RESEARCH ARTICLE

A novel attention-getting vocalization in zoo-housed western gorillas

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Abstract

As a critical aspect of language, vocal learning is extremely rare in animals, having only been described in a few distantly related species. New evidence, however, extends vocal learning/innovation to the primate order, with zoo-housed chimpanzees and orangutans producing novel vocal signals to attract the attention of familiar human caregivers. If the ability to produce novel vocalizations as a means of navigating evolutionarily novel circumstances spans the Hominidae family, then we can expect to find evidence for it in the family’s third genus, Gorilla. To explore this possibility, we conduct an experiment with eight gorillas from Zoo Atlanta to examine whether they use species-atypical vocalizations to get the attention of humans across three different conditions: just a human, just food, or a human holding food. Additionally, we survey gorilla keepers from other AZA-member zoos to compile a list of common attention-getting signals used by the gorillas in their care. Our experiment results indicated that Zoo Atlanta gorillas vocalized most often during the human-food condition, with the most frequently used vocal signal being a species-atypical sound somewhere between a sneeze and a cough (n = 28). This previously undescribed sound is acoustically different from other calls commonly produced during feeding (i.e., single grunts and food-associated calls). Our survey and analyses of recordings from other zoos confirmed that this novel attention-getting sound is not unique to Zoo Atlanta, although further work should be done to better determine the extent and patterns of transmission and/or potential independent innovation of this sound across captive gorilla populations. These findings represent one of the few pieces of evidence of spontaneous novel vocal production in non-enculturated individuals of this species, supporting the inclusion of great apes as moderate vocal learners and perhaps demonstrating an evolutionary function to a flexible vocal repertoire.

Introduction

Language is considered a uniquely human feature, though most of its components—such as vocal learning, intentionality, syntax, semantics, and other associated cognitive abilities—vaguely emerge in the communication systems of other animals [1, 2]. Yet despite the mechanical...
similarities between vocal production and perception in human and non-human primates (hereafter primates) [3] as well as our shared evolutionary history, some of these cognitive features seem to be absent from the communication systems of our closest relatives. Indeed, evidence for “complex vocal learning,” or the ability to produce novel calls through the imitation of sounds, is rare in the animal kingdom [4, 5], confirmed only in three bird orders (songbirds, parrots, and hummingbirds: [6, 7]), some cetacean [8–10], bat [11, 12], and pinniped species [13, 14], and only recently in elephants [15, 16]. Recently developed frameworks for studying vocal learning, however, have departed from distinguishing vocal from non-vocal learners based only on the presence/absence of vocal mimicry alone, and consider the ability to fine-tune the acoustic structure of species-specific vocal signals in the absence of auditory input as evidence of vocal learning [17–20].

Research has long classified primate vocalizations as innate signals not modifiable by experience [21] and as driven only by the internal state [22, 23]. New evidence, however, demonstrates otherwise: call structural plasticity [24], call convergence [25–27], turn-taking exchanges [28–30], and reinforcement-based vocal learning during development [31] all suggest that primates may at least be limited or moderate vocal learners [18, 32]. Moreover, research examining audience effect on primate communication suggests that some primates have volitional control on vocal production [33] as well as an awareness of the receiver’s perceptual state, potentially indicating some aspects of theory of mind [34, 35]. For instance, female vervet monkeys produce more alarm calls when offspring are nearby [36], male Thomas langurs stop calling only after all group members reply with a counter call [37], while chimpanzees produce exaggerated screams if nearby group members can provide support [38] and more frequent alarm calls if bystanders are unaware of imminent danger [39–41]. Audience effect also influences the production of food calls. Capuchin monkeys delay calling if other individuals are far away [42], while chimpanzees call more often when food quantity is sharable [43] or if estrous females are nearby [44]. Multiple zoo-based experiments have indicated that great apes can adjust their vocal strategies when they are tested across different conditions: specifically, (1) in the presence of visible but inaccessible food, (2) in the presence of an inaccessible and inattentive human without food, or (3) in the presence of an inaccessible and inattentive human with food. These experiments have confirmed that great apes reliably modify their responses according to the perceived attentional state of human experimenters: in other words, they show greater efforts at getting the attention of humans during the third condition [45–49], presumably since the humans could access foods that the apes themselves could not. Moreover, these apes attuned their strategies if they were not initially successful, demonstrating increased effectiveness at communication [50].

Evidence of vocal learning and/or innovation, although scant, is slowly accumulating for captive apes: orangutans can learn to produce voiced utterances [51–53] and whistles [54, 55], chimpanzees adopt new referential food calls through vocal convergence under social integration [56], and enulturated apes, such as the gorilla Koko and the chimpanzee Vicky, are able to produce a limited number of novel utterances [57, 58]. Most of these novel signals seem to emerge while communicating with human caregivers. For instance, Hopkins, Taglialatela [59] explored species-atypical attention-getting vocal strategies in chimpanzees, behaviorally and acoustically describing the “raspberry” and the extended grunt, which they explicitly classified as “novel signals invented in novel environmental circumstances” (p281). Wich, Swartz [54] showed that orangutans are able to imitate human whistling to attract and direct human attention, an ability later confirmed in at least ten other captive orangutans [55]. Furthermore, growing evidence suggests the novel call types emerging in captive settings can indeed be socially learned (chimpanzees: [60–62]; orangutans: [55]).
Despite an emerging trajectory and a growing need to catalog novel vocal signals produced in captivity, particularly those signals used to get the attention of humans, little has been reported for gorillas. Here we test whether gorillas use species-atypical vocal signals to attract the attention of humans, as reported for both orangutans and chimpanzees. We compare the vocal and gestural signals produced by the gorillas during three conditions: 1) only keeper, where a keeper sits in front of the subject’s cage, 2) only food, where a bucket of food is positioned in front of the subject’s cage, and 3) keeper holding food, where a keeper holds a bucket of food in front of the subject’s cage. We hypothesize that if gorillas use vocal and/or gestural signals to capture a human’s attention, they will use them more often during the third condition than during the first two [46]. In identifying atypical vocal signals, we provide the acoustic description and compare them to the species-specific calls that are most frequently uttered while feeding: contact calls [grunts: 63] and food-associated calls [hums: 63, 64]. Finally, we present the results of a survey of 39 gorilla zookeepers across 19 North American AZA-member zoos to assess the types of attention-getting signals used in captivity by this species.

Methods

Study subjects

We included eight gorillas (Gorilla gorilla gorilla), 2 males (19–55 years old) and 6 females (9–31 years old), in the experimental portion of the study. We conducted the experiments at Zoo Atlanta between April and May 2015. We indicate kinship, date of birth, and Studbook ID numbers for each subject in Fig 1. We included all the female gorillas from Taz’s group as well as two external adult males whose testing did not interfere with the keepers’ work plans during the days of data collection.

Testing procedure

We tested each subject in his/her indoor cage either in isolation or in pairs, and mothers always in the company of dependent infants. At all times subjects were able to see, smell, and communicate vocally with group members and other gorillas occupying the same indoor enclosure (even though they were in separate chambers during the experiment). The keeper staff generally followed a similar procedure of separating gorillas during feeding sessions to

![Fig 1. Kinship, year of birth, and studbook ID of study subjects. Light and dark gray boxes indicate female and male gorillas, respectively, and patterned background indicate gorillas not included in the experimental study but included here to indicate kinship.](https://doi.org/10.1371/journal.pone.0271871.g001)
reduce competition between group members and to ensure that all individuals received an adequate amount of food; thus, no disruption of daily gorilla routines occurred while conducting this study. Our research protocol was approved by the Zoo Atlanta Scientific Review and by the Committee Institutional Animal Care and Use Committee of the University of Georgia and complies with the ASAB/ABS guidelines for the Use of Animals in Research.

