

Kennesaw State University

DigitalCommons@Kennesaw State University

Master of Science in Integrative Biology Theses

Department of Ecology, Evolution, and
Organismal Biology

Summer 6-30-2021

Yakety sacs: laryngeal air sac usage in great apes

Chelsea Trenbeath

Follow this and additional works at: https://digitalcommons.kennesaw.edu/integrbiol_etd



Part of the [Integrative Biology Commons](#), and the [Other Ecology and Evolutionary Biology Commons](#)

Recommended Citation

Trenbeath, Chelsea, "Yakety sacs: laryngeal air sac usage in great apes" (2021). *Master of Science in Integrative Biology Theses*. 63.

https://digitalcommons.kennesaw.edu/integrbiol_etd/63

This Thesis is brought to you for free and open access by the Department of Ecology, Evolution, and Organismal Biology at DigitalCommons@Kennesaw State University. It has been accepted for inclusion in Master of Science in Integrative Biology Theses by an authorized administrator of DigitalCommons@Kennesaw State University. For more information, please contact digitalcommons@kennesaw.edu.

Yakety sacs: laryngeal air sac usage in great apes

Chelsea Trenbeath

Department of Ecology, Evolution, and Organismal Biology, Kennesaw State University

Advising Professor: Jared Tagliatela, PhD

Committee Members: Anton Bryantsev, PhD, Lisa Ganser, PhD, Bill Ensign, PhD

Statistical Analysis: Nicholas Green, PhD

Table of Contents

2	List of Figures
3	Research Summary
4	Background
4	Determining the origins of complex communication in humans
5	Laryngeal air sacs
5	Air sacs in super family Hominoidea (apes)
6	Fossil evidence for air sacs in family Hominidae (great apes)
7	Air sacs in extant members of family Hominidae
8	Air sacculitis: the expense of conserving laryngeal air sacs
9	Proposed function of air sacs in apes
9	Vocal intensity and resonance
10	Rebreathing
11	Sexual Selection
12	Research Study
12	Subjects
12	Recordings
14	Video Processing
16	Data Analysis
18	Results
22	Discussion
24	Potential drawbacks
25	Integration of Thesis Research
26	Acknowledgements
27	References

List of Figures

6	Figure 1A: Diagram of laryngeal air sacs in great apes
6	Figure 1B: Diagram of the larynx and trachea in <i>Homo sapiens</i>
6	Figure 2: Cladogram identifying air sacs in extant primates
7	Figure 3: Adult hyoid bones of <i>Gorilla gorilla</i> , <i>Pan troglodytes</i> , <i>Homo sapiens</i>
13	Figure 4: Examples of criteria for identifying viable video frames
15	Figure 5: Examples of steps to find the ROI
17	Table 1: The GLM and GLMM models fit to the data
18	Table 2: Akaike's Information Criterion (AIC) of models 1-5 & 7
19	Figure 6: Boxplot with standard deviations of datapoints for each bonobo
20	Table 3: Data snapshot of points closest to 70% probability
21	Figure 7: Plots for each bonobo comparing ΔA to the probability of a vocalization
22	Figure 8: Comparison of male and female ΔA to the probability of a vocalization

Research Summary

Except for humans, extant great apes have evolutionarily conserved lateral ventricular air sacs extending from laryngeal saccules. Humans are the only species of Hominidae that lack this anatomical feature attached to the primary vocal apparatus. As we are the only species that produces spoken language, this association has led to hypothesis that the loss of lateral ventricular air sacs was necessary for the evolution of spoken language. However, why these sacs are conserved in all other hominids remains unclear. Computer modeling has indicated that air sacs may increase resonance properties, but there are no data from great apes indicating if vocalizations include the use of air sacs during their production. For this study, we hypothesized that we could use high-frame-rate digital audio/video recordings to determine when bonobos (*Pan paniscus*) inflate their laryngeal air sacs. We identified a region of interest in the air sac area and quantified it using frame-by frame image analysis. We then compared the difference in areas between resting, swallowing, and vocalizing apes. Results suggest air sac inflation may be associated with vocal production but not with other states. The method outlined in this thesis may be utilized in a variety of settings, enabling data collection to test hypotheses regarding the putative function of laryngeal air sacs in extant great apes. Enhancing our understanding of the conservation of laryngeal air sacs in non-human great apes will strengthen hypotheses related to the loss of these sacs in humans and its relevance for the evolutionary origin of language.

Background

Determining the origins of complex communication in humans

Paleontological and archeological evidence are often used to determine the evolution of a particular trait, but the evolution of human communication is difficult to trace. Vocal communication uses soft and cartilaginous tissues, such as the tongue, brain, larynx, pharynx, epiglottis, and oral cavity, which do not fossilize well or often in any species. In the hominid fossil record, we have no record of any of these soft tissues, and even the hyoid bone (which originates from the pharyngeal arches) is often not found (and found only once in articulation with the throat) (Fitch, 2000; Hewitt et al., 2002; Albessard-Ball and Balzeau, 2018; Dunn, 2018). As we have not, and may not, be able to find significant vocal trait changes in fossil hominids, many researchers look to other species as a starting point for conserved or lost evolutionary traits (Fitch, 2000). The two most closely related species to *Homo sapiens* are in the *Pan* genus – chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) (Hewitt et al., 2002). Comparative anatomical and genomic analysis of traits in these species, as well as other primates, can give us clues to the evolutionary changes that occurred in humans (Fitch, 2000; Steele et al., 2013). Identifying a trait in one ape lineage and tracing it throughout other extant apes gives a broader picture to when the trait might have arose, what areas of the trait have been conserved through selection, and which features have changed in individual species compared to other related species.

One prominent anatomical difference in the larynges of nonhuman apes is the presence of laryngeal air sacs (Fitch, 2000; Hewitt et al., 2002; de Boer, 2008; Nishimura et al., 2007; de Boer, 2012 b; Dunn, 2018). Despite this presence, these sacs are overlooked in many studies (Fitch, 2000; Reide et al. 2008). Previous research has instead focused on studies comparing primate breathing, throat anatomy, tongue and muscular structures, and neurology to quantify what gives humans the ability to create and understand speech. Air sacs have been conserved through evolution, and the lack of air sacs in humans is phylogenetically unique (Fitch, 2000; Hewitt et al., 2002, de Boer 2012b; Dunn, 2018). Obtaining a basic understanding of how and when nonhuman apes use these sacs is the first step towards interpreting why they may have been lost in our own lineage (Fitch, 2000; de Boer, 2008, de Boer, 2012b).

Laryngeal air sacs

Tracheal and laryngeal sacculles are commonly present in many mammalian taxa as small pouches of mucosal tissue (Negus, 1949). These sacculles have convergently developed into air sacs in numerous mammalian taxa, for example, baleen whales (Mysticeti), pinnipeds, reindeer (*Rangifer tarandus*), antelope and gazelles (Bovidae), and many primates (Negus, 1949; Harrison, 1995; Frey et al., 2007; Reide et al., 2008). Common hypotheses for laryngeal air sacs include rebreathing or adding amplitude and resonance to vocalizations. In reindeer, Mongolian gazelle (*Procapra gutturosa*), and hammer-headed fruit bats (*Hypsignathus monstrosus*), air sacs seem to be a product of sexual selection, as they are significantly larger in males and are thought to be used for mating calls (Frey and Reide 2003; Frey et al., 2007; Bradbury, 2010). In primates, air sacs are also hypothesized to be used for communication (de Boer, 2008, Reide et al., 2008; Dunn, 2018). As an indication of their importance to primates, laryngeal air sacs have convergently evolved numerous times and have been classified into four differing types: lateral ventricular, subhyoid, infraglottal, and dorsal air sacs (Hewitt et al., 2002; Nishimura et al., 2007; Reide et al., 2008; Dunn, 2018). How and when these four types of air sacs evolved is unclear, as taxa within families can have differing air sacs or no air sacs at all. For example, in the new world monkey family Cebidae, some howler monkeys (*Alouatta* sp.) and capuchins (*Cebus* sp.) have subhyoid air sacs while others have lateral ventricular sacs, and related taxa are not known to have sacs at all (Hewitt et al., 2002; Frey et al., 2007). In great apes, laryngeal air sacs are found in all genera but one: *Homo* (Hewitt et al., 2002, Steele et al., 2013; Dunn, 2018).

Air sacs in super family Hominoidae (apes)

Hominoid air sacs are inflatable pouches of epithelial tissue that branch laterally off the larynx directly above the vocal folds (Figure 1) (Nishimura et al., 2007; Reide et al., 2008; de Boer 2012 a, de Boer 2012 b). These ventricular sacs connect anteriorly, and then depending upon the species, may branch and extend into the thorax and/or the throat (Hewitt et al., 2002; Reide et al., 2008). Inflation occurs when the ape exhales (Negus, 1949) and deflation occurs on inhalation. The sac can remain inflated over several breathing. Basal members of all ape lineages have lateral ventricular air sacs, and therefore this type of air sac is considered an ancestral trait of all ape species (Figure 2) (Hewitt et al., 2002, Steele et al., 2013).

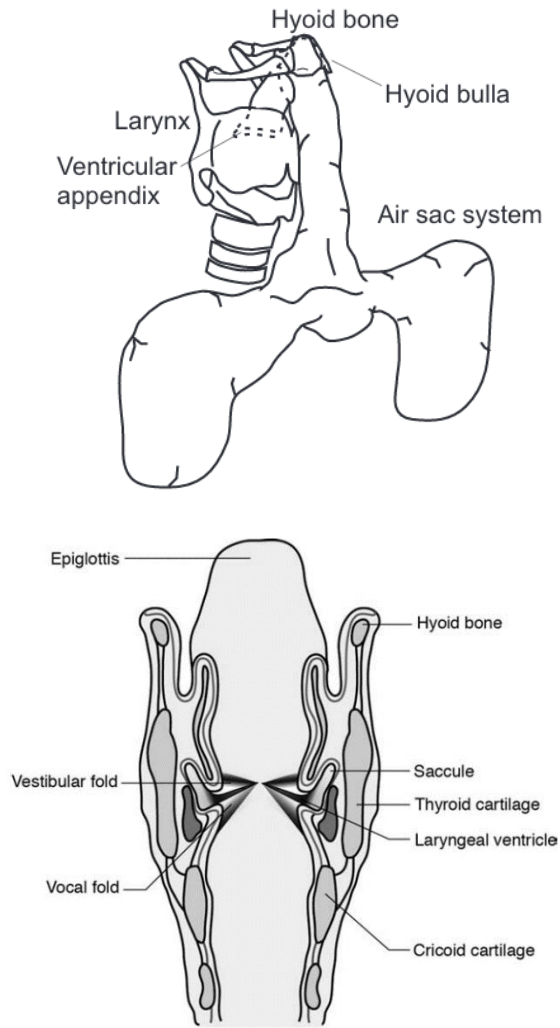


Figure 1. A. Diagram of laryngeal air sacs in great apes (de Boer, 2012b) B. Diagram of the larynx and trachea in *Homo sapiens*, cross section in posterior view. The laryngeal saccules extend anteriorly from the laryngeal ventricles (Porter and Vilensky, 2012).

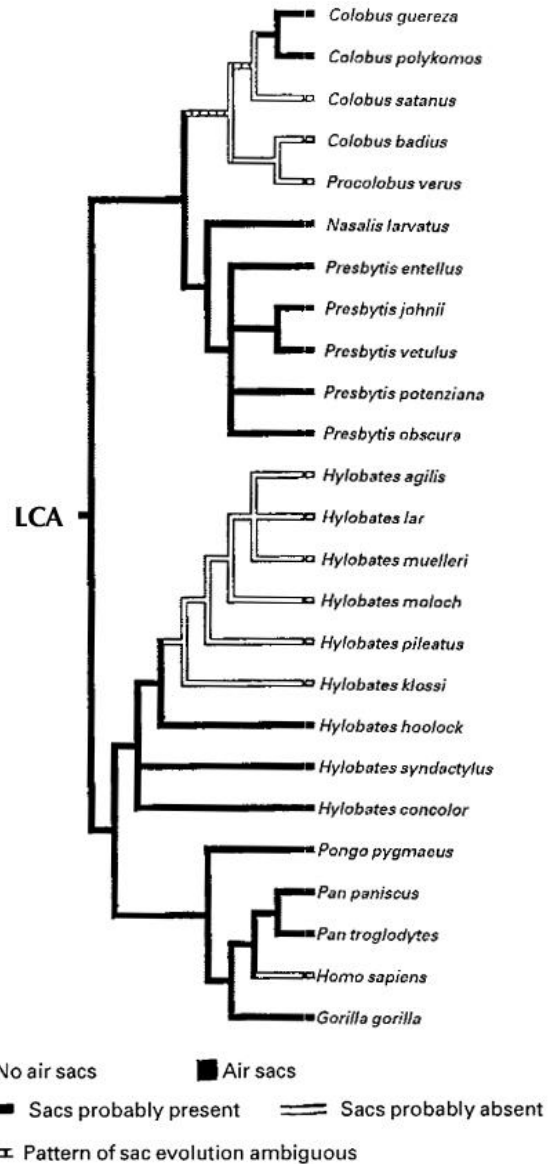


Figure 2. Cladogram identifying air sacs in extant primates of closest relation to *Homo sapiens* (Hewitt et al., 2002).

Fossil evidence for air sacs in family Hominidae (great apes)

The fossil record rarely preserves evidence of soft tissues, so scientists must discover other methods of determining the presence of air sacs in extinct Hominidae. One proposed hypothesis states that the morphology of hyoid bones often shows effects of air sac presence (Fitch, 2000; de Boer 2012 b; Steele et al., 2013; Dunn, 2018). The hyoid bone sits above the larynx in great apes, and the growth of air sacs can affect the shape and thickness of the hyoid body. Extant non-human ape hyoids have large bullas of thinned bone where air sacs can expand

(Figure 3). *Homo* species seem to have lost this trait, as modern human hyoids, as well as fossilized hyoids from *Homo neanderthalensis* and *Homo heidelbergensis*, have thick, bar-like hyoid bodies. This is in contrast with the hyoid from *Australopithecus afarensis* which has a bulla similar in size and shape to a chimpanzee, suggesting that this ancestor had air sacs (Steele et al., 2013, de Boer, 2012 a, de Boer, 2012 b).

Fossil hyoids are difficult to find, as they are articulated only by tendon and cartilage to the throat and can be easily lost in the fossil record (Fitch, 2000; Hewitt et al., 2002; Dunn, 2018). To compound upon that, only partial skulls or small bones such as fingers and toes identify many hominids. As a result, studying extant great apes and comparing them to *H. sapiens* will allow us to gain information that would not be possible to obtain from the fossil record (Fitch, 2000).



Figure 3. Adult hyoid bones of *Gorilla gorilla*, *Pan troglodytes*, *Homo sapiens*. Orientation of views (top to bottom): superior, right lateral, inferior, anterior (Steele et al., 2013).

Air sacs in extant members of family Hominidae

Extant great apes include Asian orangutans (three *Pongo* species), two genera of African apes (two *Gorilla* sp. and two *Pan* sp.), and humans (*Homo sapiens*). Air sac size appears to be larger in males than females, but for the most part, this sexual dimorphism may be due to differences in overall body size (Nishimura et al., 2007).

Orangutan species have the largest air sac to body ratio of all apes, and air volume of male orangutans has been measured as up to 6 liters. These sacs are most extensive in males,

though orangutans also have the one of the largest sexual dimorphisms for size difference between males and females in primates (Knott, 1999). The air sacs can extend along the thoracic wall and even along the jaw towards the ear (Lawson et al., 2006). These sacs seem to be used primarily used for vocalization, as orangutans are semi-solitary and call over long distances (>400 m) for mating and territorial displays (Lameira and Wich 2008). The substantial size of the sacs may increase the distance a male orangutan can broadcast calls.

African apes, such as gorillas, bonobos, and chimpanzees have smaller air sacs than orangutans. The sacs are proportionally similar between these genera after accounting for body size (Nishimura et al., 2007). Male gorillas might use them to increase resonance for displays that include thoracic drumming (chest beating), but recent studies have shown that this signals an accurate account of body size, so the increased resonance may be for improved distance transmission (Nishimura et al., 2007; Wright et al., 2021).

H. sapiens are the only extant hominids known to not have air sacs. Within human larynges are small ventricular saccules (Figure 1). These are thought to be vestigial remnants of the extensive sacs found in other apes. (Hewitt et al., 2002; de Boer, 2012 a; de Boer, 2012 b; Riede et al., 2008). Therefore, the loss of laryngeal air sacs seems to be an anatomical feature from a common ancestor to the entire *Homo* genus (de Boer, 2012 b; Steele et al., 2013).

Air sacculitis: the expense of conserving laryngeal air sacs

Despite the number of times air sacs have arisen in primate species, and how the only great ape to have lost these sacs are humans, many previous researchers in the 20th century dismissed primate air sacs as useless vestigial traits (Hewitt et al., 2002). Evolutionary pressure, however, seems to suggest otherwise. Air sacculitis, the term for common bacterial infections in primate laryngeal air sacs, can greatly reduce an individual's fitness with chronic infections, often leading to secondary, often fatal, infections with diseases such as pneumonia (de Boer, 2012 b, Kumar et al., 2012). Infections seem to occur at a higher rate in larger air sacs, so adult males, and in particular orangutans, are most susceptible. While most documented cases are in primates in captivity, air sacculitis has also been documented in a free-ranging mountain gorilla (Hastings, 1991). Selection pressures for large air sacs seems to be greater than decreases in fitness that may occur (de Boer 2012b; Steele et al., 2013). If air sacs were useless, evolutionary pressures would have selected against them over the past 30 million years and extant apes would likely not retain them as a trait.

Proposed functions of air sacs in apes

One of the earliest mentions of air sacs in primates (as referenced by Steele et al. (2013)) was Rudolf Fick's observations in 1895. Since then, the functions of the sacs have been debated (Harrison, 1995). Data on these sacs are mostly limited to post-mortem autopsies, imaging, and computer and physical modeling.

Three hypotheses for ape laryngeal air sacs remain viable. Riede et al. (2008) and Bart de Boer (2008) conducted experiments for the first hypothesis, which states that in apes, air sacs provide greater acoustic resonance than vocalizations without sacs. A second hypothesis, proposed by Hewitt et al. (2002), plays upon the previous rebreathing hypothesis and suggests that the sacs may be used to prevent hyperventilation. A third hypothesis, proposed by Dunn (2018), returns to the idea of sexual selection. Dunn states that the sexual selection may be towards vocal acoustics instead of visual displays. These hypotheses all have merit, and it may be that some or all of them are accurate in at least some species of ape.

Vocal intensity and resonance

Recent experimentation has pointed towards air sacs adding resonance to primate calls. Reide et al. (2008) used a physical model to reproduce vocal conditions with and without an air sac and found that air sacs may increase the extent to which high and low pitches can be made (Riede et al., 2008). Models by de Boer (2008) have shown similar results. De Boer used mathematical and computer modeling to reproduce the acoustic properties of apes with and without air sacs. The experiments showed two possible results: the sac could either increase the amount of lower frequency resonances or match the acoustical impedance value in the transition of sound waves between vocal cords and the air of the environment so the waves are not dampened. (de Boer, 2008) (de Boer, 2012a) (de Boer, 2012b), (Nishimura et al., 2007).

Apes often live in dense vegetation, such as rainforests in Africa and Asia. Within these areas, sight can be limited, so apes seem to rely upon calls to interact with each other. Sound experiments show that lower frequency sounds penetrate through dense foliage for longer distances with less refraction and distortion of the sound wave. Ideally, broadcast calls for communication greater than 25 m distance in dense vegetation would propagate from 1 m off the ground, have low to no frequency or amplitude modulation (as the vegetation surfaces will increase and distort both properties), and measure between 1 and 3 kHz. (Maciej et al., 2011). This does not allow for call localization, however. In studies with macaques, Brown et al. (1978)

found that frequency modulation increased a primate's ability to locate a call direction. This coincides with a study by Mennill et al. (2012) in which the researchers found it easier to localize low pitched trills over clear tonal sounds or high-pitched trills.

According to De Boer (2008, 2012a, 2012b), inflated laryngeal air sacs add extra resonance frequencies to calls. These harmonic resonances have the effect of melding with and effectively boosting the volume of the fundamental frequency produced without air sacs. This increase in volume may help propagate the call over longer distances with less attenuation. Assumptions were that air sacs would make vocalizations noisier (Dunn, 2018), but instead, they resonate with more harmonics. This also may help with long distance transmission, as tonal calls retained at least some harmonics over distances of 25 m with verifiable fundamental frequency (Mennill et al., 2012).

Sound transmission pressures for low frequency calls with trills or repetitions most likely caused selection in ape vocalizations. For example, orangutan calls (which are used most often for the longest distance communication between great apes) are low frequency with repetitions, meeting both the requirements for longer distance transmission without attenuation as well as repetition for localization. Considering they also have the largest air sac size, this leads to hypotheses that air sacs are correlated with long distance transmission. In contrast, bonobos have the overall highest frequency vocalizations. Bonobo calls still have a mean peak frequency of 2.3 KHz (de Waal, 1988) and are repeated, therefore are still within the ideal range for sound propagation over distances in thick foliage environments.

Rebreathing

Hewitt et al. (2002) proposed a modified hypothesis on rebreathing the air in laryngeal sacs. Ape calls are often drawn out over a significant time period and include many quick cycles of breathing, which could cause hyperventilation. The laryngeal sac is filled when an ape exhales, so the air inside the sac has a higher carbon dioxide concentration than the air in the ape's environment. The air in the sac could be rebreathed to keep blood oxygen levels from elevating. Small gibbon species have lost their sacs, preventing this rebreathing technique. However, Hewitt et al. noted that the behavioral patterns at the latter half of small gibbon vocalizations are often paired with increased levels of brachiation, which could be a way to reduce oxygen levels by burning more through muscular exercise (Hewitt et al., 2002)

Sexual Selection

Sexual dimorphism in laryngeal air sacs has been noted in at least five mammalian taxa: hammer-headed bats, Mongolian gazelle, orangutans, gorillas, and reindeer (Frey et al. 2007). Though sexual dimorphism is rare in bats, male hammer-headed bats are not only much larger in size than females, but their larynx fills the entire thoracic cavity (Fitch and Hauser, 2001). During mating season, male bats will congregate in specific areas and call with visibly inflated laryngeal air sacs. In reindeer and Mongolian gazelle, laryngeal air sacs are used by males when rutting, and are also visible when inflated in the neck. In gorillas, air sac inflation has been associated with chest beating behaviors. A recent study by Wright and others (2021), chest beating has been found to give an accurate representation of a male's body size. This behavior is clear connected to sexual selection, as silverback gorillas chest-beat most often during female estrus and in response to other male's encroachment on the territory.

Though most apes do not have highly visible air sac inflation as found in other mammals, sexual selection may still play a role in the evolution of their air sacs (Dunn, 2018). Exaggerated sexual dimorphism may not occur if laryngeal air sacs have more than one function. Frey et al. (2006) found that in muskox (*Ovibos moschatus*), roars used by males in rutting competition were statistically similar to roars used by females for other communication, and both sexes had similar larynx size, vocal fold length, and laryngeal out pocketing, despite a sexually dimorphic increase of the males' head size. Though air sacs may be used by both sexes, they can still be used in antagonistic competition for mate selection.

Comparatively, loud calls are not as important in human communication as in apes, which are spread out in extensive rainforests. Dunn suggested that changes in social communication might have led to the loss of air sacs in humans (Dunn, 2018). As human communication became more complex, it also became more localized. Precisely articulated syllables are most accurate in proximal communication in quieter tones (Fitch, 2000; Reide, 2008; Dunn, 2018)

Research Study

For this thesis, we tested the hypothesis that air sacs evolved to increase resonance in ape vocalizations. In other vertebrates, highly resonant vocalizations are used for mating calls and interspecific challenges. Therefore, we predicted that loud calls, or broadcast vocalizations, will more often coincide with inflated air sacs compared to more proximal calls such as food peeps. We also wished to see if sexual selection accounted for differences between male and female vocalizations.

We created methods to non-invasively determine distention of the throat (as a sign of air sac inflation) during vocal production. To do this, we compared external dimensions of the throat/upper chest during vocalization to other movements of the laryngeal apparatus (e.g. swallowing and chewing). With these data, we then analyzed whether broadcast vocalizations used inflation more than local vocalizations.

Subjects

The subjects consisted of four male and three female bonobos between the ages of 10 and 40. The bonobos were housed and recorded at the Ape Cognition and Conservation Initiative in Des Moines, Iowa. The study was conducted on bonobos in their typical daily enclosures. Facility staff recorded high speed images and audio of bonobos both vocalizing and at rest from a sagittal view ad libitum.

Individual bonobos were filmed during training and enrichment sessions with keepers encouraging bonobos to vocalize with vocal prompts and food. 149 minutes, 15 seconds of footage was analyzed, resulting in 179 samples of comparable frame sequences.

Recordings

The cameras used were the default audio/video recording applications created by Apple for the iPhone 11 (software version 14.4.2), recording at 29.97 fps and save as a MOV file, with video recorded in raw video at 1920px x 1080px resolution and audio as 44100 Hz stereo mp3s. Audio/video files were converted to AVI files and frame numbers were added to the video with the program *FFmpeg* (Tomar, 2006). Videos were watched in half speed to determine vocalizations, as well as imported into the *Fiji* program (Schindelin et al., 2012) as stacks and scanned frame by frame for targeted actions, such as vocalization, swallowing, and chewing. Two frames in near succession (between 1 and 10 frames from each other) were identified to show the range of motion of the laryngeal region and labeled as “open” and “closed”. The

“open” frame was a frame during the targeted action. The “closed” frame was either immediately before or after the action, in a resting or close to resting state as possible. Further criteria for identifying viable video frames were as follows: 1.) the frame must have the ape’s head and throat in sagittal view, 2.) the frame must show the entire of the curve of the ape’s throat, from the chest to the start of the chin, as well as the entire ear and brow, 3.) frames must be in focus enough to clearly distinguish the curve of the throat, 4.) the cranium must be centered over the torso with limited cervical extension, and 5.) both frames must have equivalent resolution and registration of the cranium (see figure 5). The individual frames were opened separately and saved as uncompressed TIFF files.

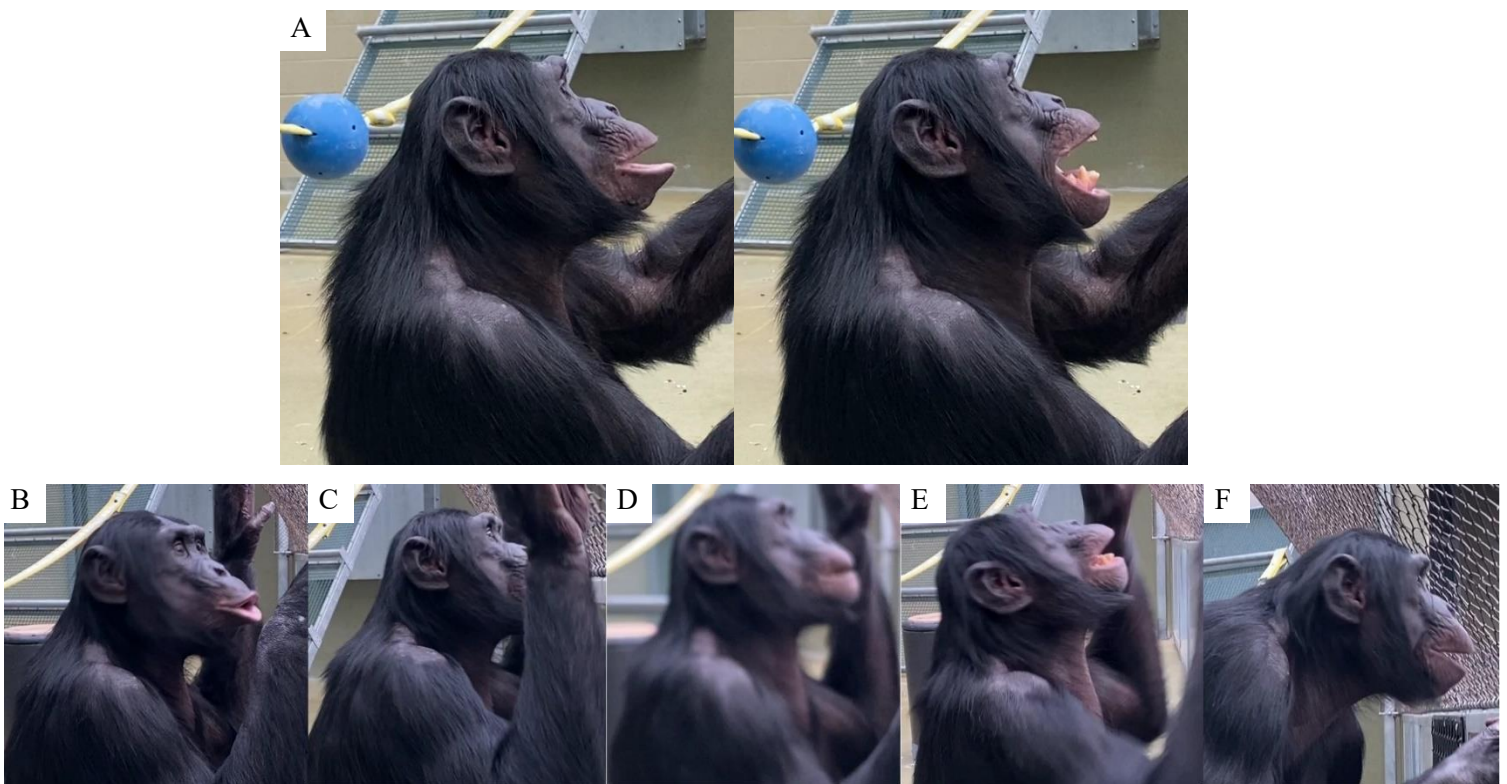


Figure 4: Examples of criteria for identifying viable video frames.

A: Two frames that conform to all five criteria, the first would be designated as the “closed” frame and the second the “open” frame.

B: This frame does not have the ape’s head completely in sagittal view, you can see both of his eyes.

C: This frame does not show the entire curve of the ape’s throat – his arm blocks view of his chin and where the throat meets the chest.

D: This frame is too blurry to clearly determine the brow and outline the throat.

E: The bonobo in this frame has too much dorsal cervical extension.

F: This frame does not show equivalent registration of the cranium compared to the other frames.

Video Processing

The region of interest (ROI) in these methods is defined as the area of the throat from just posterior of the chin to the sternum. The two frame files (the “open” and “closed” states) were imported into Fiji as a stack. To create a standardized ROI for each ape, an initial rectangular region was found using the ear and brow as landmarks (See Fig. 5 A & B). Using the Fiji rotated rectangle tool, the top of the rectangle outlined most superior point of the supraorbital ridge and pinna, one side of the rectangle outlined the anterior-most point of the supraorbital ridge, and the second side of the rectangle outlined the dorsal-most point of the pinna in relation to the brow. The height of the rectangle was equal to at least three times the pixel height of the bonobo’s ear (ensuring the rectangle included the area where the throat meets the chest). To determine standardized registration of the cranium, the angle between the superior point of the supraorbital ridge and pinna was within 5 degrees in each of the two frames. The frame outside of the rectangular selection was then removed and replaced with a black background. Differences in subject size and allometry was account for as random effects in the data analysis.

Next, the entire outline of the neck was traced with the polygon selection tool, using as many points as necessary to capture curves, and closed off with a straight line between the first and last points. This creates a segment of an elliptical shape, consisting of an irregular arc and its chord (See Fig. 5 C & D). In cases where hair covered parts of the chin, a straight line was drawn from the discernable anterior and posterior areas skin of the chin or from the edge of the rectangular area. This same length line was used in both frames to keep standardized measurements within an observed event. The shape was saved as a selection in Fiji’s ROI Manager tool. These procedures were repeated for both frames of interest, then, each shape was compared to check that the starting and ending points of each curve were comparable in relation to the area outlined. The area, perimeter, width, and height in pixels of both ROI selections were measured through the ROI Manager tool and saved in a .CSV file.

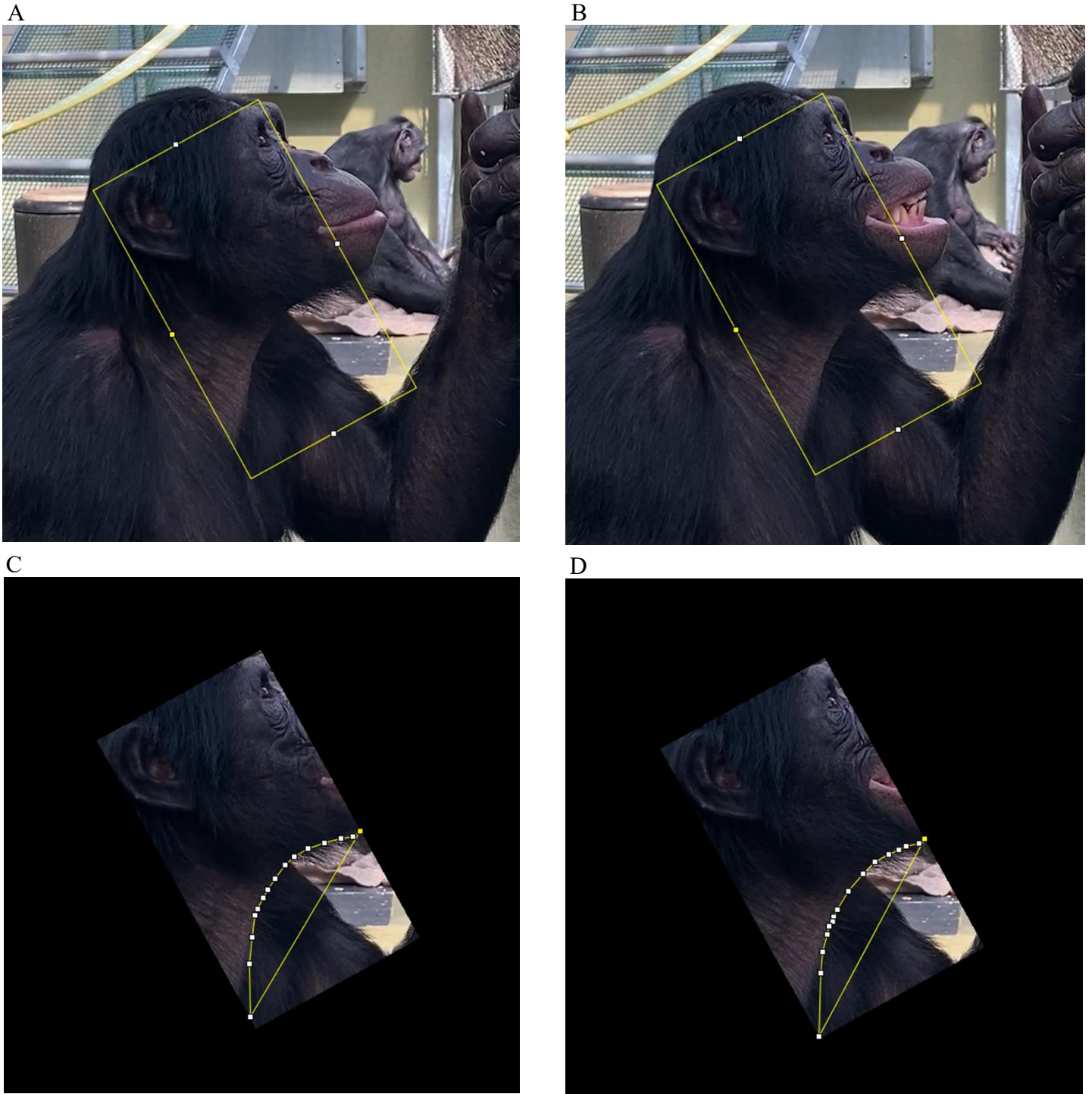


Figure 5: Examples of steps to find the ROI.

A and B: The frames are marked with rectangular selections following protocols outlined in the video processing section.

C and D: The area outside of the rectangular selections is blacked out. The edge of the throat is traced with a polygon selection and closed off to make an arched shape.

Data Analysis

As the videos were variable in depth of field and the position of the bonobo, both between videos and within the videos, we used the “closed” frame as a control for each recorded instance. Thus, each observation consisted of a pair of images taken from a single bonobo vocalization event: one open, and one closed. Using the area measured in pixels, we calculated the percent difference in area of the ROI, ΔA , as:

$$\Delta A = 100 * \left(\frac{A_{closed} - A_{open}}{A_{average}} \right)$$

where A_{closed} and A_{open} are the areas (in pixels) in the closed and open state, respectively. We used ΔA as a response variable so that changes in vocal sac size, which we assumed to be proportional to changes in external throat area, would be measured in a way that was proportional to each bonobo’s size as well as the resolution and registration of the recorded image. Negative ΔA is seen more frequently in non-vocal events. When a bonobo depresses the jaw joint, the radius of curvature in the irregular arc increases even as the chord decreases. This increases the overall area of the segment, causing the value of A_{open} to be larger than A_{closed} and therefore the value of ΔA to be negative. As both vocalizations and non-vocal events often include depression of the jaw joint, positive values of ΔA in vocalization events are caused by a decrease in the radius of curvature in the irregular arc due to distention of the laryngeal region.

We used generalized linear mixed models (GLMM; Bolker et al., 2009) to model the probability that a change in throat area was a vocalization or non-vocal event. GLM models are more flexible than standard linear regression models and are used to find the rate of change in differing sized population using logistical odds of probability. As sample sizes of recorded bonobo’s data were variable in size depending upon the quality of video retrieved, linear regression models could not fit the data and GLM models were instead used. The specific GLMM fitted was a logistic regression model (where 0 was a non-vocal event and 1 was a vocalization), with a logit link to convert linear values to probability, a binomial error distribution (as the response variable had been converted into binomial states), and with random effects fitted for individual bonobos to prevent pseudo-replication. The response variable Y_i took on value 1 if a throat movement event was a vocalization and was 0 for a non-vocalization.

We modeled Y_i as:

$$Y_i \sim \text{Bernoulli}(\theta_i)$$

$$\text{logit}(\theta_i) = \beta_0 + \beta_1 \Delta A_i$$

where θ_i was the probability of event i being a vocalization modeled by a model intercept (β_0). β_0 is the model intercept; β_1 is the effect of percent difference (ΔA); and ΔA_i is the percent difference in throat area of event i . We secondarily added models with the addition of γ_k as the effect of sex from individual j of sex k . We tested models where β_0 , β_1 , or both β_0 and β_1 could vary as a random effect of individual, as well as the addition of sex as an independent variable and models with the interaction of sex on the model. Random effects were assumed to come from a normal distribution with mean = 0 and a variance estimated from the data. Thus, we fit 9 GLMM which differed in their deterministic part and random effects structure (see Table 1).

Model	Deterministic	Random effects	Interpretation
1	$\beta_{0,j} + \beta_1 \Delta A_i$	$\beta_{0,j} \sim \text{Normal}(\mu, \sigma_{\beta_0})$	The model for Y_i with a random effect of individual on the intercept
2	$\beta_0 + \beta_{1,j} \Delta A_i$	$\beta_{1,j} \sim \text{Normal}(\mu, \sigma_{\beta_1})$	The model for Y_i with a random effect of individual on the effect of ΔA (i.e., slope)
3	$\beta_{0,j} + \beta_{1,j} \Delta A_i$	$\beta_{0,j} \sim \text{Normal}(\mu, \sigma_{\beta_0})$ $\beta_{1,j} \sim \text{Normal}(\mu, \sigma_{\beta_1})$	The model for Y_i with a random effect of individual on the intercept as well the effect of ΔA (i.e., slope)
4	$\beta_{0,j} + \gamma_k + \beta_1 \Delta A_i$	$\beta_{0,j} \sim \text{Normal}(\mu, \sigma_{\beta_0})$	Model 2 with additive effects of sex
5	$\beta_0 + \gamma_k + \beta_{1,j} \Delta A_i$	$\beta_{1,j} \sim \text{Normal}(\mu, \sigma_{\beta_1})$	Model 3 with additive effects of sex
6	$\beta_{0,j} + \gamma_k + \beta_{1,j} \Delta A_i$	$\beta_{0,j} \sim \text{Normal}(\mu, \sigma_{\beta_0})$ $\beta_{1,j} \sim \text{Normal}(\mu, \sigma_{\beta_1})$	Model 4 with additive effects of sex
7	$\beta_{0,j} + \gamma_k + \beta_1 \Delta A_i + \beta_2 \Delta A_i \gamma_k$	$\beta_{0,j} \sim \text{Normal}(\mu, \sigma_{\beta_0})$	Interactive effects of sex and ΔA , with a random effect of individual on the model intercept
8	$\beta_0 + \gamma_k + \beta_{1,j} \Delta A_i + \beta_2 \Delta A_i \gamma_k$	$\beta_{1,j} \sim \text{Normal}(\mu, \sigma_{\beta_1})$	Interactive effects of sex and ΔA , with a random effect of individual on the effect of ΔA (i.e., slope)
9	$\beta_{0,j} + \gamma_k + \beta_{1,j} \Delta A_i + \beta_2 \Delta A_i \gamma_k$	$\beta_{0,j} \sim \text{Normal}(\mu, \sigma_{\beta_0})$ $\beta_{1,j} \sim \text{Normal}(\mu, \sigma_{\beta_1})$	Interactive effects of sex and ΔA , with a random effect of individual on the model intercept as well the effect of ΔA (i.e., slope)

Table 1: The different GLM and GLMM models fit to the data with an explanation of random effects and interpretation (models 6, 8, and 9 were discarded due to singularities). σ_{β_0} is the standard deviation (SD) associated with the model's intercept and σ_{β_1} is the SD associated with the model's slope.

	df	AIC	delta	wt
mod1	3	185.0938	3.143526	0.0879
mod2	3	184.1467	2.196358	0.1412
mod3	5	184.4000	2.449659	0.1244
mod4	4	185.3834	3.433137	0.0761
mod5	4	184.0657	2.115424	0.1470
mod7	5	181.9503	0.000000	0.4234

Table 2: The degrees of freedom, Akaike’s Information Criterion (AIC) number, the amount of change between models, and the AIC weight of models 1-5 & 7. Model 7 was chosen to represent the data as it had the smallest AIC and largest AIC weight. Models 1-5 were not used as they had greater than 2 degrees of difference in AIC score than the best model (mod7).

We compared the fit of models using Akaike’s Information Criterion (AIC) and AIC weights to find the best fit (Burnham et al., 2011). Models with singular fits were discarded as they were most likely the result of small sample sizes. The model with the smallest AIC (and thus greatest AIC weight) was selected as the best fitting model and used to predict probability of vocalizations (see Table 2). We used R version 4.0.5 and R package lme4 version 1.1-23 to fit GLMM (Bates et al., 2015).

Results

140 occurrences (comparisons of “open” and “closed” states, i.e.: ΔA) were recorded for the seven bonobos (4 male, 3 female). These data points were fit to the GLM model 7, where we found the probability that an occurrence is a vocalization equals the interactive effects of sex of the individual (over the entire model) with random effects of the individual fit to the intercept of the model ($logit(\theta_i) = \beta_{0,j} + \gamma_k + \beta_1 \Delta A_i + \beta_2 \Delta A_i \gamma_k$).

For each bonobo, vocalizations showed greater change in percentage in the ROI area of the throat (ΔA , see Data Analysis section for computation). For all bonobos, the median ΔA is larger in vocalizations than nonvocal events, and for most bonobos, the spread of vocalizations were found over greater positive values of ΔA (See Figure 6). A trend is seen in the male bonobos (Kanzi, Maisha, Nyota, and Teco) as well as one female bonobo (Clara) of all data points within the 1st and 3rd quartile of vocalizations greater than the data within the 1st and 3rd quartiles of non-vocal events.

Using the best fit GLMM, the logistic regression model was plotted for each bonobo (see Figure 7). In general, data on male bonobos tended to reach higher probability of vocalization with smaller changes in ΔA and a smaller ranged spread of probability (see Figure 8 and Table 3). All bonobos show that a greater change in ΔA correlates to a greater probability the the occurrence is a vocalization.

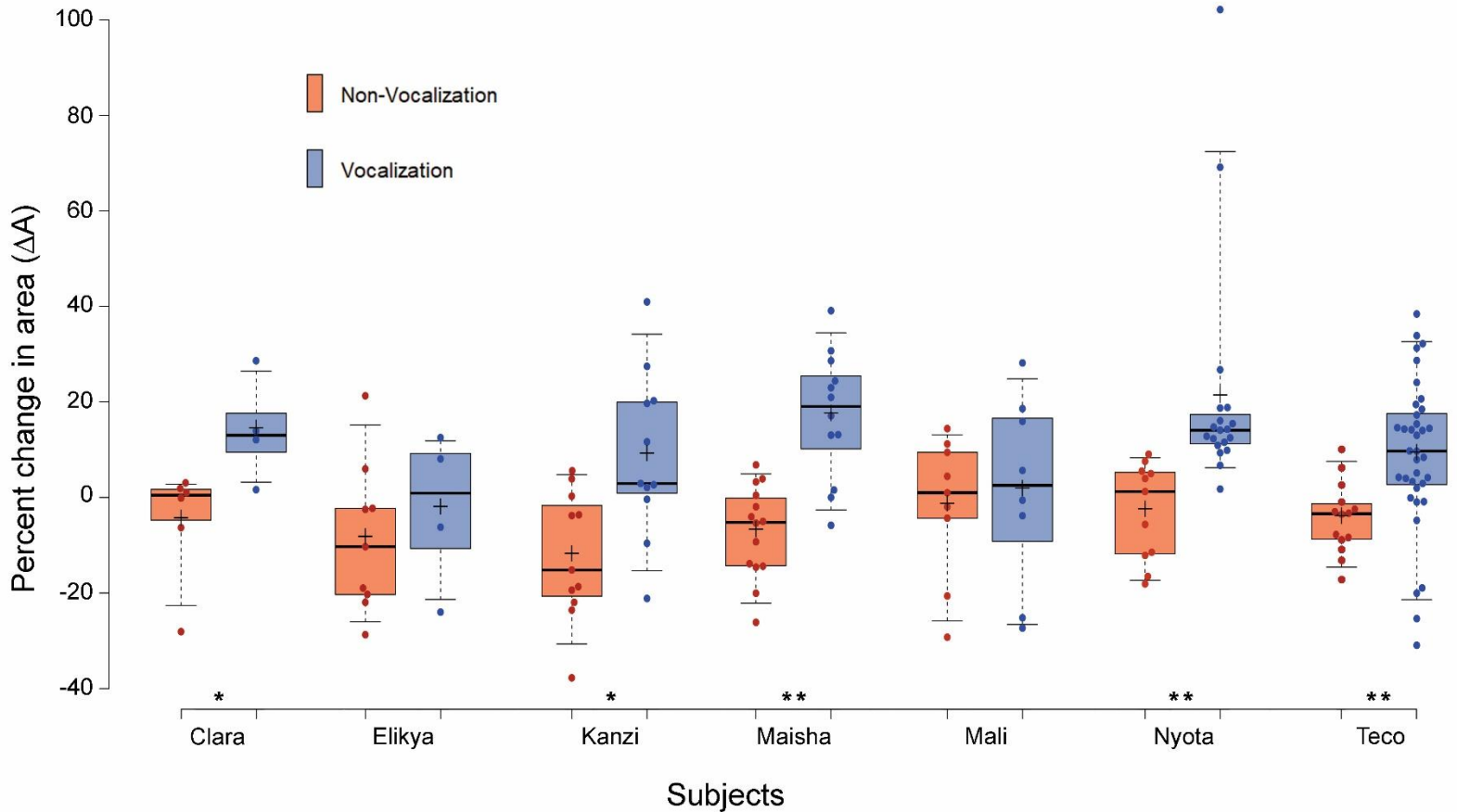


Figure 6: Boxplot with standard deviations of datapoints for each bonobo. The percent change in throat size as found by $\Delta A = 100 * ((A_{\text{closed}} - A_{\text{open}}) / A_{\text{average}})$ is shown for each individual, showing that greater change in throat size generally occurs during vocalizations (blue) in comparison to non-vocalization events (red). Mann-Whitney U tests were ran on each subject to determine significance (noted on plot with *, $p < 0.05$ and **, $p < 0.01$).

Clara: $u(9)=22$, $p=0.0252$; Elikya: $u(12)=22$, $p=0.4874$; Kanzi: $u(21)=99$, $p=0.0126$; Maisha: $u(25)=153$, $p=0.0004$; Mali: $u(16)=42$, $p=0.5317$; Nyota: $u(29)=202$, $p=0.0001$; Teco: $u(49)=411$, $p=0.0001$

Subject	Sex	ΔA	Probability of vocalization	Standard Deviation	Min Probability	Max Probability
Clara	F	13.7059494	68.2%	0.6483035	39.2%	87.7%
Elikya	F	21.3044367	72.2%	0.6310530	47.5%	88.1%
Mali	F	25.1541243	72.6%	0.6204738	50.3%	87.4%
Kanzi	M	7.8015263	70.7%	0.5315769	65.3%	75.5%
Maisha	M	8.1976315	71.0%	0.5413858	63.9%	77.2%
Nyota	M	7.1950326	69.2%	0.5380473	62.5%	75.2%
Teco	M	9.2277395	75.3%	0.5526724	66.8%	82.2%

Table 3: For this snapshot of data, data points closest to 70% probability were found for each bonobo as 72.2% probability of vocalization was the highest probability met by Elikya. The change in area of the ROI is listed as ΔA . The range of probabilities for the occurrence listed is outlined by the Min and Max probabilities.

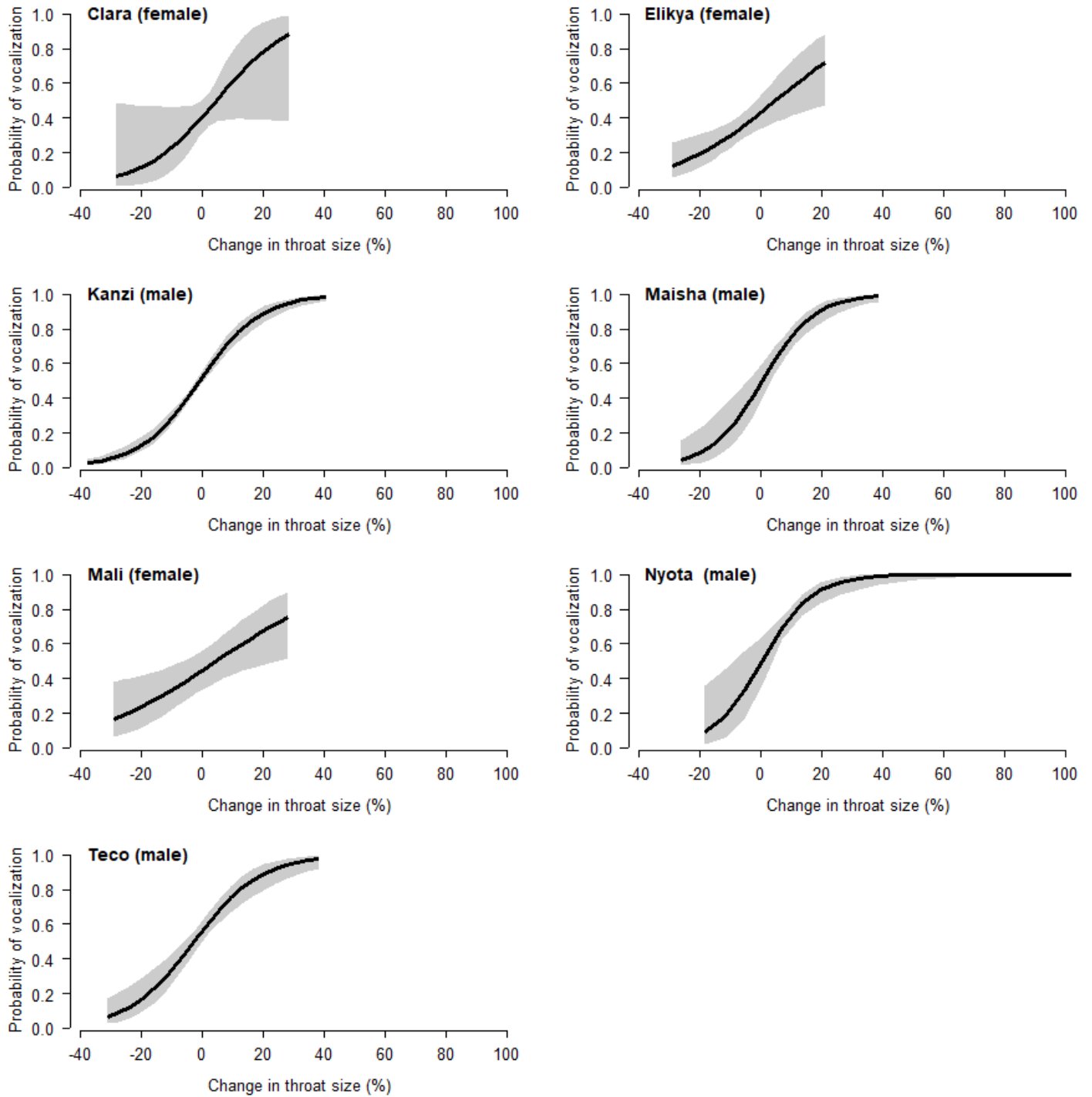


Figure 7: Plots for each individual bonobo comparing the percent change in throat size (ΔA as found by $\Delta A = 100 * ((A_{\text{closed}} - A_{\text{open}}) / A_{\text{average}})$) to the probability that the event recorded is a vocalization, margin of minimum and maximum potential probability shown in gray.

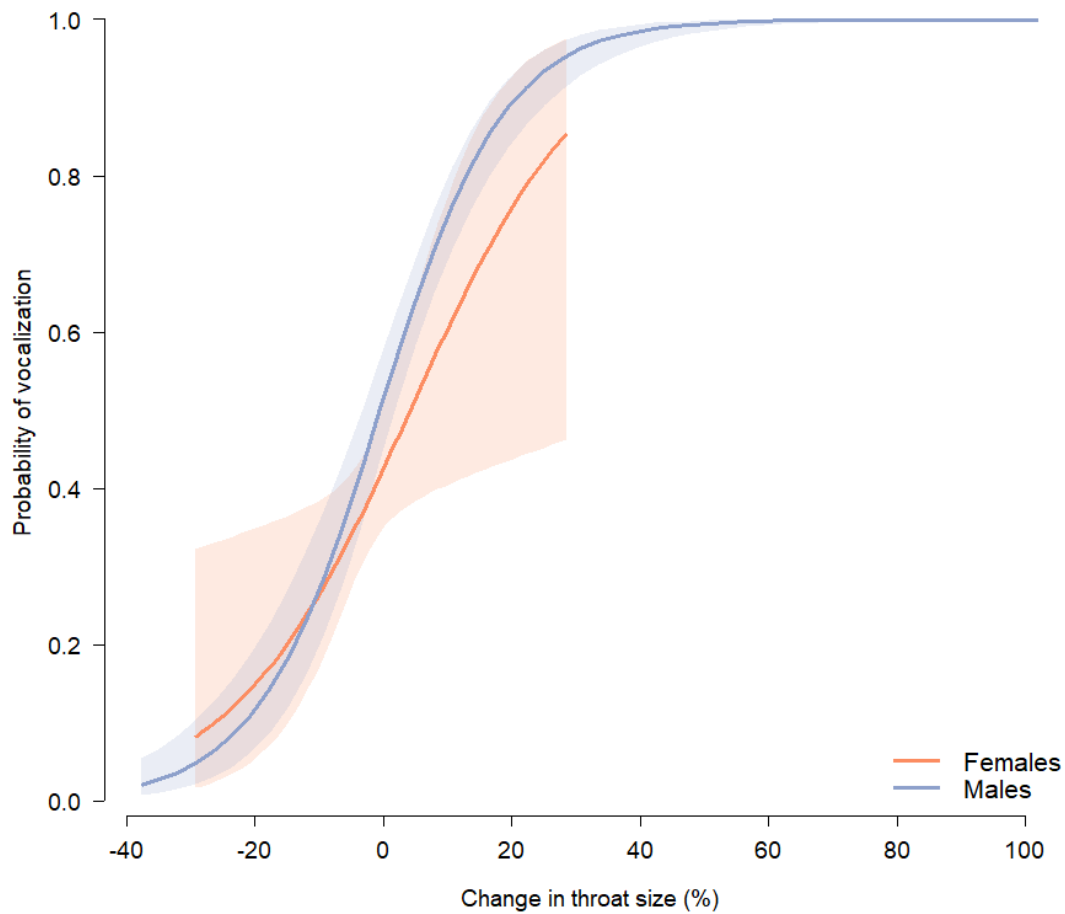


Figure 8: Plot for female bonobos (red) and male bonobos (blue) comparing the percent change in throat size (ΔA as found by $\Delta A = 100 * ((A_{\text{closed}} - A_{\text{open}}) / A_{\text{average}})$) to the probability that the event recorded is a vocalization, with of minimum and maximum potential probability.

Discussion

Each data point used was a comparison between a control reference frame of the larynx in a resting state and an active state of vocalization, swallowing, or chewing. When analyzed, there was a significant trend showing a larger difference in the two areas during vocalization than non-vocal laryngeal movements. This provides evidence that the laryngeal apparatus is significantly changing in size specifically during vocalizations. While this is not direct evidence of laryngeal air sac inflation, as we have not specifically measured the air sac itself, there is limited anatomy in the region that would move except for a laryngeal air sac, therefore, it is highly likely we are measuring occurrences of air sac inflation.

During observations of the bonobos, there was often an anterior movement of the laryngeal area with all types of vocalizations, and broadcast vocalizations were often accompanied by distention of the throat which are likely to be air sac inflation. Due to this, most vocalizations could be visually differentiated from non-vocal movement of the mouth and trachea. Nyota and Teco were observed to distend their throats when aroused, rather than specifically to create a louder vocalization; this may be akin to humans unconsciously raising their vocal volume when excited. Nyota, in particular, often presented a distended throat for an extended time after loud call vocalizations. Teco distended his throat in response to loud calls from other bonobos or excited human voices, even though he was rarely recorded producing a broadcast call in response. Maisha had too few recorded broadcast calls in view of the camera to make reliable behavioral observations on his laryngeal apparatus.

While the male bonobos all visibly showed evidence of air sac inflation through throat distention, none of the female bonobos were recorded with a significant change in area in the laryngeal area, even when loud calling in an excited state. As confirmed by the data analysis, in females, there was an overlap in the change of area (ΔA) of vocalizations and non-vocal events. There are numerous possible hypotheses for this discrepancy. First, air sacs may be (at least partially) conserved by sexual selection, and males may predominately use air sacs to amplify calls. While previous literature has focused on chimpanzees and noted no significant size difference in air sacs between males and females, no studies have focused on comparing male and female bonobo air sac sizes. It is inconclusive whether bonobo female air sacs are large enough to increase resonance during vocalization. Second, the male bonobos at the Ape Initiative are more closely related than the female bonobos, and two of the three females have been recently introduced to the facility. The excessive throat distention in the male bonobos may be due to genetic differences or learned behaviors within their familial group. Third, female bonobos generally have greater subcutaneous fat deposits than males (Zihlman and Bolter, 2015), and this may be obscuring movement in the laryngeal apparatus. Fourth, it has been noted that other mammalian taxa can temporarily lower their larynges, a behavior most often seen in male antagonistic and mating calls (Frey et al., 2020). There is a chance that the throat distention is at least in part due to the larynx dropping to increase the vocal tract length. Further studies would be needed to determine if this is a possibility.

An unlikely potential hypothesis for differences in air sac inflation is the health of the bonobo. Kanzi, a male, and the eldest bonobo, has a history of air sac infections, including surgeries such as placement of a stoma within the air sac wall. Despite this, he shows significant air sac inflation during vocalizations. Mali, a relatively young and healthy female bonobo, did not show as significant a difference between vocal and non-vocal events.

Potential drawbacks

First, the research in this thesis was only able to analyze observations from a small population of bonobos. Long-term studies using larger, more diverse populations should give more conclusive evidence of air sac usage in bonobos. Similar studies on other ape species could give comparing analyses for air sac usage between species closely related to humans.

Second, methods for data collection are highly specific and resulted in many instances of vocalizations that were unable to be used, as bonobos are highly active and often combine behaviors such as running and climbing to broadcast vocalizations. The most viable data came from bonobos that were more motivated to interpret and follow directions of the keeper to remain relatively still and use only one hand to reach for food. Data recording was also the most successful when only one bonobo was in the enclosure yet still had vocal interactions with other bonobos calling throughout the facility.

Third, the data collection methods are not highly precise. The methods seemed to be most accurate when the bonobo was completely still except for movement in the larynx. Any movement of the head, arms, or position of the body created a slight difference in registration of frames, even at recording speeds of 30 frames per second. This difference may slightly alter the endpoints of the ROI selection, even with the standardized rectangular area as a guide. In cases that were extremely visually obvious, the selections were nudged in manual adjustment with frequent comparison of the two frames.

Despite these drawbacks, the methods were able to produce results consistent with visual observations. While precision and accuracy were not ideal, they were sufficient at capturing differences in area of the throat during vocalization and yielding significant results. These methods should be viable for similar applications of measuring variable objects at a distance. Parties interested in using similar methods are encouraged to improve upon the ones outlined in this thesis, and hopefully there will be an increase in technological ability to register a moving, flexible object with few external identifiable markings.

Integration of Thesis Research

The research, background, and applications of this thesis are integrative in nature. The subject deals with archeology, primatology, comparative morphology, anatomy, acoustics, and linguistics. Other applications for these methods can be used for measuring anatomical structures in other species that cannot be safely handled.

Acknowledgements

I would like to thank the Graduate College of Kennesaw State University for funding my thesis research. Next, I would like to thank my advisor Dr. Jared Tagliatela for his support, ideas, and patience over the past two years. I would have been lost on so many occasions without your input and guidance on methods and techniques. I came up with a harebrained idea and you listened, improved upon, and helped make it work. I would also like to thank my committee members for all their patience and input. Thank you, Lisa, for being understanding and supportive. Thank you, Anton, for realistic guidance and keeping me on track. Thank you, Bill, for agreeing to join the project last minute so I could complete everything. Thank you, Nick, (though not on my committee), you took time out of your summer to create and explain to me statistical analyses and how to program them into R. Finally, I would like to thank Amanda Epping and the staff at the Ape Institute for all the time, patience, and effort they spent listening to what I needed, gathering videos, then listening to multiple renditions of changes I wanted made, working with the bonobos to encourage certain vocalizations and postures, and gathering more video for me. Without them, I would not have data. They saved my research project when pandemic travel restrictions prevented me from obtaining video in person.

References

1. Albessard-Ball , L. and Balzeau, A. (2018) Of Tongues and Men: A Review of Morphological Evidence for the Evolution of Language. *Journal of Language Evolution*, 3(1): 79-89. doi:10.1093/jole/lzy001
2. Bates, D.; Mächler, M.; Bolker, B.; Walker, S. (2015) Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1). doi:10.18637/jss.v067.i01
3. Bolker, Benjamin M. et al. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24(3), 127 – 135. doi:10.1016/j.tree.2008.10.008
4. Bradbury, J. W. (1977). Lek Mating Behavior in the Hammer-headed Bat. *Zeitschrift Für Tierpsychologie*, 45(3), 225–255. doi:10.1111/j.1439-0310.1977.tb02120.x
5. Brown, C. H.; Beecher, M. D.; Moody, D. B.; Stebbins, W. C. (1978) Localization of Primate Calls by Old World Monkeys. *Science*, 201(4357), 753-754. doi:10.1126/science.97785
6. Burnham, K. P.; Anderson, D. R.; Huyvaert, K. (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, 65:23–35 doi:10.1007/s00265-010-1029-6
7. de Boer, B. (2008) The acoustic role of supralaryngeal air sacs. *The Journal of the Acoustical Society of America*, 123(5): 37-79. doi:10.1121/1.2935420
8. de Boer, B. (2012)a Air sacs and vocal fold vibration: Implications for evolution of speech. *Theoria et Historia Scientiarum*, 9: 13-28. doi:10.12775/v10235-011-0002-5
9. de Boer, B. (2012)b Loss of air sacs improved hominin speech abilities. *Journal of Human Evolution*, 62(1): 1-6. doi:10.1016/j.jhevol.2011.07.007
10. de Waal, F.B.M. (1988) The Communicative Repertoire of Captive Bonobos (*Pan Paniscus*), Compared To That of Chimpanzees. *Behaviour*, 106(3/4): 183-251. doi:10.1163/156853988X00269
11. Dunn, J. C. (2018) Sexual selection and the loss of laryngeal air sacs during the evolution of speech. *Anthropological Science*, 126(1): 29-34. doi:10.1537/ase.180309
12. Fitch, W. T. (2000) The evolution of speech: a comparative review. *Trends in Cognitive Sciences*, 4(7): 258-267. doi:10.1016/S1364-6613(00)01494-7

13. Fitch W.T. and Hauser M.D. (2003) Unpacking “Honesty”: Vertebrate Vocal Production and the Evolution of Acoustic Signals. In: Acoustic Communication. Springer Handbook of Auditory Research, vol 16. New York, NY, Springer. doi:10.1007/0-387-22762-8_3
14. Frey, R.; Gebler, A.; Fritsch, G. (2006) Arctic roars - laryngeal anatomy and vocalization of the muskox (*Ovibos moschatus* Zimmermann, 1780, Bovidae). *Journal of Zoology*, 268(4), 433–448. doi:10.1111/j.1469-7998.2006.00053.x
15. Frey, R.; Gebler, A.; Fritsch, G.; Nygrén, K.; Weissengruber, G. E. (2007) Nordic rattle: the hoarse vocalization and the inflatable laryngeal air sac of reindeer (*Rangifer tarandus*). *Journal of Anatomy* 210(2): 131-59. doi:10.1111/j.1469-7580.2006.00684.x
16. Frey, R. and Reide, T. (2003) Sexual Dimorphism of the Larynx of the Mongolian Gazelle (*Procapra gutturosa* Pallas, 1777) (Mammalia, Artiodactyla, Bovidae). *Zoologischer Anzeiger - A Journal of Comparative Zoology*, 242(1): 33-62. doi:10.1078/0044-5231-00086
17. Frey, R.; Volodin, I. A.; Volodina, E. V.; Efremova, K. O.; Menges, V.; