls during all modes of behavior and were often accompanied by constant side-to-side tail wagging.

Only adult males produced *Bark* calls, which had a mean rate of 0.01 ± SE 0.002 calls/individual/minute (Table S2). Individuals often barked continuously for several

seconds or sometimes minutes and called in short bursts at a rate of up to 2.3 calls/s. *Barks* appeared particularly common in individuals who were alone or in small groups far from the main group. Individuals on the extreme edges of groups often gave *Barks*. Occasionally, uakaris gave *Barks* at the end of a rest period. Sometimes monkeys ignored *Barks*, but these calls usually elicited *Hics*. Occasionally, uakaris responded *Barks* with the same call, resulting in sequences of alternating *Barks* between two individuals. When individuals gave *Bark* calls, a single, deep forward tail wag accompanied each *Bark*; this front-to-back tail wagging has not reported before, to our knowledge.

Uakaris produced *Chicks* (Table II) at a mean rate of 0.03 ± SE 0.003 calls/individual/minute. This call type has a range of variations that are not easily defined. Uakaris emitted quieter *Chicks* in response to loud noises (e.g., falling trees), *Kreeks* and *Wa* calls emitted by aggressed individuals, or when less habituated groups reacted to researchers. Individuals uttered louder "strong" *Chicks* in response to threats, such as birds of prey. On hearing a "strong" *Chick* alarm call, other individuals became alert and looked up. Occasionally, we heard very loud, "strong" *Chicks*, which were followed by rapid descent by monkeys, eliciting further "strong" *Chicks* and *Hics*. Monkeys often responded "quiet" *Chick* calls with *Hics* or with similar "quiet" *Chick*s, but individuals did not always look up or stop the activity they were doing. Uakaris, especially adults, often wag their tails side-to-side when hearing *Chicks*.

Discussion

Using supervised random forest analysis, we provide a quantitative description and classification of the vocal repertoire of a bald or red uakari species. We identified 12 reliable acoustic categories or call types. The Ucayali bald uakaris' vocal repertoire includes calls that appear to function to stay in contact and coordinate movement (*Hics*, *Chyooks* and *Barks*), regulate conflict (*Rhäs*, *Kreeks*, *Shrieks,* and *Wa calls*), facilitate social bonding (*Wee-ook* and *Kik*), and alert group members to potential threats (*Chick* and *High-chicks*).

Although the random forest analyses indicated the reliability of 12 call types (Table I), the t-SNE showed a considerable degree of acoustic overlap in Ucayali bald uakaris' vocal repertoire. However, the level of gradedness differed between call types. For example, *Hics*, *Chicks*, and *Purrs* showed very little gradation in the acoustic space, indicating that these are discrete calls. Moreover, *Chick* calls, Ucayali bald uakaris' main alarm call, were acoustically distinct from other calls and had the lowest classification errors of all call types. This supports Cheney & Seyfarth's (1990) suggestion that predator alarm calls should be highly discrete, as any ambiguity is potentially deadly for recipients. In contrast, vocalizations that are highly context-dependent and have a variety of functions, such as those given during agonistic interactions (*Rhäs* and screams: *Kreeks, Shrieks*, and *Wa* calls), showed more gradation. Our findings are similar to those for Campbell's monkey (*Cercopithecus campbelli*) and chimpanzee (*Pan troglodytes*) vocal systems, where vocalizations

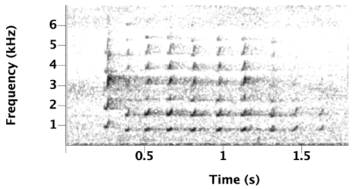
Fig. 1 Spectrograms of call types in the updated repertoire of Ucayali bald uakaris at Lago Preto Conservation Concession, Peru, March 2003 to June 2005, and June to July 2015. The *Hic* spectrogram contains a series of ten calls. The call type and the number of calls represented are above each spectrogram. The axes of the spectrograms vary in length. We created spectrograms using Raven with the following settings: 1024 FFT, Hamming window, 75% overlap, 22.05 kHz sampling frequency. Corresponding audio clips for each spectrogram are in the electronic supplementary material. ▶