We tested the subjects once per three conditions: *only keeper* (K), *only food* (F), and *keeper holding food* (KF). During each condition, we positioned the keeper and/or food out of reach and in clear sight of the gorilla subject at 1 meter from their enclosure. In the first condition (K), the keeper sat on a stool facing sideways (body and face turned 90˚ from the subject). In the second condition (F), the keeper placed fresh grapes in a bucket on a stool, tilting the bucket to ensure its contents were in complete sight of the subject. The keeper conducting the experiments has worked with the Zoo Atlanta gorillas for over 15 years, currently serves as the Assistant Curator of Primates, and is one of the present study’s co-authors (JC). We tested each subject consecutively in all three conditions, with an interval of 1 min between conditions. We randomized the sequences of the conditions across subjects. Each experiment lasted 120 seconds, and we recorded the results with a Panasonic HC-VX870 4K Ultra HD Camcorder and/or a Canon Powershot G12 with a built-in microphone. To ensure high quality recordings of vocal behavior during the experiments, we also positioned a Sennheiser MKH 416 short shotgun microphone at 1–1.5 m from the subject’s cage, protecting it with a foam windshield (MZW415ANT) and connecting it to a Professional Solid State Recorder Marantz PMD671. Additionally, because the acoustic quality of recordings was variable and not many calls were produced during the experiments, we complemented the vocal sample with *ad libitum* acoustic recordings of single grunts, hums, and attention-getting sounds (the same calls produced during the experiments) from 7 Zoo Atlanta gorillas (including all of the females that participated in the experiments, plus another female, Shamba) during 26 days of data collection between January and October 2015, using the same equipment described above.

MS coded the videos, categorizing attention-getting strategies as either vocalizations (distinguishing types: e.g., attention-getting call, grunts, grumbles) or gestures. We further categorized gestures as either auditory (e.g., handclapping, chest-beating, or enclosure-banging) or non-auditory (e.g., tool-use, attempting to touch oneself or another gorilla, or reaching fingers through the mesh toward the food and/or keeper). To test for coding reliability, MS recoded twenty percent of the videos one year later. We used frequencies of occurrence of attention-getting sounds, other vocalizations, and gestures to assess intra- and inter-rater reliability using a two-way mixed, absolute agreement, intra-class correlation [65]. The resulting intra-class correlation coefficients (ICC) were all in optimal range [ >0.90; 65], indicating high intrarater consistency: test-retest correlation for attention-getting sounds was 0.98, for other vocalizations was 0.96, and for gestures 1.00. We repeated the same procedure but for different raters after the experimenter (RS) recoded twenty percent of the videos and obtained again significant and high correlations for each signal type considered (1.00, 0.93, and 0.94 respectively).

**Acoustic analysis**

We made all digital recordings at a sampling frequency of 48 kHz and saved them as uncompressed WAV files (PCM format). To facilitate the measurements of acoustic and temporal parameters, we converted the sampling frequency of all calls to 11,025 Hz, using the Avisoft SASLab Pro software (R. Specht, Berlin, Germany). We generated spectrograms using a
frequency resolution of 1024 points and the Hamming Window option. We selected only good quality recordings (low background noise-call ratio) for a total of 64 calls. Gorilla vocalizations can be produced in isolation, in series [63], or in combination [66]. We considered the unit of analysis the single segment (since the three call types were never combined with other calls during the experiments) and measured for each call one temporal parameter, the call duration, and 4 frequency parameters, the mean frequency 1st dfa (distribution of frequency amplitude), the mean frequency 2nd dfa, the minimum difference between 1st and 2nd df (dominant frequency bands), and the maximum peak frequency, to broadly describe temporal and spectral call characteristics, using a custom software program [LMA: 67]. In cases where calls were given in bouts (series), we also reported the mean duration of the silent interval between calls. Mean values of call parameters are given as value±SD.

To determine if the calls labeled as attention-getting were acoustically distinct from the other calls produced during the experiments (i.e., single grunts and food calls or hums: [63, 64]), we performed a discriminant function analysis [DFA: 68] and a leave-one-out cross validation DFA using the five acoustic parameters mentioned above [69]. For this analysis we included calls of high quality recorded during the experiments as well as other recordings of the same call types recorded ad libitum at another time (as before mentioned). We included calls produced by all 6 of the female gorillas that participated in the experiments plus the grunts of one additional Zoo Atlanta female gorilla, Shamba, to increase the sample size of this call type (see Table 2 in S1 File for each female sample size; and S1 Data for the entire dataset). In addition, to account for non-independence, we ran a permuted DFA (pdfa.incomplete—since not all callers contributed to each call type) using the function written by Roger Mundry in R (version 4.2.0; Core Team 2013), based on the function lda of the MASS R Package [70]. The procedure includes 100 random selections and 1000 iterations, allows to control for caller ID, and provides the statistical significance (equivalent to p-value) of the mean effect size of cross-validated classification. We then assessed whether the parameters significantly associated with the DFA functions (r > 0.5) were statistically useful to discriminate across call types using linear mixed models [LMM: 71] when controlling for repeated (Caller ID as random factor) and unequal sampling among individuals (Satterthwaite approximation). We adjusted for multiple analyses using Sequential Bonferroni method. With the exception of the pDFA described above, all statistical analyses were conducted using SPSS 25.0 (IBM Corp., NY USA).

Attention-getting and other novel sounds in other zoos

To obtain a robust sampling of attention-getting behaviors used by zoo gorillas toward their human caregivers, we created a fourteen-question survey in Qualtrics (S1 Appendix) and distributed it to 47 AZA member zoos housing gorillas in the United States and Canada. We used both closed-ended questions (those requiring a yes or no answer or those where respondents were asked to list the ages and sexes of gorillas) as well as open-ended questions (those where respondents were asked to qualitatively describe a particular behavior). We asked respondents to meet the following conditions in order to take part in the survey: (1) to have at least one year of experience working directly with the gorillas on whom they reported and (2) to be able to recognize the individual gorillas on sight. We also requested at least two individual survey responses from each zoo, but this request was not a requirement.

Results

Experiments

The Zoo Atlanta gorillas produced three types of vocalizations during the experiments, listed here in order of frequency: a novel call type indicated here as an attention-getting sound (AG)
(29), single grunts (3), and hums (2) (Table 1). Interestingly, only half of the individuals we tested produced the novel attention-getting sound (Table 1), and they were all adult female gorillas. Three of them are closely related: Sukari and Kudzoo are sisters, and Macy is Kudzoo’s first daughter (see Fig 1). The attention-getting gestures produced during the experiments included those that were auditory (i.e., gestures executed in order to produce a distinct audible component, such as hand-clapping, chest-beating, or enclosure-banging) and those that were non-auditory (i.e., gestures that did not invariably produce a distinct audible component, such as tool-use, attempting to touch oneself or another gorilla, or reaching fingers through the mesh toward the food and/or keeper). Table 2 Column B lists all attention-getting strategies exhibited by Zoo Atlanta gorillas.

