

Gorillas may use their laryngeal air sacs for whinny-type vocalizations and male display

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Abstract

Great apes and siamangs—but not humans—possess laryngeal air sacs, suggesting that they were lost over hominin evolution. The absence of air sacs in humans may hold clues to speech evolution, but little is known about their functions in extant apes. We investigated whether gorillas use their air sacs to produce the staccato ‘growling’ of the silverback chest beat display. This hypothesis was formulated after viewing a nature documentary showing a display by a silverback western gorilla (Kingo). As Kingo growls, the video shows distinctive vibrations in his chest and throat under which the air sacs extend. We also investigated whether other similarly staccato vocalizations—the *whinny*, *sex whinny*, and *copulation grunt*—might also involve the air sacs. To examine these hypotheses, we collected an opportunistic sample of video and audio evidence from research records and another documentary of Kingo’s group, and from videos of other gorillas found on YouTube. Analysis shows that the four vocalizations are each emitted in rapid pulses of a similar frequency (8–16 pulses per second), and limited visual evidence indicates that they may all occur with upper torso vibrations. Future research should determine how consistently the vibrations co-occur with the vocalizations, whether they are synchronized, and their precise location and timing. Our findings fit with the hypothesis that apes—especially, but not exclusively males—use their air sacs for vocalizations and displays related to size exaggeration for sex and territory. Thus changes in social structure, mating, and sexual dimorphism might have led to the obsolescence of the air sacs and their loss in hominin evolution.

Key words: laryngeal air sacs; Gorilla display; speech evolution; vocalization

1. Introduction

Humans are distinct among the great apes in that they lack inflatable air sacs extending from their larynx (Fitch 2000). Laryngeal air sacs are common across many tetrapod vertebrates, including many mammals, and especially primates, which exhibit rich morphological diversity in their air sacs (Negus 1949; Harrison 1995; Fitch and Hauser 2003; Frey et al. 2007;). The great apes in particular, as well as the closely related siamang, are distinguished by the presence of large, lateral

ventricular air sacs that extend into the pectoral and axillary regions of their upper torso (Fitch 2000, 2002; Hewitt et al. 2002; Nishimura et al. 2007).

Despite various hypotheses, the specific functions for which the great apes use their laryngeal air sacs remain largely uncertain (Fitch 2000; Hewitt et al. 2002). Yet, for one reason or another, humans lost their air sacs over the course of hominin evolution. All that remains are vestigial structures of the lateral ventricles, and only in rare pathological cases do humans have small air sacs

(Stell and Maran 1975). Some researchers have proposed that this derived feature of the human vocal tract holds important clues to the evolution of speech (MacLarnon and Hewitt 1999; Fitch 2000; Fitch and Hauser 2003; de Boer 2012a). Might humans have lost their air sacs as a consequence of selection pressures arising from the evolution of the increasingly complex vocal communication that led to speech? In the current study, we aim to shed light on this question by examining the function of the laryngeal air sacs in extant apes—gorillas in particular. By studying what apes do with their air sacs, we may gain insight into why they were lost during hominin evolution.

1.1 Laryngeal air sacs and the evolution of speech

Evidence from fossilized hyoid bones suggests that human ancestors lost their air sacs somewhere along the evolutionary path from *Australopithecus afarensis* to *Homo erectus*. The hyoid is a small, horseshoe shaped bone positioned in the throat, near the larynx. Great apes, with the derived exception of orangutans (Brown and Ward 1988), typically have a bullate hyoid, characterized by a thin-walled shell into which the air sacs extend (Fitch 2010). The fossil hyoid bone from a juvenile *A. afarensis* skeleton estimated at 3.3 million years old exhibits the ape-like bullate shape (Alemseged et al. 2006). However, a fossil hyoid bone from a *Homo erectus* skeleton estimated at 400,000 years old lacks the bulla shape (Capasso et al. 2008). Consistent with this finding, a hyoid fossil from a *Homo heidelbergensis* skeleton, estimated to be 600,000 years old, also lacks the bulla shape (Martínez et al. 2008). The absence of a bullate hyoid in these specimens suggests that they no longer possessed laryngeal air sacs. This time frame roughly aligns with fossil evidence of an increase in diameter of the thoracic vertebral canal present in Neanderthals, but not in early *Homo erectus* dated at 1.6 million years old. This may reflect that increased thoracic innervation for the enhanced breath control required for complex vocalizations like speech and singing did not arise until after early *H. erectus* (MacLarnon and Hewitt 1999, 2004).

Recent studies with both physical and computer vocal tract models suggest more specifically that human ancestors might have lost their laryngeal air sacs because of their interference with the articulation of complex vocalizations, such as in speech or singing (de Boer 2012b). Physical models show that air sacs increase the instability of vocalization by inducing nonlinear coupling between the source and filter of the vocal tract (Riede et al. 2008). In addition, computer models reveal

that air sacs can cause changes to the resonance patterns of the vocal tract (de Boer 2009). Vocalizations take on the low frequency resonances of the air sacs, and the original resonances of the vocal tract are shifted up in frequency, which causes them to be closer together. Consequently, people were worse at discriminating between vowels filtered through a physical vocal tract model when it connected to an air sac (de Boer 2012b).

If human ancestors did lose their air sacs due to interference with vowel-like or other complex vocalizations, it would imply a substantial degree of vocal sophistication in place at the time when the air sacs disappeared, dating back at least 400–600 thousand years ago. This date significantly predates some prominent estimates concerning the persistence of predominantly gestural linguistic communication over speech until as recently as 150,000 years ago (e.g., Tomasello 2008) or even 50,000 years ago (e.g., Corballis 2003). However, it is also possible that the laryngeal air sacs were lost in human evolution for reasons unrelated to the evolution of speech. For example, it may be that they were discarded as a consequence of changes in the hominin lifestyle that caused them to become obsolete (e.g. the transition from arboreal to bipedal locomotion, reduced competition between males). Such a scenario is particularly plausible because the air sacs are highly susceptible to infection, making them costly to maintain (Hastings 1991; Lawson et al. 2006; Kumar et al. 2012). In this case, the disappearance of the air sacs in human evolution reflects that they were no longer useful, but does not mark the advent of more sophisticated vocal precursors of speech.

1.2 Functions of laryngeal air sacs in apes

An assessment of these two alternatives—whether our ancestors lost their air sacs because of interference with increasingly sophisticated vocal communication, or because of obsolescence—requires that we understand the function of air sacs in extant great ape species. What is it that apes do with their laryngeal air sacs? It turns out that there is little data to bear on this question. Nevertheless, scholars have, over the years, offered various more-or-less speculative hypotheses, including several possible functions unrelated to vocalization. For example, the physiologist Negus (1949) proposed that the air sacs aid respiration during strenuous activity. Another proposal was that apes inflate their air sacs to support their body during arboreal locomotion (Hayama 1998). And after considering multiple alternatives, Harrison (1995) concluded that the air sacs lack

any function altogether, although the susceptibility of the sacs to infection renders this possibility unlikely.

More recently, researchers mostly concur that the laryngeal air sacs of great apes serve a function related to vocalization (Fitch 2000; Hewitt et al. 2002). One current hypothesis is that air sacs enable animals to produce faster sequences of calls by reducing the risk of hyperventilation. On this idea, animals are able to exhale used air into their sacs, and then recycle this carbon dioxide-enriched air to prevent hyperventilation during the production of faster vocalization sequences—analogueous to breathing into a brown paper bag (Hewitt et al. 2002; Fitch and Hauser 2003). This hypothesis is supported by findings that primate species possessing air sacs tend to produce call sequences at faster rates than expected based on their body weight (Hewitt et al. 2002). The fast rate of pant hoot sequences by chimpanzees—produced at a rate of 300 cycles/minute, compared to their resting breathing rate of 20 cycles/minute—may exemplify this function. Similarly, western gorillas hoot at a rate greater than 200 cycles/minute, which is also much faster than their resting breathing rate (Salmi, unpublished data).

Another hypothesis is that air sacs function to enhance the impression of the size of the vocalizer (Fitch and Hauser 1995). Especially when fully inflated, air sacs may serve as a low-frequency resonator, enabling an animal to produce extremely low frequency calls. Through impedance matching, and thus the more efficient radiation of low-frequency sound, air sacs may also increase the amplitude of the call. Louder, lower pitched calls make the vocalizer sound bigger and stronger. This impression may serve to intimidate rivals for territory or access to mates, and it may also be attractive to potential mates. In addition, by providing extra air, air sacs could possibly be used to extend the duration of vocalizations, also contributing to an effect of greater size (Fitch and Hauser 2003; although Hewitt et al. (2002) failed to find evidence of this). Lower-pitched, louder, longer calls would also propagate for greater distances in a jungle environment (cf. Marten et al. 1977).

Apes may also use their laryngeal air sacs for more idiosyncratic species-specific vocalizations and displays. For example, Haimoff (1981) observed that siamangs produce their characteristic boom call by inflating their air sac, and de Boer's (2009) theoretical model of a siamang vocal tract with an air sac suggests that the call acoustics are consistent with this conclusion. Booms are produced by both males and females during their territorial duets.¹ Two types—short and long booms—are produced by males and females, but only males produce an ascending boom. A few studies have also noted that the air sacs appear to be involved in the visual size

exaggeration display of male orangutans (Marler and Tenaza 1977; Tuttle 1986). In addition, there are several anecdotal observations that silverback gorillas inflate their air sacs to amplify thoracic percussion during chest beating, which is often the climax of a ritualized display serving to intimidate threats or rivals (Schaller 1963; Marler and Tenaza 1977; Tuttle 1986). For instance, Schaller observed that the sudden inflation of air sacs on each side of the throat is readily apparent before the silverback begins to chest beat, and he proposed that the air sacs function as resonators.

1.3 Male vocalization and display in gorillas

In the current study, we examine the possibility that the laryngeal air sacs play a role in the vocalizations and chest beating displays of male, silverback gorillas. The chest beating display of silverbacks is an impressive performance (Schaller 1963/1976). According to Schaller's (1963/1976) description of mountain gorillas, the display consists of nine elements: hooting, rising, throwing, chest beating, leg kicking, running, slapping and tearing vegetation, ground thumping and symbolic feeding. However, particular displays do not always involve the complete sequence, and they can vary in the elements they include, and to some extent, in the order of elements. The display may be enacted partially by females or juveniles, but typically only mature males perform the full display. According to Fossey's (1972) observations of mountain gorillas, females and blackback males rarely produced hoot series or performed chest beating during their displays. In western gorillas, the combination of hooting and chest beating is typical of the silverback display, although hoot series alone are used by all age-sex classes in non-agonistic contexts (Salmi et al. 2013; Salmi and Doran-Sheehy 2014).

In a complete silverback display, the intensifying hoot series and the culminating chest beating are two of the most salient elements. Notably, the hooting is often described as accelerating into a sort of 'growling' sound. As Schaller described it, 'A complete display includes a series of some ten to forty distinct hoots gradually fusing into a slurred growling sound at the climax of the display' (p. 223). Similarly, Fossey (1972) noted that a hoot series is sometimes terminated by 'a growl sound (merged hoots) and a chest-beat'. And Emlen (1962) described it, '[T]he hoots again coming in a slow deliberate manner. Gradually and irregularly the tempo

1 For example, see https://www.youtube.com/watch?v=YWabd_3AEfo, or <https://www.youtube.com/watch?v=k3cD1Nd302k>.

increased and with it the volume, until individual hoots merged into a long hoarse growl . . .’ (p. 517).

In addition to the chest beating display, silverback gorillas are also distinctive in their use of a particular vocalization known as the *whinny*. Fossey (1972) first used this term to describe some odd sounds produced by a silverback and a blackback mountain gorilla—just five observations in total. She described the whinny as an ‘unusual’ vocalization. She explained that, ‘Although sounds resembling whinnies were sometimes heard during prolonged durations of the belch vocalization, these were part of a complex of sound and were not uttered in a single unit’ (p. 51). Salmi et al. (2013) observed the much more frequent use of whinnies (or ‘horse-like sounds’) by a western lowland silverback at the Mondika field site in the Central African Republic. This study also identified a second type of whinny—a *sex whinny*—which the silverback male (Kingo) directed toward a specific receptive female as an invitation to mate.

Salmi et al. (2013) noted that a call resembling the whinny was called a *train grunt* in the study of Harcourt et al. (1993), which also observed that train grunts and *copulatory grunts* sound very similar to human observers. Like whinnies and train grunts, copulation grunts are emitted in rapid sequences of a repeated sound. Unlike whinnies and train grunts, however, they can last for the entire duration of the mating act, including, in some cases, more than 80 repeated pulses (like ‘huh, huh, huh’; Salmi et al., 2013). Another difference is that, whereas whinnies are typically only produced by males, copulation grunts are produced by both males and females.