with less specific functions (i.e., chimpanzee *'barks'* and *'screams'* and Campbell's *'krak-oo'* and *'hok-oo'*) show high levels of gradation, which may facilitate flexible usage and the capacity to convey different types of information (Crockford & Boesch, 2003; Keenan *et al.*, 2013; Marler, 1976). Our results show that the vocal repertoire of Ucayali bald uakaris shows aspects of both strong gradedness and discreteness depending on the call type, probably associated with the functions of the calls, as shown in other primate species (Campbell's monkeys: Keenan *et al.*, 2013; Lemasson & Hausberger, 2004, 2011; red-capped mangabeys, *Cercocebus torquatus*: Bouchet *et al.*, 2012; chacma baboons, *Papio hamadryas ursinus*: Rendall *et al.*, 2009; gray mouse lemurs, *Microcebus murinus*: Leliveld *et al.*, 2011).

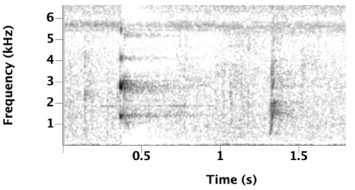
The vocal repertoire reported here matched most of the calls previously described for captive individuals of uncertain geographical origin and taxonomic classification (Fontaine, 1981). One important difference with Fontaine's work, however, is that we propose to include the *Rhork* call in the *Rhä* call. We found that *Rhorks* were more often classified as *Rhäs* than their own call type category, suggesting that these vocalizations are a single acoustic category. Based on three vocalizations, Fontaine (1981) described *Rhorks* as "complexly modulated sounds with tonal and atonal portions," which are given during "mild aggressions" and in "proximity to threatening stimulus." Thus, it is likely that these vocalizations were rare variations of *Rhä* calls. A second difference with existing work is that we were unable to relate the *Hiss* and the *Keh* calls reported by Fontaine (1981) to any of the calls that we recorded. Fontaine described these calls as common but difficult to record due to their low amplitude, which makes them "inaudible to humans at more than three or four meters," and they seem to be mainly given by juveniles and infants during play activity (Fontaine, 1981, p. 487). We only recorded *Hics* and *Kiks* from juveniles and infants when playing, both of which are high amplitude sounds with distinctive acoustic structures. Because uakaris usually use the middle and upper levels of the forest (Emmons & Feer, 1997), it is possible that we did not record Fontaine's *Hiss* and *Keh* calls due to distance and the elusive behavior of immature individuals. Thus, they may represent additional call types in the species' vocal repertoire, rather than being acoustic variants of the *Hics* or *Kiks* that we describe.

We recorded *High-chicks*, an alarm call given to middle disturbances (e.g., fights, chases, and falling branches), which Fontaine did not distinguish from *Chicks* (Fontaine, 1981). Ucayali bald uakaris frequently give alarms in the form of *High-chicks* and *Chicks* to nonthreatening stimuli (i.e., vultures) but only react strongly (rushing down through the canopy) to very loud and intense *Chicks* given to raptors and, occasionally, terrestrial predators (JL and MB personal observations). This pattern resembles the alarm call system of bonnet macaques (*Macaca radiata*), which uses acoustic properties of their calls, such as the harmonics-to-noise ratio, to specify

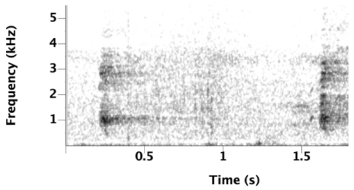
Hic (n = 10)



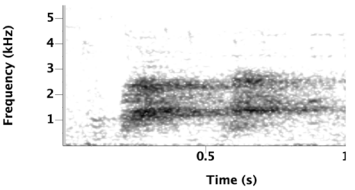
Chyook (n = 2)



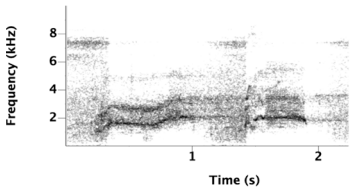
Bark (n = 2)



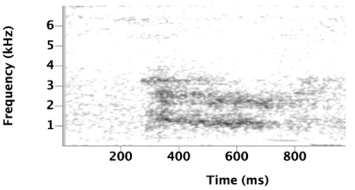
Rhä (n = 2)



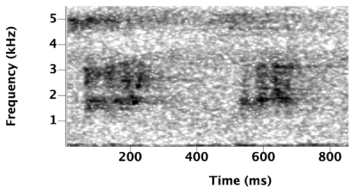
Scream–Kreek (n = 2)



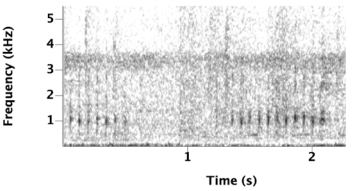
Scream–Wa (n = 1)



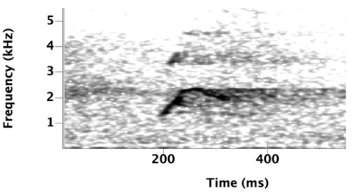
Scream– Shriek (n = 2)



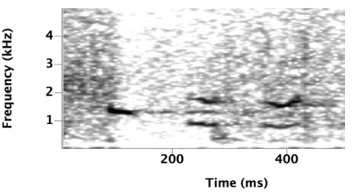
Purr (n = 2)



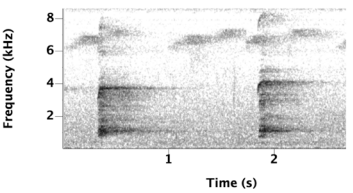
Wee-ook (n = 1)



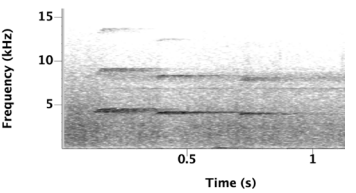
Kik (n = 3)



Chick (n = 2)



High chick (n = 3)



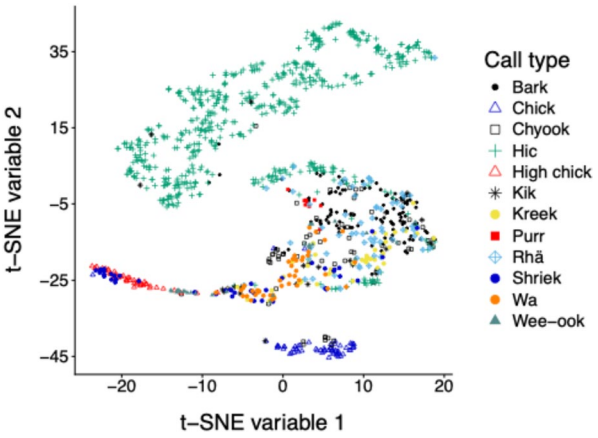


Fig. 2 t-SNE scatterplot illustrating how 12 call types in the updated vocal repertoire cluster together based on similarity in their acoustic structure. Each point represents a call, colored and shaped according to the call types of Ucayali bald uakari at Lago Preto Conservation Concession, Peru, March 2003 to June 2005, and June to July 2015

their assessment of urgency and potential danger, rather than use acoustically distinct alarm calls based on predator type (Coss *et al.*, 2007). Moreover, the bald uakari *Chick* is produced by the combination of a *High-chick* with a low-frequency element, which gives *Chicks* their distinctive metallic sound. This pattern suggests that combinatorial capacity and pragmatics are involved in the alarm call system of the Ucayali bald uakari, as in the alarm call systems of other primate species. For example, various primate species combine two types of alarm calls or signals to communicate about predator type, location, urgency of threats, and the caller's identity and intention (putty-nosed monkeys, *Cercopithecus nictitans*: Arnold & Zuberbühler, 2006, 2008; black-fronted titi monkeys, *Callicebus nigrifrons*: Cäsar *et al.*, 2013; olive colobus, *Procolobus verus*: Gallot *et al.*, 2024). This pattern suggests that primates of different taxonomic groups incorporate diverse, rule-governed combinatorial elements and pragmatic principles into their alarm call systems.

We also recorded *Shrieks*, a third type of scream produced only by infants and juveniles, mostly during aggressive interactions, which can be differentiated from the *Kreeks* and *Wa* calls described by Fontaine (1981). Screams are one of the most distinct vocalizations produced by primates and animals in general. They are usually loud, high-pitched calls that are primarily associated with agonistic contexts but often exhibit great context-dependent acoustic variation. For example, in vervet monkeys (*Chlorocebus pygerythrus*), victims produced longer and higher-pitched screams than aggressors, and screams produced in severe conflicts (e.g., chase or physical contact) showed higher entropy than those in mild conflicts (e.g., charge or displace) (Mercier *et al.et al.*, 2019). Although acoustically graded, the three types of screams given by Ucayali bald uakaris (*Kreeks*, *Shrieks*, and *Wa* calls) vary consistently in some acoustic features and context. *Kreeks*, emitted in severe conflicts, lasted longer, and had lower frequencies and smaller entropy values than *Wa* calls, which are emitted in mild conflicts. Our results are similar to those reported in red-fronted lemurs (*Eulemur fulvus*), and capuchin (*Cebus capucinus*) and squirrel monkeys (*Saimiri sciureus*), where frequencies, duration, amplitude, and upward shifts of frequencies increased with the arousal or risk perceived by the caller (Fichtel *et*

Table II Updated vocal repertoire, based on random forest analysis, and behavioral contexts for Ucayali bald uakaris at Lago Preto Conservation Concession, Peru, March 2003 to June 2005, and June to July 2015

	Call type	Description	Context
Contact	Hic[1,2]	A short staccato 'he' or 'hic', with 2–8 harmonics, and given singly or in series of two to >20 notes (mean = 4.7 notes per call). Under high arousal, *Hics* seem to have higher frequencies and shorter intervals between notes; in this context, *Hics, Chyooks,* and alarm calls are often combined in long call sequences.	Contact call produced in a wide variety of contexts; very common during the early morning, while foraging and after disturbances (e.g., aggression or loud noise). Given by all age-sex classes, but much less frequent in adult males (103 calls; 7.2% of occurrences) than females (687 calls; 47.8%). *Hics* are often accompanied by side-to-side tail wagging.
	Chyook[1]	A short quiet sound, similar to a *Hic* call, with a harder, more defined ending, and highly variable. May sound like 'wick' or 'wook', or have a whistle-like element. Usually given as a single note but can be produced in short series of up to four or five calls.	Given in response to loud noises and, occasionally, when uakaris find highly preferred food. Emitted predominantly by adults, but more in females (44 calls; 59.5%) than males and very rarely in juveniles (3 calls; 2.7%).
	Bark[3]	A loud, harsh dog-like bark, with 2–3 harmonics, given in single notes which are often repeated in long sequences of up to >130 calls. When startled, callers appear to increase the energy of the second harmonic, which produces higher pitched *Barks*. This call may intergrade with the *Rhä*.	Only heard given by adult males. Often before a group moves after a resting period, or changes direction. Common in individuals who forage far from the rest of the group. Accompanied by front-to-back tail wagging.

Table II (continued)

	Call type	Description	Context
Social interactions: agonistic	Rhä[1]	Long, harsh, guttural low-pitched calls. Usually loud, but occasionally given as shorter quieter 'hiss-like' calls. Often given in long series of up to 20 calls by the same caller.	Given by juveniles and adults as an apparent sign of distress and during aggressive encounters, often combined with screams. Produced by both, aggressors and victims.
	Scream–Kreek[1]	Long high-pitched calls, with flat-like shape but complex structure. Can exhibit up to 4 overtones, and can be modulated or not, with fast rises and falls in its frequency. Broadband sound.	Given by juveniles and adults of both sexes during episodes of intense apparent stress (chases) and mild, non-persistent aggressive encounters. Produced by the victim. Very common during agonistic interactions.
	Scream–Wa[1]	Strident long high-pitched calls, higher pitched and louder than the *Wa* scream. Often given in sequences up to 30 s or more. More tonal than the *Kreek* scream.	Given by juveniles and adults of both sexes during intense agonistic interactions (aggression with contact). Produced by the victim. Common when the victim was attacked by a coalition of uakaris.
	Scream-Shriek[4]	Short chain of discrete 3–5 pulses of uniform structure and high frequency (higher than *Kreek* and *Wa* screams). Possibly the infant version of screams. Tonal call.	Given by infants during apparently frightening situations or when rejected by the mother. Can elicit maternal approach and retrieval.
Social interactions: affiliative	Purr[1]	Lower-pitched than most calls. Given in a chain of 4–11 discrete pulses of variable numbers but uniform structure. Emitted with a mean inter-pulse interval of 44 msec (range: 22–128 msec). Sounds similar to the purr of a domestic cat.	Apparently friendly contact. Produced by all age-sex classes. Infant, juveniles and adult females purr during dorsal mounting and nursing. Adult males purr during friendly approaching to other males and during urine washing, piloerection can occur while producing this call.
	Wee-ook[1]	High-pitched, bird-like whistles which vary considerably in their structure. Has an arch form, with initial frequencies usually lower than terminal frequencies. Sometimes grade into *Chyooks*.	Produced by juveniles (28 calls; 63.6%) and, rarely, by adults (4 calls; 9.1%). Emitted during times of apparent frustration (e.g., when other individual monopolize food) or when a nearby individual is aggressed.
	Kik[1]	Whimper-like pulses, emitted either as a single note or in series of > 10 notes. Usually with 1–3 harmonic. Tonal call.	Given by infant and juveniles during play activity, and aggression. Seems to mark swift transitions from playful to fearful-like motivation (pre-aggression) and to signal conflict avoidance (post-aggression).

Table II (continued)

	Call type	Description	Context
Alarm	Chick[1]	Loud, high-pitched call with metallic ringing notes. Variable in volume and pitch. Tonal call. Often repeated several times. It has two sound bands, a low and a high frequency band, with the later one having most of the energy and duration. The lower band has a harsh sound similar to the *Bark* call.	Given by all independent age-sex classes. General alarm call given in response to predators and common disturbances. *Chicks* were often given as false alarms (e.g., to vultures) and only occasionally, when very loud and intense, elicited strong reactions (moving rapidly down in the canopy).
	High Chick[4]	Very short, loud, high-pitched call. Corresponds to the high frequency band of the *Chick*. Can be distinguished from the *Chick* by the absence of the metallic sound contained in *Chicks*' low bands. Very tonal call.	Given as a signal of apparent distress and arousal, in response to mild disturbances (falling branches) and aggression. Juveniles produce it when they are unable to jump from one tree to another or when the mother does not give them access to food. Usually heard with *Rhäs*.

Described in Fontaine,[1] Ayres (1986, as *Ca-Ca-Ca-Ca*),[2] Heymann (1990).[3] Call type not reported before[4]

Table III Bioacoustic measurements (mean ± SEM) of Ucayali bald uakari call types at Lago Preto Conservation Concession, Peru, March 2003 to June 2005, and June to July 2015.