The frequency of attention-getting sounds (AG), other vocalizations (VOC), and gestures (GES) differed significantly between experimental conditions (Friedman test: AG: $\chi^2 = 7.54$; $p = 0.023$; VOC: $\chi^2 = 8.00$; $p = 0.018$; and GES: $\chi^2 = 10.23$; $p = 0.006$; auditory and non-auditory). S = sex; A = age in 2015; F = food; K = keeper; KF = keeper with food. Note: Total gestures include those that are non-auditory and auditory. Of the total gestures, we indicated the # of auditory gestures in parentheses.

![Fig 2](https://doi.org/10.1371/journal.pone.0271871.g002)

**Table 1. Number of signals for each individual in the three conditions.**

| Subject | S | A | Attention-Getting Calls | Other Vocalizations | Gestures |
|---------|---|---|-------------------------|---------------------|----------|
|         |   |   | $F$ | $K$ | $KF$ | $F$ | $K$ | $KF$ | $F$ | $K$ | $KF$ |
| Kudzoo  | F | 21 | 0  | 0  | 7   | 0  | 0  | 0   | 0 (0) | 0 (0) | 2 (1) |
| Kuchi   | F | 30 | 0  | 0  | 2   | 0  | 0  | 1   | 0 (0) | 0 (0) | 7 (0) |
| Lulu    | F | 15 | 0  | 0  | 0   | 0  | 0  | 0   | 0 (0) | 0 (0) | 11 (9) |
| Sukari  | F | 16 | 0  | 0  | 7   | 0  | 0  | 2   | 0 (0) | 0 (0) | 2 (0) |
| Macy    | F | 9  | 0  | 1  | 12  | 0  | 0  | 0   | 1 (0) | 5 (1) | 26 (4) |
| Kazi    | F | 9  | 0  | 0  | 0   | 0  | 0  | 0   | 4 (0) | 0 (0) | 2 (0) |
| Charlie | M | 19 | 0  | 0  | 0   | 0  | 0  | 1   | 1 (0) | 0 (0) | 1 (0) |
| Ozzie   | M | 54 | 0  | 0  | 0   | 0  | 0  | 1   | 0 (0) | 0 (0) | 12 (12) |

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auditory gestures did not differ significantly and thus are analyzed together ($Z = -1.29 \ p = 0.65$)—when analyzed separately they both differed between conditions: auditory gestures: $\chi^2 = 7.54; \ p = 0.02$, non-auditory gestures: $\chi^2 = 8.44; \ p = 0.015$). The gorillas produced all three types of signals more often during the KF condition than compared to either the F or K condition alone (Fig 2). However, the small sample size (N = 8) prevented us from finding

| Description | Column A | Column B |
|-------------|----------|----------|
| Attention-getting vocalizations | | |
| Attention-getting call: Per respondent, a call where the lips are puckered, mouth is open and one to three short vocalizations are produced | >5<33⁴ | 4 |
| Grumble/rumble/purr/hum: A low, long call of irregular length and dense harmonics bearing varying degrees of noise and produced by an open or closed mouth [63] | 27 | 3 |
| Raspberries: A voiceless call where the lips buzz or sputter to produce the sound [57, 98] | 11 | 0 |
| Bark: A loud, harsh, and abrupt call most often produced as a single call but occasionally in repetition by adult males [63] | 7 | 0 |
| Kiss/squeak/lip smack: A voiceless, ingressive sound produced by the lips [22, 94] | 5 | 0 |
| Grunt: A soft, guttural single- or double-syllable call with noisy harmonics, produced with an open or closed mouth at a low frequency [65] | 4 | 5 |
| Cry/scream: A call with high, sparse harmonics, varying degrees of noise, and produced in a sequence of varying lengths [65] | 3 | 0 |
| Burp: Per respondent, also referred to as a “frog burp” and used by the gorilla to startle people | 1 | 0 |
| Unspecified vocalization: No further description provided by respondent | 1 | 0 |
| Attention-getting gestures, auditory | | |
| Banging/knocking/hitting/tapping the mesh/enclosure/window/wall/door | 27 | 3 |
| Hand clapping | 15 | 1 |
| Chest beating | 3 | 1 |
| Attention-getting gestures, non-auditory | | |
| Shaking/waving/tapping/lifting part of body | 5 | 3 |
| Pushing objects through mesh, trading for object, using tools to reach object | 8 | 0 |
| Staring | 3 | 0 |
| Following keeper | 2 | 0 |
| Soliciting play | 1 | 0 |
| Throwing hay | 1 | 0 |
| Presenting/pushing body against mesh (4); biting mesh (4) | 0 | 8 |
| Reaching toward mesh (4), grabbing (1) | 0 | 5 |
| Displaying | 0 | 1 |

**NOTE:** Through the analysis of videos and recordings of 15 gorillas from other zoos, we were able to confirm the use of the target call in 6 gorillas. The number of gorillas reported to use the target call from keepers totaled 33: Calgary Zoo (2), Columbus Zoo and Aquarium (2), Dallas Zoo (5), Houston Zoo (1), North Carolina Zoo (1), Oklahoma City Zoo (1), Riverbanks Zoo and Garden (3), Utah’s Hogle Zoo (1), WCS Bronx Zoo (5), Woodland Park Zoo (11), Zoo Knoxville (1).

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 auditory gestures did not differ significantly and thus are analyzed together ($Z = -1.29 \ p = 0.65$)—when analyzed separately they both differed between conditions: auditory gestures: $\chi^2 = 7.54; \ p = 0.02$, non-auditory gestures: $\chi^2 = 8.44; \ p = 0.015$). The gorillas produced all three types of signals more often during the KF condition than compared to either the F or K condition alone (Fig 2). However, the small sample size (N = 8) prevented us from finding
significant pairwise comparisons when adjusting for multiple analyses with the Bonferroni method, except for gestures being produced significantly more often during the KF condition than the K condition (Wilcoxon rank test: K vs. KF: z = -2.53; p < 0.025).

Attention-getting call

Captive gorilla attention-getting calls resemble a sound between a sneeze and a cough that we named "snough" or AG (video clip in S1 Video). The gorillas at Zoo Atlanta generally produced these signals as single calls, but in a few cases, they were part of a longer series with 2 to 4 calls spaced on average by 0.8±1.2 s (min = 0.09 s, max = 2.5 s; see Fig 3 for bout samples of three females). The mean duration of the single call was 212.4±63 ms, with Macy and her mother Kudzoo having shorter calls than those of the other two adult females. On average, the mean frequencies of the 1st and 2nd df (distribution of frequency amplitude) were 553±281 Hz and 1110±43 Hz, respectively. The minimum difference in frequency between the 1st and 2nd dominant frequency bands was in average below 200 Hz (195.5±43.0), while the maximum peak frequency was almost 1000 Hz (997.6±357.6) (see Table 3). The calls produced by the three related females (Sukari, Kudzoo, and Macy) were often accompanied by an exaggerated mouth opening and/or a gentle but fast repeated slapping/covering of head or face.