1.4 Current study: Do silverbacks use their air sacs for display vocalizations?

Although anecdotal accounts suggest that silverback gorillas inflate their laryngeal air sacs during chest beating (Schaller 1963; Marler and Tenaza 1977; Tuttle 1986), little is known about the particular involvement of the air sacs and whether they might play a role in vocalizations associated with the display. In this article, we examine whether silverbacks might use their laryngeal air sacs specifically to produce the staccato growling sound that is part of the hoot–chest beat display.

We initially formulated this hypothesis after viewing a nature documentary with footage of a silverback performing a display (*Secret Gorillas of Mondika*, 2005, British Broadcasting Corporation). (See Table A.1 in the Appendix for links to all audio and video files used in



Figure 1. Illustration of a silverback gorilla with the laryngeal air sacs superimposed in white. The air sacs extend into the neck and under the pectoral musculature (Illustration by H. Little).

this article.) The display was performed by Kingo, a western gorilla from a wild group living at the Mondika site in the Republic of Congo.² The close-up video footage of Kingo is remarkable in the clear view of his chest and neck during the episode, particularly during the part of the display in which his hoots fuse into the staccato growl. Along with the change in vocalization, the video distinctly shows his pectoral muscles trembling in a rather striking and peculiar way. The narrator (Charlotte Uhlenbroek) noted this too, commenting that, ‘His whole chest just shimmers’. Additionally, the video shows that vibrations were also visible in his throat. The laryngeal air sacs of gorillas and other great apes are known to extend into the neck and under their pectoral musculature (Raven 1950; see Fig. 1). Therefore, it is plausible that the trembling in Kingo’s chest and throat resulted from action of the laryngeal air sacs in connection to the co-occurring growling vocalization.

In our preliminary investigation of this hypothesis, we listened to a sample of Kingo’s other vocalizations. In doing so, we noted that the slurred growling of Kingo’s display sounded similar to his whinnies and sex whinnies—which are also male-specific vocalizations. In

2 This is the same group studied by the second author, and the basis for the catalog of vocalizations described in Salmi et al. (2013).

particular, all three calls consist of staccato pulses of sounds that are produced at a frequency on the order of about 10 pulses per second. This raised the further speculative hypothesis that the display growling is part of a broader class of *whinny*-type calls that might involve action of the laryngeal air sacs. Listening to Kingo's other vocalizations, we also noted that his copulation grunts seem to be produced in pulses of roughly similar frequency, which fits with Harcourt et al.'s (1993) observation that the whinny-like *train grunts* and *copulatory grunts* sound very alike to human listeners. This led us to investigate whether copulation grunts, although they are produced by both sexes, might also fit within the whinny class.

2. Methods

Ideally, to examine these hypotheses, we would be able to make high-quality audio-video recordings of silverback gorillas producing the vocalizations of interest. However, we were unable to do this for several reasons, including a lack of funds for adequate audio-video recording equipment, as well as a lack of access to gorilla subjects. Even with optimal equipment and access to subjects, such a study would nevertheless present considerable challenges due to the size and strength of silverback gorillas, and especially the excitable, mobile, potentially aggressive nature of the display. Additionally, whinnies and copulation grunts may not be observed until gorillas are fully habituated to human observers, making these vocalizations difficult to record.

Thus, in order to flesh out our speculative hypotheses, we collected an opportunistic sample of video and audio evidence—drawing from the second author's previous recordings of Kingo and the Mondika gorillas, another documentary featuring Kingo (*Mystery Gorillas*, 2010, National Geographic Wild), and also from videos on YouTube of various other gorillas (using search terms like 'gorilla chest beating', 'silverback display', and 'gorilla chest slapping'). Our aim was to find high quality audio-video recordings that clearly showed the chest of a gorilla while producing any of the four vocalizations of interest (i.e., the display growl, simple whinnies, sex whinnies, and copulation grunts).

2.1 Video and audio recordings

The original BBC video of Kingo turned out to be the best recording we could find, but we did uncover six additional videos relevant to a preliminary assessment of our hypotheses. These included three additional videos of Kingo from Salmi's research records, and a fourth of

Kingo from the National Geographic Wild documentary. The other three videos were found on YouTube: two of wild silverback mountain gorillas and a third of a captive lowland western gorilla (housed at Disney's Animal Kingdom). Table 1 shows the details of all seven videos, including information on the behavior and the gorilla that produced it. Links to the video files are provided in Table A.1 in the Appendix.

In addition, we obtained a larger sample of relevant audio-only recordings of Kingo's vocalizations from Salmi's research records (see Table A.1). These included seven simple whinnies, six sex whinnies, six display growls, and two series of copulation grunts. Because copulation grunts are typically produced in highly overlapping series, it is generally difficult to distinguish which animal produced which sound. The two series of grunts used in our analysis were the only ones that allowed us to confidently distinguish between the series of the male and female, which was necessary to reliably measure their pulse frequencies.

2.2 Analysis

Our analyses focused on three primary objectives. First, we wanted to ascertain whether the growl was acoustically distinct from the hoot series and chest beating of the display. Second, we searched for visual evidence to assess whether chest and neck vibration might be generally associated with the display growl, and also whether it might be associated with whinnies and copulations grunts. Such evidence would help to determine whether the visible vibrations reflect a mechanism for producing the growl and other similar vocalizations, or whether they were a coincidental part of the display. Ideally, we would also have been able to measure the synchrony between the audible pulses and the visible vibrations in any video recorded episodes, but even the highest-quality BBC video was too short in duration and too unstable for a reliable measurement (D. Abney, personal communication). Third, we wanted to compare some basic properties of the different vocalizations—particularly their pulse rate and duration—to make a preliminary evaluation of whether they might be produced by a similar mechanism. Measurements of hooting and chest beating were included in our analyses for comparison.

For acoustic analyses, we measured the pulse rate of each vocalization by visual inspection of the waveform and spectrogram to determine its duration and number of pulses (audio recordings of the videos were extracted from the video file). When present, we also measured the rate of hoots and chest beating in the same manner. Waveforms and spectrograms were created in Praat

Table 1. Details on video recorded episodes.

Video	Gorilla	Sub-species	Location	Call type	Context	Visible vibration	Pulse freq.	Hoot freq.	CB freq.	Source
Video 1	Silverback (Kingo)	Western lowland	Mondika	Slurred growl	Display with hooting, chest beating	Good view of chest, throat	12.7	3.3	8.7	BBC, <i>Secrets of Mondika</i>
Video 2	Silverback (Kingo)	Western lowland	Mondika	Whinny	Directed at female, without copulation	Distant view of lower torso	9.8	n/a	n/a	Salmi's research records
Video 3	Silverback (Kingo)	Western lowland	Mondika	Sex whinny	Directed at female preceding copulation; Directed at female during copulation	Good view of torso, esp. back	9.8; 9.7; 8.6	n/a	n/a	Nat Geo Wild, <i>Mystery Gorillas</i>
Video 4	Silverback (Kingo) & Female	Western lowland	Mondika	Cop. grunts	Mating	Not clear				Salmi's research records
Video 5	Silverback	Mountain	Bwindi	Slurred growl	Display with hooting, chest beating	Limited view of chest	13.0	3.1	16.7	YouTube
Video 6	Silverback	Mountain	Rwanda	Slurred growl; whinny	Display with chest beating; After display without chest beating	Not clear	12.5; 8.7		13.2	YouTube
Video 7	Silverback	Western lowland	Animal Kingdom	Slurred growl	Display with hooting, chest beating	Not clear	16.8	4.4	9.1	YouTube

Note: Frequencies in pulses per second.

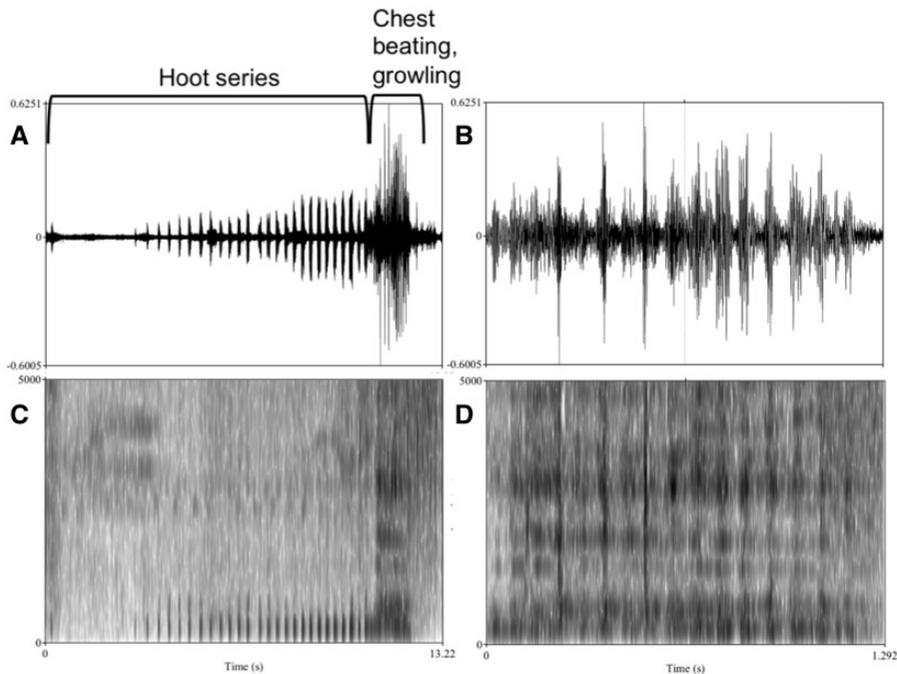


Figure 2. (A) shows the waveform, and (C) the spectrogram of Kingo's complete display. (B) shows a zoomed-in waveform and (D) a zoomed-in spectrogram of the chest beating and growling portion of the display. Frequency on the y-axis of the spectrograms ranges from 0 to 5000 Hz, and intensity on the y-axis of the waveforms ranges from -0.6005 and 0.6251 Pascals. Compare to Fig. 58A in Schaller (1963).

(Boersma and Weenink 2016) and Avisoft SASLab pro (R. Specht, Berlin, Germany). Gorilla calls have very low frequencies (high-pitched hoots are lower than 5000 Hz), and so it was sometimes useful to downsample the recording for a better view of the call in the spectrogram. For this, we converted the sampling frequency from 44.1–11.0 or 5.5 kHz using Avisoft SASLab Pro 5.

3. Results

We first consider Kingo's display in the original BBC Video 1 in more detail, and assess whether the growl is distinct from the rest of the display. Figures 2A and 2C show the waveform and spectrogram of the roughly 13 seconds of the display from the first hoot to its end. Figures 2B and 2D show a zoomed-in spectrogram and waveform for the short slurred growling portion with chest beating. The display begins at about 33 seconds in the video when Kingo begins a series of hoots. After about 12 seconds, the hoots transition into a short series of chest beats and growling, which persists after the chest beating ceases. The spectrogram shows the staccato pulses of the growl, with about 16 pulses occurring over a span of about 1.2 seconds—a frequency of

roughly 13 pulses per second (pps). In comparison, Kingo produced five hoots in the preceding 1.2 seconds—a frequency of about 4 pps. Based on visual inspection of the video, we counted that Kingo performed four chest beats during a span of about 0.5 seconds, which are visible as spikes in the waveform in Fig. 3B.

Next we compared the BBC video of Kingo's display growl to video recordings of his whinnies and copulation grunts. Video 2 shows Kingo producing a whinny at about 14 seconds, when he directs the call at the female Mama. The sound consisted of about 11 pulses emitted over a period of 1.2 seconds (10 pps). Kingo is too far from the camera for detailed observation, but some trembling can be seen in his lower torso. Video 3 shows Kingo producing sex whinnies and copulation grunts. First at about 21 seconds, and again at about 42 seconds, Kingo produces a sex whinny, directed at a receptive female shortly before copulation. In these two episodes, the trembling in Kingo's torso is clearly visible. It is even commented on by the narrator (Mireya Mayor), who noted, 'When the silverback is ready to mate, he makes this deep grunting sound, and his whole body trembles and vibrates'. Video 4 shows Kingo with a female (Emily) mating and producing copulation