Call type	Duration (s)	Peak frequency (Hz)	Low frequency (Hz)	High frequency (Hz)	Delta frequency (Hz)	Average entropy (bits)
Hic	0.04 ± 5e-4	885.27 ± 7.34	775.55 ± 7.19	1004.86 ± 7.82	229.31 ± 2.58	1.64 ± 0.01
Chyook	0.05 ± 3e-3	1430.50 ± 53.25	944.48 ± 40.88	1998.23 ± 94.11	1053.75 ± 100.44	2.96 ± 0.11
Bark	0.12 ± 0.01	1208.98 ± 11.94	977.87 ± 12.06	1400.27 ± 14.26	422.40 ± 17.59	2.63 ± 0.06
Rhä	0.19 ± 0.02	1293.46 ± 29.21	1046.79 ± 28.21	1469.22 ± 30.52	422.44 ± 27.08	2.38 ± 0.06
Scream–Kreek	0.50 ± 0.04	1517.72 ± 46.60	1211.68 ± 32.08	1777.58 ± 48.49	565.89 ± 40.30	2.71 ± 0.06
Scream–Wa	0.33 ± 0.03	1762.72 ± 55.53	1293.29 ± 43.99	2125.53 ± 43.82	832.24 ± 39.34	2.99 ± 0.08
Scream-Shriek	0.41 ± 0.03	2592.30 ± 155.84	2221.36 ± 159.17	2838.28 ± 158.18	616.93 ± 43.35	2.72 ± 0.08
Purr	0.48 ± 0.06	1088.54 ± 42.63	777.39 ± 20.29	1302.60 ± 31.61	525.21 ± 44.29	2.84 ± 0.12
Wee-ook	0.16 ± 0.01	2052.08 ± 137.05	1638.48 ± 152.16	2291.13 ± 132.26	652.65 ± 51.86	2.53 ± 0.10
Kik	0.09 ± 0.01	1591.95 ± 105.51	1350.81 ± 91.23	1845.64 ± 142.36	494.84 ± 75.92	2.25 ± 0.13
Chick	0.90 ± 0.02	1998.72 ± 157.79	935.67 ± 54.88	3988.27 ± 72.56	3052.60 ± 85.71	4.41 ± 0.06
High Chick	0.34 ± 0.02	3555.04 ± 73.74	3310.81 ± 74.80	3783.35 ± 71.01	472.54 ± 20.64	2.43 ± 0.06

Two of the call types used and validated in the classification analyses, the *High-chick* and the *Shriek*, were call types not described before (Table II). *High-chicks* are a single-note, high-pitched version of *Chicks*, the alarm call, which were given in response to middle disturbances (e.g., fights and chases, or falling branches). *Shrieks* are a third type of scream, the highest-pitched one, and infants and juveniles produced them during frightening situations

al., 2001, 2005; Fichtel & Hammerschmidt, 2002; 2003). Moreover, *Shrieks* were the screams with the highest frequencies, probably because they are emitted by immature individuals, who have smaller bodies than adults; aligning with empirical evidence showing a strong inverse relationship between body size and vocalization frequencies in primates and other mammals (Bowling *et al.*, 2017). Further research should test if this acoustic variation is meaningful for the Ucayali bald uakaris and if they are capable of distinguishing between these calls despite their highly graded nature, an ability well documented in other primates (Barbary macaques, *Macaca sylvanus*: Fischer, 1998; chimpanzees: Slocombe & Zuberbühler, 2005; Slocombe *et al.*, 2009).

One of the main characteristics of *Cacajao* is its distinctive shortened, nonprehensile tail, which accounts for 34–36% of the length of the head and body and is unique among platyrrhine genera (Hershkovitz, 1987). Although we did not quantify it during data collection, side-to-side tail wagging was a very common, at times almost constant, behavior in Ucayali bald uakaris, along with the emission of *Hics* (particularly in young individuals), *Chicks* (particularly in adults), and all three scream types. We also reported front-to-back tail wagging, which occurs along with the emission of *Barks*, a call type reported by Heymann (1990). Reports describe tail wagging concurrent with vocalizations in bald uakaris, possibly to draw the attention of other group members (Bowler, 2007; Fontaine, 1981; Walker & Ayres, 1996). Because primates rely heavily on their tails to balance and for guiding leaps, Walker & Ayres (1996) suggest that the selection pressures for tail reduction in uakaris must have been great to overcome the advantages for its use in balance but not strong enough to overcome the selection pressure to maintain it for display, which could be related to the role of uakari tail in their acoustic-visual multimodal communication.