To test whether the novel attention-getting call we identify here differs acoustically from common gorilla calls such as grunts and food calls, we ran a discriminant function analysis (DFA). For this analysis, we used call recordings only from the female gorillas since the males never produced the attention-getting calls and since male and female calls may vary greatly due to the large difference in body size [170.4 vs. 71.5 kg; 72]. The DFA distinguished among the three call types, with a classification accuracy of 92% for both the original and cross-

Table 3. Individual acoustic measurements of attention-getting calls, or "snough", for each female. Listed are the following: duration of single element; duration of silent interval between calls (number of intervals considered) when given in bouts; mean frequency 1st df (distribution of frequency amplitude) (Q1mean); mean frequency 2nd df (Q2mean); Minimum difference between 1st and 2nd df (dominant frequency bands) (Diffmin); and Maximum peak frequency (Pfmax).

| Subject  | Call n | Duration (ms) | Intercall interval (s) | Q1mean (Hz) | Q2mean (Hz) | Diffmin (Hz) | Pfmax (Hz) |
|----------|--------|---------------|------------------------|-------------|-------------|-------------|------------|
| Sukari   | 18     | 233.0±100.0   | 0.15±0.1 (n = 20)      | 365.2±103.8 | 762.3±270.0 | 171.9±44.6  | 642.9±295.5 |
| Kuchi    | 3      | 288.1±39.5    | 2.50±1.8 (n = 2)       | 478.0±209.0 | 1187.7±532.8| 152.0±17.7  | 990.3±1056.8 |
| Macy     | 3      | 141.1±73.9    | 0.10±0.1 (n = 3)       | 968.3±88.9  | 1634.7±222.2| 208.3±46.3  | 1489.0±273.9 |
| Kudzoo   | 7      | 187.3±75.0    | 0.19±0.2 (n = 4)       | 401.4±186.1 | 854.3±317.8 | 249.7±80.1  | 867.3±760.4  |
| Female Mean | 212.4±62.9 | 0.8±1.2 | 553.2±280.7 | 1109.8±394.8 | 195.5±43.0 | 997.6±357.6 |

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validated DFAs (Wilks’ $\lambda = 0.078; \chi^2 = 152.99; df = 6; p < 0.001$), indicating that the profiles derived from the calls are highly stable [73]. Two canonical discriminant functions were generated: Function 1 explained 91.7% and Function 2 8.3% of the variance. While Function 1 was primarily correlated with the call duration ($r = 0.95$), Function 2 was correlated with the mean frequency of the $2^{nd}$ dfa ($r = 0.73$) and the minimum difference in frequency between the $1^{st}$ and $2^{nd}$ dominant frequency bands ($r = -0.65$). The percentages of corrected assigned calls varied between 87% (attention-getting calls) to 100% (food calls or hums) (Table 4). Misclassified calls were only recorded between attention-getting (AG) calls and grunts, with 1 grunt classified as AG call and 4 AG calls misclassified as grunts (Fig 4). The permuted DFA (pDFA) indicated that the calls were still significantly different when controlling for caller ID, with 78% of cross-classified calls assigned correctly ($p = 0.028$). Linear Mixed Model results had confirmed that the three acoustic parameters used in the DFA differed significantly among calls when controlling for caller ID (duration: $F_{(2, 51)} = 157.95; p < 0.001$; $q_2^{\text{mean}}: F_{(2, 58)} = 31.56; P < 0.001$; diffmean: $F_{(2, 54)} = 9.34; p < 0.001$). While duration differed significantly

| Call Type | N   | AG calls | Grunts | Hums |
|-----------|-----|----------|--------|------|
| AG calls  | 31  | 87.1% (27) | 12.9 (4) | 0    |
| Grunts    | 17  | 0        | 100% (17) | 0    |
| Hums      | 16  | 6.3% (1)  | 0      | 93.8% (15) |

92.2% of original and cross-validated grouped cases correctly classified.

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![Fig 4. Plot of the two canonical discriminant functions for the three call types in captive western gorilla.](https://doi.org/10.1371/journal.pone.0271871.g004)
between each call type pairs, the mean frequency of the 2nd dfa distinguished attention-getting calls from the other two calls, the minimum difference in frequency between 1st and 2nd dominant frequency bands distinguished grunts from attention-getting calls and hums (Fig 5; see S2.1 Table in S1 File for pairwise comparison results).

**Attention-getting signals and presence of the novel call across AZA-member zoos**

Between August 2020 and February 2021, we received 39 individual survey responses from keepers at 19 AZA-member zoos hosting ~118 gorillas, which was roughly a third of the total gorilla population in AZA facilities during that time [74]. All survey respondents reported having previously observed attention-getting strategies directed toward them by one or more gorillas in their care, and 34 respondents (87.2%) from 17 institutions (89.5%) described at least one type of vocalization. Overall, auditory signals accounted for over 84% of all attention-getting strategies reported, including vocalizations (e.g., grumbles, purrs, and raspberries: 47.2%) and auditory gestures (e.g., banging, chest beating, and hand clapping: 35.4%), while non-auditory gestures accounted for only 15.7% of attention-getting strategies reported (Fig 6; Table 2 Column A). Eighteen survey respondents (46.2%) confirmed the presence of the target vocalization in the vocal repertoires of at least one of the gorillas in their care. In total, these respondents attributed the vocalization to 33 gorillas (F = 23, M = 10) at 11 zoos (58% of the zoos returning survey responses). All respondents reported a context for the target call that was about one or a combination of the following: food, keeper-gorilla interactions (e.g., training sessions), and/or the gorillas being interested in something and/or seeking/wanting attention.

We followed up with 11 zoos with requests for vocalization recordings when one or both of the following occurred: (1) at least one keeper confirmed the presence of the target vocalization in their gorilla group but did not supply a recording of the call or (2) at least one keeper provided a qualitative description of an attention-getting vocalization that we interpreted to be a potential description for the target vocalization (e.g., “soft barking,” “short, dry cough,” “huff noise”). Between our solicitations as well as the recordings already provided by some respondents with the original surveys, we received a total of 17 videos and/or audio clips of different gorillas from 11 facilities. Among these, and after selecting recordings of sufficiently high quality (n = 15), we confirmed the use of the target call by 6 gorillas (5 females and 1 male) housed at 4 different zoos. One of these gorillas (Macy) was also the subject of our experimental study at Zoo Atlanta, suggesting long-term use of the target call even after transferring between institutions.

**Discussion**

In this study we explored whether zoo-housed western gorillas selectively used species-typical and/or species-atypical vocal signals to attract the attention of humans. We repeated an experiment known to elicit attention getting signals in great apes [46] and found that gorillas at Zoo Atlanta produced vocalizations and gestures significantly more often when human and food were present together than when either stimulus was presented alone. This was also true for a novel vocalization not previously described in the species repertoire and produced mostly during the keeper-food condition, which we named the attention-getting sound (AG) or “snough”. We then showed that the AG call was acoustically distinct from other gorilla calls produced in the same context: the food call or hum and the single grunt [63, 64]. Moreover, the results of the zookeeper survey suggest that the AG call is not idiosyncratic to the Zoo Atlanta gorillas, as survey respondents attributed its use to as many as 33 gorillas housed at 11
different zoos across the US and Canada. By examining video footage of 45% of these gorillas (15/33), we confirmed that the AG call was in fact produced by at least 6 gorillas (5 females and 1 male) housed at 4 different facilities. These results demonstrate that gorillas can modify their calls to produce a novel sound and furthermore confirm that they can produce their calls and gestures intentionally to modify the attention status of their caregivers.

Western gorillas at Zoo Atlanta use diverse signals to attract human attention, including vocalization and auditory/non-auditory gestures, with soft vocalizations of low frequency, banging or hand clapping, and shaking/waving a body part being some of the most common signals used. Although our sample size was small (n = 8 gorillas), all three communicative signals tested (i.e., the AG call, other vocalizations, and gestures) followed a similar pattern: they were all more frequently produced during the keeper-food condition compared to when either stimulus was presented alone. Regarding the gestures, contrary to our expectation, gorillas produced both auditory and non-auditory gestures more often in the third condition, possibly because the keeper position (at 90˚ instead of 180˚) permitted the gorillas to see one of the keeper eyes, which might have led to the use of silent gestures to attract their attention. Among the vocalizations produced during the experiment, the most common call type was the novel attention-getting sound (85%), even if only half of the subjects used it (n = 4). The other call types (grunts and hums) were rare and in fact were never produced during the food-only or keeper-only conditions. Thus, in contrast to chimpanzees (see [75]), gorillas did not produce significantly more food calls (or hums: [63, 64]) when food was presented alone, indicating differing call functions between the two species. While chimpanzees produce food calls upon initial discovery to recruit specific individuals to the food source [76], western gorillas produce them only during food consumption [63, 64], potentially to coordinate spatial distances and/or reduce aggression between group members while feeding. However, since our study subjects were separated from other adults and were not provided food during the experiment,
these potential food call motivations were not present. This may explain why we recorded only two hums throughout all trials.

The novel call type, the AG sound, has not previously been described in the repertoire of wild gorillas [63, 77–79]. Indeed, our study results indicate that it is used specifically to attract the attention of humans, suggesting that gorillas, as other apes, are able to produce novel sounds when encountering novel contexts (e.g., the chimpanzee raspberry: [59]; orangutan whistling: [54, 55]). However, because the vocal behavior of wild western gorillas (the gorilla species found in US and Canadian zoos) has only recently been described [63, 66], we cannot exclude the possibility that future studies may document the target call in wild populations, as well. Nevertheless, in our study, the AG call was never used by captive gorillas when communicating with one other (J. Carrigan pers. Comm.; R. Salmi unpublished data), supporting the idea that it is a novel sound not part of the typical gorilla-gorilla communication repertoire and that it emerged to address the communicative need of attracting human attention in captive settings. This, however, does not exclude the possibility that the same call may be separately innovated and used for different purposes in wild populations. The AG sound, in fact, is not the first vocal invention noted in gorillas. Perlman and Clark (57) attributed several novel utterances to the female gorilla Koko during interactions with caregivers. These included a fake cough/sneeze, which was accompanied by a hand gesture and an open mouth and strongly resembled our study’s AG sound, and a raspberry, used by Koko to obtain/request nuts and produced by lingual-labial fricative (i.e., folding her tongue length-wise, pressing it between her lips, and blowing). Indeed, across our survey, 11 participants representing 5 zoos reported raspberries as a common attention-getting strategy exhibited by the gorillas in their care, although no further details on how the gorillas articulated them were provided. The same call was recently described as potential vocal tradition in some wild populations of the congeneric mountain gorillas, though individuals there used it in a different context and with a different function [80]. Thus, vocal inventions and traditions, although rare, are present in the genus Gorilla and, in some cases, are shared by all great apes [81, 82].

The AG call is acoustically different to other gorilla calls commonly used during feeding (namely, hums and grunts), being of shorter duration and/or higher frequency yet still within the known vocal range of this species (R. Salmi pers. comm.). At Zoo Atlanta, the novel AG call was produced alone or in a series of calls by four gorilla females, equal to only 50% of our sample. Our analyses of video/audio recordings of potential samples of the AG call from gorillas at other zoos, however, yielded further insight: (1) it confirmed the AG call’s presence outside of Zoo Atlanta, (2) it provided evidence that the call is used by both sexes, and (3) it indicated that the number of gorillas to which survey respondents had attributed the AG call was most probably an overestimation. Though respondents attributed the target call to at least 33 gorillas, the number might be closer to 13 individuals (40%; considering the proportion of gorillas producing the target call among those for whom we received good quality recordings: 6/15). Misclassification of similar-sounding gorilla calls by the survey respondents was expected, particularly since the vocal repertoire of gorillas is highly graded [83] with no clear boundaries between call types and since call identification by ear, without visual inspections of spectrograms, is prone to error.

Although confirmed in some zoo gorilla populations in the US and Canada, the AG call is likely not as common as the more prominent raspberry call used by captive chimpanzees [62], which may indicate that zoo gorillas only recently adopted this sound for the purpose of getting the attention of humans. Moreover, the call may spread more slowly than the chimpanzee raspberry owing to the lower intensity of affiliative interactions [84], smaller social groups [85], and smaller captive population sizes of gorillas when compared to chimpanzees (~ 400 vs. ~1600 in 2019, North America; [74, 86]).
Since the presence of the AG sound is sparse even within institutions, social learning and independent innovation as opposed to genetic or ecological factors may better explain its distribution, similar to other ape calls that emerged in captive settings (chimpanzees: [60–62]; orangutans: [55]). The novel AG call and its usage could be learned during early ontogenetic developmental stages by those gorillas exposed to the signal, which could explain why most of the individuals using the AG call at Zoo Atlanta were related to one other, either vertically (mother-daughter) or horizontally (sister-sister). Among the 6 gorillas confirmed to use the call outside Zoo Atlanta, two females belong to the same group and are distantly related, two adult females are not related but are part of the same social group, the other two gorillas lived in different zoos, with one being Macy, who transferred from Zoo Atlanta after participating in our study. Although the use of the same call by gorillas within and outside Zoo Atlanta for the same purpose suggests transmission via social learning and/or parallel independent innovations, our study does not explain how the innovation/s occurred. Whether the AG (or snough) call has emerged randomly or has been learnt/modelled by observing humans, as seems to be the case for Koko’ fake cough and the orangutans’ whistle [55], remains unknown. We can only speculate that a sound somewhere between a cough and a sneeze would instinctively attract the attention of caregivers, whose responsibilities include the daily monitoring of their gorillas’ health. This in turn could explain independent innovation of the same call at different institutions where learning did not play a role in its spread. Future studies are needed to quantitatively assess the spread of the AG call and to determine its origin and transmission patterns across the captive gorilla population. Moreover, because the current study is unable to confirm whether the novel AG is a case of vocal usage learning (i.e., the use of an existing call-type in a novel context) or vocal adjustment learning (i.e., the modulation of an existing call-type) [87], future studies should also compare it to the entire vocal repertoire of captive gorillas.

Although, the vocal repertoires of primates, including those of apes, are characterized by innate calls at the species and possibly the genus level [88], our research contributes to a small but growing body of knowledge showing that primates do modify their vocal output based on experience [81], making them limited or moderate learners [18, 32]. The ability to generate novel acoustic signals represents an important characteristic of human language [89] with potentially early evolutionary roots, since all great ape species have been shown to generate novel sounds, although rarely, when encountering novel environments with novel communicative needs (i.e., captivity) (chimpanzee: [59]; orangutan: [54, 55]; bonobo; [82, 90]; gorilla: [57, this study]). This ability may not be limited to great apes, since examples of vocal accommodations to ecological and social contexts [e.g., 25, 91], the use of putative distinct vocal signals from populations of the same species [92], combinatory ability of vocal signals [e.g., 93–96], and the influence of parental vocal responses on the vocal development of infants [marmosets: 3], are some of the examples suggesting learning processes in the production of monkey calls as well. We thus support a paradigm shift in the study of vocal learning that (1) overcomes the dichotomous classification of vocal learners vs. non-vocal learners based on vocal mimicry alone and (2) embraces the multidimensionality of this complex continuum trait [17, 18, 20, 32, 97] to better explore the mechanisms involved in vocal learning [27] and the factors influencing its evolution.