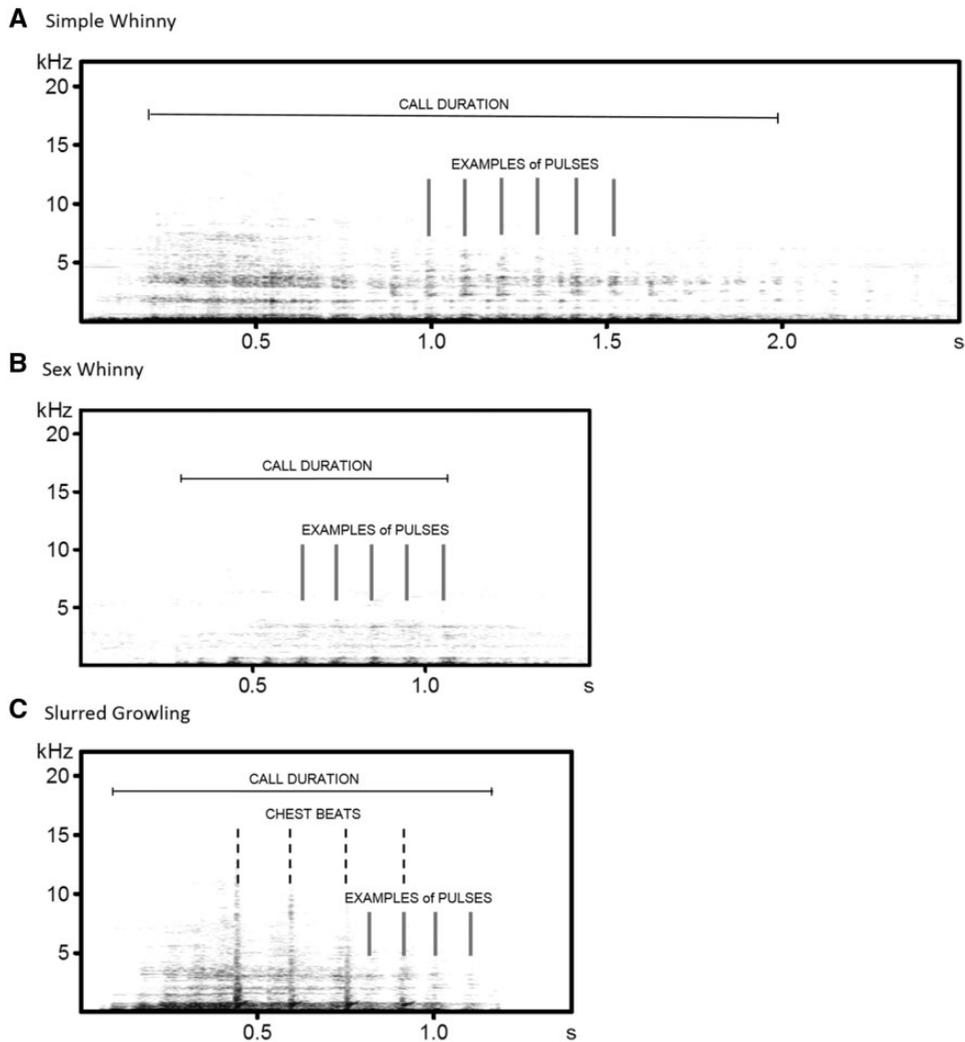


Figure 3. Spectrograms for (A) Simple whinny, (B) Sex whinny, (C) Slurred growling of a male display vocalization. In (C), notice the overlap of chest beats and pulses.

grunts. The grunts begin at about 48 seconds and continue throughout the mating act, which is completed about 60 seconds later. On a few occasions (e.g. at about 90 seconds), it sounds as if the gorilla breaks from grunting to take in a sharp breath of air before continuing with another bout. Partly due to Kingo's copulatory movements, the video does not allow one to determine whether his body is vibrating in any way.

The other three videos, found on YouTube, contain records of vocalizations of interest produced by different gorillas. Video 5 shows a display performed by a silverback mountain gorilla, observed in Bwindi Forest National Park in Uganda. The gorilla hoots, chest beats and growls during the display. Of note, near the end of

the episode at about 19 seconds, his right side is visible, and pectoral vibrations very similar to Kingo's in Video 1 are apparent. The growling consists of about 18 pulses over 1.4 seconds (~13 pps). In comparison, he produced five hoots over a preceding span of about 1.5 seconds (3 pps), and approximately 8 chest beats in a span of 0.5 seconds (16 pps).

Video 6 shows a display performed by another mountain silverback from a wild group located in Rwanda. At about 15 seconds, he rises and charges along with growling and chest beating. The growling continues briefly after the chest beating stops. Notably, the pulse frequency of growling leading up to the chest beating is about 12.5 pps, whereas it is slower, about

8.9 pps, after the chest beating. This difference in rate matches the pattern from the previous examples of Kingo, in which the display growling was comparably faster than the whinnies. The video quality is not sufficient to detect any vibration in the gorilla's body.

Finally, Video 7 shows a hoot–chest beat display performed by a captive western lowland silverback, located at Disney's Animal Kingdom. He performs a series of hoots, slurred growling, and chest beating. The camera has a direct line of view of the gorilla's chest, and there is some hint of trembling in his pectoral region and shoulder at the end of the display. However, the movement is too pixilated to clearly determine this. The slurred growling of this display is relatively fast: roughly 13 pulses in 0.8 seconds (~16.2 pps). In comparison, he produced 4 hoots over the preceding 0.9 seconds (4.4 pps).

In summary, our analysis of the videos suggests that the slurred growling is distinct from other components of the display. It is emitted in pulses of a distinctive frequency range (12.5–16.2 pps) that is considerably faster than hooting (3.1–4.4 pps). The growling is more similar in frequency to chest beating (8.7–16.7), but it is also clear that these are distinct, as each was observed to occur without the other. The observed pulse frequency of the display growling was a little faster than that observed for the simple whinny and sex whinny (8.7–9.8 ppm), but the limited data prevents any more general inference based on this difference. The videos also show visual evidence that growling, the simple whinny, and the sex whinny are all associated with distinctive vibration and trembling across different portions of the body, especially the chest, throat, and torso.

Next, we examined Kingo's vocalizations based on a larger sample of audio-only recordings. These included 7 simple whinnies, 6 sex whinnies, and 6 display growls produced with chest beating and hooting. Figure 3 shows spectrograms of the vocalizations, noting the individual pulses in each. Table 2 shows mean values and standard deviations for duration and pulse frequency for each call type. Within displays, we found a significant difference in frequency between chest beating, hooting, and growling (repeated measures ANOVA: $F_{2, 10} = 672.11, p < 0.001$; see Fig. 4). Between call types, the number of pulses per second

differed significantly by a Welch one-way ANOVA, $F_{(2, 9.44)} = 38.12, p < 0.001$. A Games-Howell post-hoc test revealed that the number of pulses was significantly lower in the normal whinny (10.57 ± 0.54 per sec) than either the display growling (13.07 ± 0.50 per sec; $p < 0.001$) or the sex whinny (13.13 ± 1.22 per sec; $p < 0.001$). There was no difference between the number of pulses in growling and sex whinnies ($p = 0.993$). The duration of the entire vocalization also differed significantly in the three call types, $F_{(2, 16)} = 8.76, p = 0.003$. A Tukey's post-hoc test revealed that the normal whinny (2.53 ± 1.07 sec) was significantly longer than either the growling (1.28 ± 0.26 sec; $p = 0.016$) or the sex whinny ($0.98 \pm 0.44, p = 0.003$). There was no significant difference between the duration of growling and sex whinnies ($p = 0.751$).

Finally, we examined the two series of copulation grunts for which we were able to—at least in some sections—separate the vocalizations of the male from those of the female. Figure 5 shows a spectrogram of a portion of one of the series with overlapping male and female copulation grunts, which includes short grunts by the male and female, and a 'long' grunt by the male. While both sexes use the staccato short grunts with similar frequency, males also occasionally give longer grunts. Long grunts are acoustically different from the vocalizations of focus here—in particular, they lack the staccato quality—and therefore, these are not discussed further. Table 3 shows the mean pulse frequency of the two series, along with their standard deviation and range. We found that the pulse frequency of the copulation grunts was similar to that observed in Video 3 (8.9 pps). The copulation grunts of both the male and female are produced at a comparable rate (8.8–10.0 pps) to slurred growling and the two kinds of whinnies.

In summary, analyses of the audio-only recordings found that there are some differences in the pulse frequency and duration of the different vocalization types. Display growling and sex whinnies are emitted at higher frequencies than the simple whinny and copulation grunts, and they also tend to have a shorter overall duration. Nevertheless, the vocalizations are all similar in that they are emitted in staccato pulses at frequencies within the distinctive range of about 9–16 Hz.

Table 2. Duration and pulse mean and range frequency (pps: pulse/unit per second) of different vocalization types.

Call type	N	Duration (s) (sec: mean \pm SD)	Pulse frequency (pps: mean \pm SD)	Pulse frequency range (pps: min-max)
Simple whinny	7	2.53 \pm 1.07	10.6 \pm 0.5	9.6–11.1
Sex whinny	6	0.98 \pm 0.43	13.1 \pm 0.5	11.3–14.3
Slurred growling	6	1.28 \pm 0.23	13.1 \pm 1.2	12.5–13.8

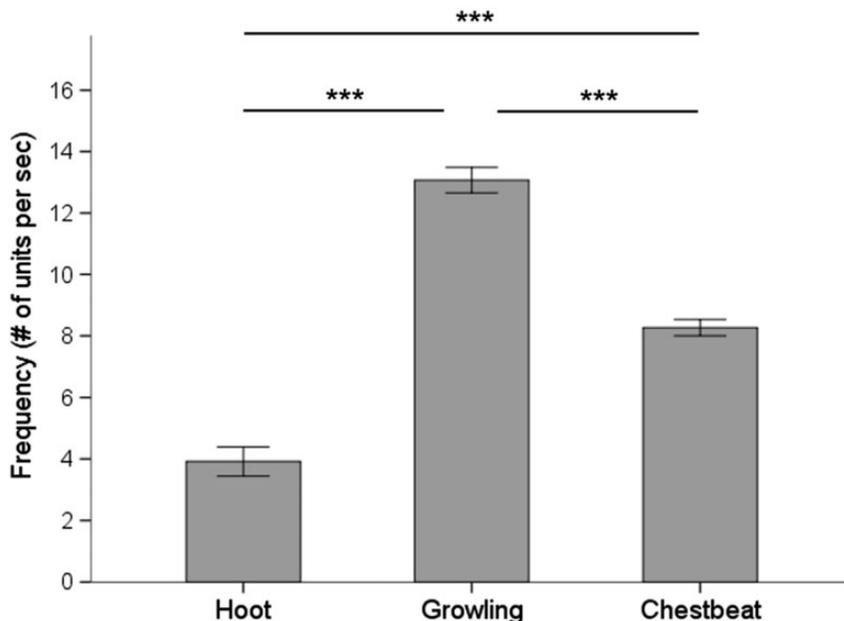


Figure 4. Frequency (number of units per second) of hoots, slurred growls and chest beats in the western silverback Kingo's displays ($n=6$). ***: $p < 0.001$ (post-hoc with Bonferroni correction; error bars represent Standard Errors).

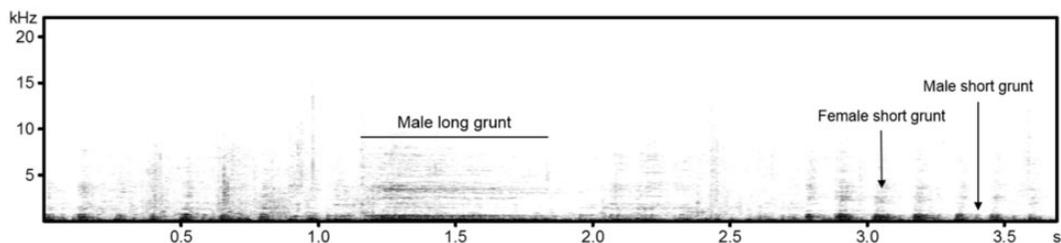


Figure 5. Short portion of a copulation series lasting over 27 seconds, showing the male and female short grunts and a long male grunt (.wav file of this section is available as Supplemental Material).

Table 3. Pulse mean and range frequency (pps) of male and female copulation grunts from two series of overlapping calls.

	Sex	N sections	N pulses	Pulse frequency (pps: mean \pm SD)	Pulse frequency range (pps)
Long copulation grunt	M	1	3	0.24	–
Short copulation grunt	M	3	20	8.8 \pm 0.3	8.6–9.1
Short copulation grunt	F	3	26	9.0 \pm 1.0	8–10.0

4. Discussion

The great apes and siamangs—but not humans—possess laryngeal air sacs, suggesting that they were discarded sometime during hominin evolution. The question of why we lost our air sacs potentially has significant implications for understanding the evolution of speech, and

yet, little is known about their functions in extant apes. In the current study, we examined whether gorillas might use their laryngeal air sacs to produce the ‘slurred growling’ component of the characteristic silverback hoot-chest beat display (see Schaller 1963/1976). We originally formulated this hypothesis after viewing a

nature documentary showing a silverback western gorilla (Kingo) performing a noteworthy display. The video shows a clear view of Kingo's chest during the growling portion of the display, revealing distinctive vibrations in his chest and throat—regions under which the air sacs extend. Based on previous literature (Harcourt et al. 1993; Salmi et al. 2013) and other audio recordings of Kingo, we also examined the possibility that some other similar-sounding vocalizations might also involve the laryngeal air sacs. These included the simple *whinny*, *sex whinny*, and *copulation grunt*, which, along with display growling, are all emitted in series of pulses at frequencies of roughly 10 per second.

To investigate our hypotheses, we collected an opportunistic sample of video and audio evidence from research records and another documentary of the Mondika gorillas (Kingo's group), as well as of other gorillas from YouTube. Previously the growling portion of the display has evaded clear description, and observers have tended to conflate it with the surrounding hoot series (e.g., Schaller, 1963/1976). However, our analyses show that the growling is acoustically distinct from the series of hoots, as well as from the chest beating. We also found that while the different vocalizations—the display growling, whinnies, and copulation grunts—vary somewhat in pulse frequency, they were all emitted within the distinctive range of 8–16 pulses per second. Although clear video of the behaviors was limited, the evidence we reviewed is consistent with the possibility that chest and neck vibrations are generally associated with each of the vocalizations. Nevertheless, it is possible that the visible vibrations are caused by a mechanism unrelated to the laryngeal air sacs. For example, they could be caused by the lungs, or by the intercostal muscles—although in this latter case, one might expect more vibration to be visible in the stomach region. The vibrations could also be caused by action of the pectoral muscles, which impinge on the lungs.

More observations are necessary to determine whether the whinny-type vocalizations do, in fact, always co-occur with visible vibrations, which would provide further evidence that they are connected to a common production mechanism. In addition, to confirm that they are caused by the same mechanism, future research would need to determine whether the vocalizations and visible vibrations are synchronized. Unfortunately, even the highest-quality recording analyzed here—from the BBC documentary—was not sufficient for us to make a valid measurement of synchrony. Given that the vocalizations are produced at a frequency range of about 8–16 pps, future research should seek to obtain clear video recordings of the subject's torso at a

frame rate of minimally 48 or 60 frames per second with progressive scan. (The standard 30 frames per second may not be fast enough.) High quality video recordings would also allow more precise inspection of where and when the torso and neck are inflated during the display and vocalizations, which may help to determine whether the laryngeal air sacs are involved. Ideally, video recordings could be supplemented with audio recordings with as little background noise as possible. Information about the distance of the subject from the microphone would facilitate synchrony analysis. Additionally, more audio recordings of each of the vocalizations would enable larger scale acoustic analyses, including a proper formant analysis, which may provide clues to the production mechanism and whether it involves the laryngeal air sacs.

In the current study, we examined the behavior of just a few gorillas, but our data spans western lowland and mountain gorillas and includes those living in wild and captive settings. Thus our findings may reflect genus-wide vocal behavior. However, one exception may be the sex whinny, which to date, has only been observed in the western species (Salmi et al. 2013). Notwithstanding, all four of the vocalizations have received relatively little study, and more research is needed for comparison between different species and sub-species of gorillas.

It is interesting that the display growling has evaded clear documentation, and also that, to our knowledge, no one has previously considered whether the laryngeal air sacs may be involved in its production or that of the other whinny-type vocalizations, as we have proposed. Some of the explanation for the poor understanding of display growling may lie in its characteristic occurrence within a noisy mix of hooting and chest beating, making it difficult to identify as a distinct vocalization. Compounding this problem, silverback gorillas are big, strong animals, and their displays are typically performed in aggressive or otherwise emotionally charged contexts, often with threatening behaviors like rising up and charging. Consequently, unobstructed close-up observation of a display is rare.

In the case of non-display whinnies and copulation grunts, a reason for their limited documentation may be that they are used in more intimate contexts between individual males and females. Thus they are observable only once gorillas have become fully habituated to human observers. This may explain why Fossey (1972: 51) noted just five whinnies, which were emitted in atypical circumstances. Two were produced by a young blackback, and the other three were produced by 'one ailing silverback who later died', apparently of

pneumonia and pleurisy, according to a biopsy. Fossey observed that the animal, ‘was unable to give any other type of vocalization. He emitted the whinny in the same context in which hoot barks or wraaghs were heard and elicited similar responses from the group members’. This anecdote invites speculation that the silverback was no longer able to vocalize normally because of the lung disease, but could still whinny because his laryngeal air sacs remained functional.

According to our hypothesis, another reason that these whinny-type vocalizations have all resisted clear description is that they are produced by—what is to human observers—a rather odd and foreign mechanism. The sound and associated movement produced by the laryngeal air sacs could be strange compared to vocalizations produced by our own sac-less vocal tract. Indeed, the sight of the gorillas’ trembling torsos was sufficiently striking to draw explicit commentary by the narrator in both documentaries.

Finally, although our study did not focus on the production of hoot series in the display, it is worth noting that our results fit with a second hypothesis concerning the function of the laryngeal air sacs in great apes. [Hewitt et al. \(2002\)](#) noted the high hoot rate of chimpanzees (300 cycles/minute), and proposed that they may recycle air through their laryngeal air sacs to prevent hyperventilation. The hoot series of gorillas analyzed here were produced at an average rate of about 4 hoots per second (240 cycles/minute), accelerating to an even faster rate near the end of the series (but still much slower than the display whinny). This suggests that gorillas might also use their laryngeal air sacs to prevent hyperventilation during hooting. Thus, three major components of the silverback display could potentially involve the laryngeal air sacs—hooting, chest beating, and whinny-type growling.

4.1 Implications for the evolution of speech

If future research were to confirm our hypothesis that gorillas use their laryngeal air sacs to produce whinny-type calls, what would this imply for the evolution of speech? Computer and physical vocal tract models demonstrate that laryngeal air sacs can interfere with the discriminability of speech sounds ([de Boer 2012b](#)), and so selection pressure may have been placed on humans to discard their air sacs to improve the intelligibility of their increasingly flexible vocalizations. However, it is also possible that hominins lost their air sacs for reasons unrelated to the advent of complex vocalizations. The air sacs are susceptible to infection and are therefore costly to maintain. If the laryngeal air sacs no longer

played an active function in the lives of our hominin ancestors, then they may have been selected against due to the cost of infection. In order to evaluate these alternatives, it is necessary to understand the functions of the laryngeal air sacs in our ape relatives.

Our current findings tentatively suggest at least one function: silverback gorillas use their laryngeal air sacs for male vocalizations and display. Our initial hypothesis related specifically to the slurred growling produced during the silverback display, and to our knowledge, the complete display—involving a series of accelerating hoots, chest beating, and the staccato growl—is performed only by silverback males. In addition, simple whinnies and sex whinnies also appear to be male-specific vocalizations, although these differ in that they are typically directed at individual females ([Harcourt et al. 1993](#); [Salmi et al. 2013](#)). Thus, if the laryngeal air sacs are involved in the production of these whinny-type vocalizations, this would indicate that they play an especially significant role in the vocal repertoire of male gorillas, particularly in territorial displays and interactions with females. However, we also found evidence that the air sacs might be used for the production of copulation grunts, which are emitted by both males and females during mating. Additionally, both males and females produce hoot series ([Salmi et al. 2013](#)), and so if the air sacs function to prevent hyperventilation, this would be a second way that they are utilized by both sexes.

The boom vocalization of the siamang is the only other ape call that is known to be connected to the laryngeal air sacs ([Haimoff 1981](#)), and there is some rough similarity between the contexts in which booms and whinnies are used. While booms are produced by both males and females during territorial duets, one of the three types—the ascending boom—is produced just by males. Thus, in both gorilla whinnies and siamang booms, there appears to be a bias towards the communication of sexual and territorial information, especially, but not exclusively, by males.

Related to sex and territory, gorilla whinnies and siamang booms may serve to enhance the impression of the animal’s size (cf. [Fitch and Hauser 1995](#)). Indeed, the display growling of the silverback appears to achieve this in spectacular fashion, especially in conjunction with the added effects of hooting and chest beating. This is also consistent with anecdotal reports that male orangutans inflate their sacs as part of a visual size exaggeration display ([Marler and Tenaza 1977](#); [Tuttle 1986](#)). If size exaggeration for sex and territory is a primary function of the laryngeal air sacs in apes, especially for males, then changes in social structure, mating behavior, and sexual dimorphism may have been driving

forces leading to their obsolescence and loss in hominin evolution. For example, compared to other apes, humans show less sexual dimorphism in body size and in the size of their canines. This suggests the possibility that reduced competition between males may have deflated the usefulness of male display, and so the laryngeal air sacs were eventually discarded.

However, the human vocal tract still shows evidence of strong shaping by male competition and mate choice (Pisanki et al. 2016). The ratio of the fundamental frequency of a male's voice to a female's is smallest in humans compared to the other apes (Puts et al. 2016), exaggerated by the secondary descent of the larynx in human males at puberty (Fitch 2000). Moreover, both men and women with low frequency voices tend to be judged as more dominant, physically larger and stronger, and more masculine (Pisanki and Bryant 2016). Thus, the descent of the larynx in hominin evolution may have fulfilled two functions: enabling a larger vocal repertoire (Fitch 2000), and also exaggerating the vocal impression of qualities like size, strength and dominance. This suggests that although humans, especially males, may have lost the capacity to produce impressive sounding vocalizations with their laryngeal air sacs, they have gained a more flexible mechanism for display through the fundamental frequency of their voice.

5. Conclusion

Fitch (2000) suggested, 'that the loss of air sacs in humans is as noteworthy as our gain of a descended larynx' (p. 261). At the same time, he noted that, 'virtually nothing is known about their ... adaptive significance. ... Unfortunately, until more is known about the function of air sacs in living species, it is premature to speculate about their loss in our hominid ancestors' (p. 261). In this study, we have examined and found tentative evidence for the hypothesis that gorillas use their laryngeal air sacs to produce four different vocalizations—display growling, the simple whinny, sex whinny, and copulation grunts. In doing so, we have brought particular attention to the growling portion of the silverback display, which was not previously recognized as a vocalization distinct from the hooting that typically precedes it. We hope that our preliminary investigation leads to more controlled and detailed studies of the function of air sacs in gorillas and other apes. Between fossilized hyoid bones and the untapped potential of studies with extant ape species, research on the laryngeal air sacs and their loss in the human lineage presents an especially exciting and tangible direction for the study of language evolution.

Acknowledgments

We thank Drew Abney, Tecumseh Fitch, and Bart de Boer for their helpful comments and discussions. We thank the Ministère de la Economie de Foret of Congo Republic for the permission to conduct research in the Nouabale-Ndoki Park and to the Wildlife Conservation Society (WCS) for logistic and administrative support. We are also grateful to Hannah Little for her illustration of a silverback gorilla and his laryngeal air sacs.

Funding

This research was partially supported by a grant from the Max Planck Institute for Psycholinguistics. Recording of wild gorillas at the Mondika Research Center was funded by the Leaky Foundation, Wildlife Direct and Richard Leaky, the Primate Action Fund, Primate Conservation Inc., Sigma Xi, and Stony Brook University.

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Appendix

Table A.1. Links to video and audio files.

Episode	File type	File location
1	YouTube	https://www.youtube.com/watch?v=pSif5MR9nq8
	Video	gorillagestures.info/airSacVideos/Video1_Kingo_BBC.mp4
2	Audio	gorillagestures.info/airSacVideos/Audio1_Kingo_BBC.wav
	YouTube	N/a
3	Video	gorillagestures.info/airSacVideos/Video2_Kingo_Salmi.mov
	Audio	gorillagestures.info/airSacVideos/Audio2_Kingo_Salmi.wav
4	YouTube	https://www.youtube.com/watch?v=1dCf_VM-zAE
	Video	gorillagestures.info/airSacVideos/Video3_Kingo_NatGeo.mp4
5	Audio	gorillagestures.info/airSacVideos/Audio3_Kingo_NatGeo.wav
	YouTube	https://www.youtube.com/watch?v=4Rk8GjeRjKA
6	Video	gorillagestures.info/airSacVideos/Video4_Mountain_Bwindi.mp4
	Audio	gorillagestures.info/airSacVideos/Audio4_Mountain_Bwindi.wav
7	YouTube	https://www.youtube.com/watch?v=9C8OEDsclUA
	Video	gorillagestures.info/airSacVideos/Video5_Mountain_Rwanda.mp4
8	Audio	gorillagestures.info/airSacVideos/Audio5_Mountain_Rwanda.wav
	YouTube	https://www.youtube.com/watch?v=7u53q8J7GHg
9	Video	gorillagestures.info/airSacVideos/Video6_Western_Kingdom.mp4
	Audio	gorillagestures.info/airSacVideos/Audio6_Western_Kingdom.wav
10	Youtube	N/a
	Video	gorillagestures.info/airSacVideos/Video7_KingoMating_Salmi.mov
	Audio	gorillagestures.info/airSacVideos/Audio7_KingoMating_Salmi.wav

Note. The frame rate of each video is 29.97 FPS.