We have provided a quantitative compilation of the vocal repertoire of a bald uakari species, while avoiding subjective classification of call types as much as possible. However, our dataset was unbalanced (*Hics* represented 53.9% of all analyzed calls), which might have impacted the classification performance of the categories with small sample sizes (Arnaud *et al.*, 2023). We are confident in the random forest's performance because the classification accuracy did not vary with sample size. For example, despite *Chicks* having a sample size ten times smaller than *Hic*s, they were the call type with the smallest classification error. Likewise, *Purrs*, which had the smallest sample size overall (n = 9 calls), performed third-best in the call classification. Although we could analyze only nine *Purrs*, various individuals from all age-sex classes produced them, and both our observations and previous reports show that this call is not particularly uncommon (Fontaine, 1981). *Chicks* and *Purrs* were among the calls with less gradation, but their small sample sizes may also have reduced the likelihood of capturing within-call gradation, potentially contributing to their apparent acoustic distinctiveness. At the same time, more graded calls (*Rhäs*, *Kreeks*, and *Wa* calls) had moderate-to-good performances in the call classification. As in most studies of calls of wild primates who use the upper parts of the canopy (Bowling *et al.*, 2017; Maciej *et al.*, 2011; Reichard & Anderson, 2015), a second limitation of our study is that calls with low amplitude and emitted by smaller individuals are likely to be underrepresented or not recorded, as may be the case of the *Hiss* and *Keh* calls reported by Fontaine (1981), that we did not record. Future studies, focusing on increasing the

sample size of low-amplitude and rare calls and recording immature individuals, are needed to establish whether or not these vocalizations represent reliable call types. Moreover, although we were not able to individually identify callers, we are confident that we sampled a wide range of the species' acoustic variation by recording different call types produced by several individuals from various units and groups within the studied troop. Nevertheless, individual identification will be necessary for future questions about vocal signature and recognition, and vocal ontogeny. Despite these limitations, our dataset sheds light on the complex communication system of the Ucayali bald uakari, one of the least-known primates.

This study lays the groundwork for future studies that should explore the functional aspects of the call types described here using playback experiments. This experimental approach is essential to empirically validate the social and ecological functions of the different call types, to directly test how listeners respond to each of them, and to examine the cognitive mechanisms and adaptive values behind these responses (Fischer *et al.*, 2013). Moreover, given the Ucayali bald uakari's patchy distribution on the broad Amazon landscape, acoustic surveys based on this vocal repertoire could serve as an effective method to locate, survey and monitor these rare primates in habitats that are difficult to traverse (Bowler *et al.*, 2025). Bald uakaris are also a promising study model for investigating combinatorial capacities and multimodal communication in primates. They possess a varied vocal repertoire, as well as highly conspicuous facial and body signals, which allow for analyses of how discrete and graded calls integrate with visual cues during communication. Additionally, their large troops and high fission–fusion dynamics and visually and acoustically challenging forest habitats create social and ecological pressures that are thought to favor combinatorial and multimodal complexity (Fröhlich & van Schaik, 2018; Krams *et al.*, 2012; McComb & Semple, 2005; Peckre *et al.*, 2019).

In sum, Ucayali bald uakaris have a vocal repertoire with at least 12 different call types. Some of these call types are age-, sex-, and context-specific and some show aspects of both gradedness and discreteness depending on the context of emission and its apparent function. At least one of the calls (*Chicks*) seems to be the product of signal combinations, and at least half of the call types are involved in multimodal communication. Our results suggest that Ucayali bald uakaris, like most primates, rely strongly on their vocalizations to coordinate and regulate group activities and dynamics. Compiling the vocal repertoire of Ucayali bald uakaris offers valuable insights into their communication, socioecology, and behavior and highlights the complexity and adaptability of primate communication systems in dense and dynamic environments, such as the Amazon Forest.

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Author Contributions JL: conceptualization, data collection, data curation, formal analysis, investigation, methodology, visualization, writing – original draft. MB: Conceptualization, data collection, investigation, methodology, funding acquisition, project administration, review & editing.

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