Supporting information
S1 Appendix. Summary of the questionnaire distributed to survey respondents at AZA institutions. (DOCX)
S1 File. Pairwise comparison between call types.  
(DOCX)

S1 Video. Video of the novel attention getting call (Sukari–Zoo Atlanta).  
(MOV)

S1 Data. Acoustic data used in discriminant function analysis.  
(CSV)

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References
1. Snowdon CT. Social processes in the evolution of complex cognition and communication. In: Oller DK, Griebel U, editors. Evolution of Communication Systems: A Comparative Approach. Cambridge MA: MIT Press; 2004. p. 131–50.
2. Fishbein AR, Fritz JB, Idsardi WJ, Wilkinson GS. What can animal communication teach us about human language? Philosophical Transactions of the Royal Society B: Biological Sciences. 2020; 375 (1789):20190042. https://doi.org/10.1098/rstb.2019.0042 PMID: 31735148
3. Ghazanfar AA, Liao DA, Takahashi DY. Volition and learning in primate vocal behaviour. Animal Behaviour. 2019; 151:239–47. https://doi.org/10.1016/j.anbehav.2019.01.021 WOS:000467013300024.
4. Janik VM, Slater PJB. The different roles of social learning in vocal communication. Animal Behaviour. 2000; 60:1–11. https://doi.org/10.1006/anbe.2000.1410 WOS:000086673400001. PMID: 10924198
5. Tomasello M. Origins of human communication: MIT Press; 2010.

6. Jarvis ED. Learned birdsong and the neurobiology of human language. In: Zeigler HP, Marler P, editors. Behavioral Neurobiology of Birdsong. Annals of the New York Academy of Sciences. 10162004. p. 749–77.

7. Bradbury JW, Balsby TJS. The functions of vocal learning in parrots. Behavioral Ecology and Sociobiology. 2016; 70(3):293–312. https://doi.org/10.1007/s00265-016-2068-4

8. Janik VM. Cetacean vocal learning and communication. Current Opinion in Neurobiology. 2014; 28:60–5. https://doi.org/10.1016/j.conb.2014.06.010 WOS:000343633000012. PMID: 25057816

9. Abramson JZ, Victoria Hernandez-Lloreda M, Garcia L, Colmenares F, Abotiz F, Call J. Imitation of novel conspecific and human speech sounds in the killer whale (Orcinus orca). Proceedings of the Royal Society B-Biological Sciences. 2018; 285(1871). https://doi.org/10.1098/rspb.2017.2171 WOS:000423774700009. PMID: 29386364

10. Tsukasa M, So I, Hiroshi K, Kazutoshi A. Vocal imitation of human speech, synthetic sounds and beluga sounds, by a beluga (Delphinapterus leucas). International Journal of Comparative Psychology. 2014; 27(3):368–84.

11. Vernes SC, Wilkinson GS. Behaviour, biology and evolution of vocal learning in bats. Philosophical Transactions of the Royal Society B. 2019; 375. https://doi.org/10.1098/rstb.2019.0061 PMID: 31735153

12. Knörnschild M. Vocal production learning in bats. Current Opinion in Neurobiology. 2014; 28:80–5. https://doi.org/10.1016/j.conb.2014.06.014 PMID: 25050812

13. Ralls K, Fiorelli P, Gish S. Vocalizations and vocal mimicry in captive harbor seals, Phoca vitulina. Can J Zool. 1985; 63:1050–6. https://doi.org/10.1139/85-157

14. Fitch WT, Schusterman RJ, Reichmuth C, Spasikova M, Mietchen D. Vocal learning in pinnipeds: A model system for human speech evolution. The Journal of the Acoustic Society of America. 2008;123(5):3507-. https://doi.org/10.1121/1.2934401 WOS:000423774700009. PMID: 29386364

15. Poole JH, Tyack PL, Stoeger-Horwath AS, Watwood S. Elephants are capable of vocal learning. Nature. 2005; 434(7032):455–6.

16. Stoeger AS, Mietchen D, Oh S, de Silva S, Herbst CT, Kwon S, et al. An Asian elephant imitates human speech. Current Biology. 2012; 22(22):2144–8. https://doi.org/10.1016/j.cub.2012.09.022 WOS:000311523800023. PMID: 23122846

17. Arriaga G, Jarvis ED. Mouse vocal communication system: Are ultrasounds learned or innate? Brain and Language. 2013; 124(1):96–116. https://doi.org/10.1016/j.bandl.2012.10.002 WOS:000314390000010. PMID: 23295209

18. Martins PT, Boeckx C. Vocal learning: Beyond the continuum. Plos Biology. 2020; 18(3). https://doi.org/10.1371/journal.pbio.3000672 WOS:000558340000012. PMID: 32226012

19. Wirthlin M, Chang EF, Knörnschild M, Krubitzer LA, Mello CV, Miller CT, et al. A modular approach to vocal learning: Disentangling the diversity of a complex behavioral trait. Neuron. 2019; 104(1):87–99. https://doi.org/10.1016/j.neuron.2019.09.036 PMID: 31600518

20. Tyack PL. A taxonomy for vocal learning. Philosophical Transactions of the Royal Society B-Biological Sciences. 2020; 375(1789). https://doi.org/10.1098/rspb.2018.0406 WOS:0005068580700005. PMID: 31735157

21. Egnor SER, Hauser MD. A paradox in the evolution of primate vocal learning. Trends in Neurosciences. 2004; 27:649–54. https://doi.org/10.1016/j.tins.2004.08.009 PMID: 15474164

22. Juergens U. The neural control of vocalization in mammals: A review. Journal of Voice. 2009; 23(1):1–10. https://doi.org/10.1016/j.jvoice.2007.07.005 WOS:000262492200001. PMID: 18207362

23. Tomasello M. Origins of human communication. Cambridge, MA: MIT Press; 2008.

24. Snowdon CT. Plasticity of communication in nonhuman primates. In: Naguib M, Zuberbuhler K, Clayton NS, Janik VM, editors. Advances in the Study of Behavior, Vol 40. Advances in the Study of Behavior. 402009. p. 239–76.

25. Candiotti A, Zuberbuhler K, Lemasson A. Convergence and divergence in Diana monkey vocalizations. Biology Letters. 2012; 8(3):382–5. https://doi.org/10.1098/rsbl.2011.1182 WOS:000303933300019. PMID: 22337503

26. Mitić J, Gros-Louis J. Chorusing and call convergence in chimpanzees: Tests of three hypotheses. Behaviour. 1998; 135(8–9):1041–64. https://doi.org/10.1163/156853998792913483

27. Fischer J, Wegdell F, Trede F, Dal Pesco F, Hammerschmidt K. Vocal convergence in a multi-level primate society: insights into the evolution of vocal learning. Proceedings of the Royal Society B: Biological Sciences. 2020; 287(1941):20202531. https://doi.org/10.1098/rspb.2020.2531 PMID: 33323082
28. Takahashi DY, Fenley AR, Ghazanfar AA. Early development of turn-taking with parents shapes vocal acoustics in infant marmoset monkeys. Philosophical Transactions of the Royal Society B-Biological Sciences. 2016; 371(1693). https://doi.org/10.1098/rstb.2015.0370 WOS:000375333600007. PMID: 27069047

29. Snowdon CT, Cleveland J. "Conversations" among pygmy marmoset. American Journal of Primatology. 1984; 7(1):15–20. https://doi.org/10.1002/ajp.1350070104 PMID: 32138463

30. Lemasson A, Glas L, Barbu S, Lacroix M, Remuef K, et al. Youngsters do not pay attention to conversational rules: is this so for nonhuman primates? Sci Rep. 2011; 1:22. Epub 2012/02/23. https://doi.org/10.1038/srep00022 PMID: 22355541; PubMed Central PMCID: PMC3216510.

31. Petkov C, Jarvis E. Birds, primates, and spoken language origins: behavioral phenotypes and neurobiological substrates. Frontiers in Evolutionary Neuroscience. 2012; 4(12). https://doi.org/10.3389/fnevo.2012.00012

32. Call J, Tomasello M. Does the chimpanzee have a theory of mind? 30 years later. Trends in Cognitive Sciences. 2008; 12(5):187–92. https://doi.org/10.1016/j.tics.2008.02.010 PMID: 18424224

33. Kalan AK, Boesch C. Audience effects in chimpanzee food calls and their potential for recruiting others. Behavioral Ecology and Sociobiology. 2015; 69(10):1701–12. https://doi.org/10.1007/s00265-015-1982-1 WOS:000360845600014.

34. Di Bitetti MS. Food-associated calls and audience effects in tufted capuchin monkeys, Cebus apella nigritus. Animal Behaviour. 2005; 69:911–9. ISI:000228511900018.

35. Brosnan SF, de Waal FBM. A proximate perspective on reciprocal altruism. Human Nature. 2002; 13 (1):129–52. https://doi.org/10.1007/s12110-002-1017-2 PMID: 26192598

36. Cartmill EA, Byrne RW. Orangutans modify their gestural signaling according to their audience's comprehension. Current Biology. 2007; 17(15):1345–8. https://doi.org/10.1016/j.cub.2007.06.069 WOS:000248669600031. PMID: 17883939
48. Leavens DA, Russell JL, Hopkins WD. Multimodal communication by captive chimpanzees (Pan troglodytes). Animal Cognition. 2010; 13(1):33–40. https://doi.org/10.1007/s10071-009-0242-z PMID: 19504272

49. Leavens DA, Russell JL, Hopkins WD. Intentionality as measured in the persistence and elaboration of communication by chimpanzees (Pan troglodytes). Child Dev. 2005; 76(1):291–306. https://doi.org/10.1111/j.1467-8624.2005.00845.x WOS:000226771500020. PMID: 15693773

50. Genty E, Neumann C, Zuberbuehler K. Bonobos modify communication signals according to recipient familiarity. Scientific Reports. 2015; 5. https://doi.org/10.1038/srep16442 WOS:000364385000001. PMID: 26552655

51. Lameira AR, Hardus ME, Bartlett AM, Shumaker RW, Wich SA, Menken SBJ. Speech-like rhythm in a voiced and voiceless orangutan call. Plos One. 2015; 10(1). https://doi.org/10.1371/journal.pone.016136 WOS:000348168000005. PMID: 25569211

52. Lameira AR, Hardus ME, Mielke A, Wich SA, Shumaker RW. Vocal fold control beyond the species-specific repertoire in an orang-utan. Scientific Reports. 2016; 6(1):30315. https://doi.org/10.1038/srep30315 PMID: 27461756

53. Hardus ME, Lameira AR, Singleton I, Morrogh-Bernard HC, Knott CD, Ancrenaz M, et al. A description of the orangutan’s vocal and sound repertoire, with a focus on geographic variation. Wich SA, Atmoko SSU, Setia TM, VanSchaik CP, editors2009. 49–64 p.

54. OhショーSA, Swartz KB, Hardus ME, Lameira AR, Stromberg E, Shumaker RW. A case of spontaneous acquisition of a human sound by an orangutan. Primates. 2009; 50(1):56–64. https://doi.org/10.1007/s10329-008-0117-y WOS:000262652800008. PMID: 19052691

55. Lameira AR, Hardus ME, Kowalsky B, Vries H, Spruijt BM, Sterck EHM, et al. Whistling and implications for the emergence of an open-ended call repertoire: A replication and extension. The Journal of the Acoustical Society of America. 2013; 134(3):2326–35. https://doi.org/10.1121/1.4817929 PMID: 23967963

56. Watson SK, Townsend SW, Schel AM, Wilke C, Wallace EK, Cheng L, et al. Vocal learning in the functionally referential food grunts of chimpanzees. Current Biology. 2015; 25(4):495–9. https://doi.org/10.1016/j.cub.2014.12.032 WOS:000349375900027. PMID: 25660548

57. Perlman M, Clark N. Learned vocal and breathing behaviour in an enculturated gorilla. Animal Cognition. 2015; 18(5):1165–79. https://doi.org/10.1007/s10071-015-0889-6 WOS:000359992500018. PMID: 26139343

58. Hayes KJ, Hayes C. The intellectual development of a home-raised chimpanzee. Proceedings of the American Philosophical Society. 1951; 95:105–7. ZOOREC:ZO OR0880 0006548.

59. Hopkins WD, Taglialatela JP, Leavens DA. Chimpanzees differentially produce novel vocalizations to capture the attention of a human. Animal Behaviour 2007; 73(2):281–6. https://doi.org/10.1016/j.anbehav.2006.08.004 PMID: 17389908

60. Losin EAR, Russell JL, Freeman H, Meguerditchian A, Hopkins WD. Left hemisphere specialization for oro-facial movements of learned vocal signals by captive chimpanzees. Plos One. 2008; 3(6). https://doi.org/10.1371/journal.pone.0002529 WOS:000263288000044. PMID: 18575610

61. Taglialatela JP, Reamer L, Schapiro SJ, Hopkins WD. Social learning of a communicative signal in captive chimpanzees. Biology Letters. 2012; 8(4):498–501. https://doi.org/10.1098/rsbl.2012.0113 WOS:000306361700006. PMID: 22438489

62. Salmi R, Hammerschmidt K, Doran-Sheehy DM. Western gorilla vocal repertoire and contextual use of vocalizations. Ethology. 2013; 119(10):831–47. https://doi.org/10.1111/eth.12122

63. Luef EM, Breuer T, Pika S. Food-associated calling in gorillas (Gorilla g. gorilla) in the Wild. Plos One. 2016; 11(2). https://doi.org/10.1371/journal.pone.0144197 WOS:000371164700001. PMID: 26909518

64. McGraw KO, Wong SP. Forming inferences about some intraclass correlation coefficients. Psychological Methods. 1996; 1(4):30–46.

65. Hedwig D, Hammerschmidt K, Mundry R, Robbins MM, Boesch C. Acoustic structure and variation in mountain and western gorilla close calls: a syntactic approach. Behaviour. 2014; 151(8):1091–120. https://doi.org/10.1163/1568539x-00003175 WOS:000391402000001.

66. Hammerschmidt K. Individual vocal pattern of Barbary macaques Macaca sylvanus: An approach towards the understanding of their vocal communication. Berlin, Germany: FU Berlin; 1990.

67. Klecka W. Discriminant analysis. Beverly Hills, CA: Sage; 1980.
69. Fischer J, Noser R, and Hammerschmidt K. Bioacoustic field research: A primer to acoustic analyses and playback experiments with primates. American Journal of Primatology 2013; 75: 643–663. https://doi.org/10.1002/ajp.22153 PMID: 23592340

70. Mundry R and Sommer C. Discriminant function analysis with nonindependent data: Consequences and an alternative. Animal Behaviour 2007; 74: 965–976.

71. Smith RJ, Welch KB, Galecki AT. Linear mixed models: a practical guide using statistical software: Chapman & Hall/CRC; 2006.

72. Smith RJ, Jungers WL. Body mass in comparative primatology. Journal of Human Evolution. 1997; 32 (6):523–59. https://doi.org/10.1006/jhev.1996.0122 PMID: 9210017

73. Schel AM, Machanda Z, Townsend SW, Zuberbuehler K, Slocombe KE. Chimpanzee food calls are directed at specific individuals. Animal Behaviour. 2013; 86(5):955–65. https://doi.org/10.1016/j.anbehav.2013.08.013 PMID: 27603668

74. Schaller GB. The mountain gorilla: ecology and behavior. Chicago: University of Chicago Press; 1963. xvii, 431 p.

75. Fossey D. Vocalizations of mountain gorilla (Gorilla gorilla beringei). Animal Behaviour. 1972; 20(1):36–53. ISI:A1972N633200006.

76. Harcourt AH, Stewart KJ, Harcourt DE. Vocalizations and social relationships of wild gorillas: a preliminary analysis. In: Taub DM, King FA, editors. Current prospects in primate social dynamics. New York: Van Nostrand Reinhold Co.; 1986. p. 346–56.

77. Schaller GB. The mountain gorilla: ecology and behavior. Chicago: University of Chicago Press; 1963. xvii, 431 p.

78. Harcourt AH, Stewart KJ, Harcourt DE. Vocalizations and social relationships of wild gorillas: a preliminary analysis. In: Taub DM, King FA, editors. Current prospects in primate social dynamics. New York: Van Nostrand Reinhold Co.; 1986. p. 346–56.

79. Robbins MM, Ando C, Fawcett KA, Grueber CC, Hedwig D, Iwata Y, et al. Behavioral variation in gorillas: Evidence of potential cultural traits. Plos One. 2016; 11(9):18. https://doi.org/10.1371/journal.pone.0160493 PMID: 27603668

80. Lameira AR. Bidding evidence for primate vocal learning and the cultural substrates for speech evolution. Neuroscience & Biobehavioral Reviews. 2017; 83:429–39. https://doi.org/10.1016/j.neubiorev.2017.09.021 PMID: 28947156

81. Clay Z, Archbold J, Zuberbühler K. Functional flexibility in wild bonobo vocal behaviour. PeerJ. 2015; 3: e1124–e. https://doi.org/10.7717/peerj.1124 PMID: 26290799.

82. Marler P. Social organization, communication and graded signals: the chimpanzee and the gorilla. In: Bateson PPG, Hinde RA, editors. Growing points in ethology. Cambridge: Cambridge University Press; 1976. p. 239–80.

83. Cordoni G, Norscia I, Bobbio M, Palagi E. Differences in play can illuminate differences in affiliation: A comparative study on chimpanzees and gorillas. PLOS ONE. 2018; 13(3):e0193096. https://doi.org/10.1371/journal.pone.0193096 PMID: 29513698

84. Meder A. Great Ape Social Systems. In: Henke W, Tattersall I, editors. Handbook of Paleanthropology: Vol I:Principles, Methods and Approaches Vol II:Primate Evolution and Human Origins Vol III:Phylogeny of Hominids. Berlin, Heidelberg: Springer Berlin Heidelberg; 2013. p. 1–34.

85. Ross SR. North American Regional Studbook for Chimpanzees. Chicago, IL: Lincoln Park Zoo; 2020.

86. Fischer J, Hammerschmidt K. Towards a new taxonomy of primate vocal production learning. Philosophical Transactions of the Royal Society B. Biological Sciences. 2020; 375(1789):20190045. https://doi.org/10.1098/rstb.2019.0045 PMID: 31735147

87. Hauser MD, Chomsky N, Fitch TW. The faculty of language: What is it, who has it, and how did it evolve? Science. 2002; 298(5598):1569–79. https://doi.org/10.1126/science.298.5598.1569 PMID: 12446899

88. Vernes SC, Kriengwatanaa BP, Beeck VC, Fischer J, Tyack PL, ten Cate C, et al. The multi-dimensional nature of vocal learning. Philosophical Transactions of the Royal Society B: Biological Sciences. 2021; 376(1836):20200236. https://doi.org/10.1098/rstb.2020.0236 PMID: 34482723

89. Hopkins WD, Savage-Rumbaugh ES. Vocal communication as a function of differential rearing experiences in Pan paniscus: A preliminary report. International Journal of Primatology. 1991; 12(6):559–83. https://doi.org/10.1007/BF02547670
91. Ruch H, Zürcher Y, Burkart JM. The function and mechanism of vocal accommodation in humans and other primates. Biological Reviews. 2018; 93(2):996–1013. https://doi.org/10.1111/brv.12382 PMID: 29111610

92. Ouattara K, Zuberbühler K, N’Goran EK, Gomber J-E, Lemasson A. The alarm call system of female Campbell’s monkeys. Animal Behaviour. 2009; 78(1):35–44. https://doi.org/10.1016/j.anbehav.2009.03.014

93. Coye C, Ouattara K, Arlet ME, Lemasson A, Zuberbühler K. Flexible use of simple and combined calls in female Campbell’s monkeys. Animal Behaviour. 2018; 141:171–81. https://doi.org/10.1016/j.anbehav.2018.05.014

94. Robinson JG. Syntactic structures in the vocalizations of wedge-capped Capuchin monkeys, Cebus-Olivaceus. Behaviour. 1984; 90:46–79. ISI:A1984TJ19600003.

95. Cleveland J, Snowdon CT. The complex vocal repertoire of the adult cotton-top tamarin (Saguinus oedipus oedipus). Zeitschrift fuer Tierpsychologie. 1982; 58:231–70.

96. Cáscar C, Byrne R, Young RJ, Zuberbühler K. The alarm call system of wild black-fronted titi monkeys, Callicebus nigrifrons. Behavioral Ecology and Sociobiology. 2012; 66(5):653–67. https://doi.org/10.1007/s00265-011-1313-0

97. Lattenkamp EZ, Vernes SC. Vocal learning: a language-relevant trait in need of a broad cross-species approach. Current Opinion in Behavioral Sciences. 2018; 21:209–15. https://doi.org/10.1016/j.cobeha.2018.04.007

98. Lameira AR, Vicente R, Alexandre A, Campbell-Smith G, Knott C, Wich S, et al. Proto-consonants were information-dense via identical bioacoustic tags to proto-vowels. Nature Human Behaviour. 2017; 1 (2):0044. https://doi.org/10.1038/s41562-017-0044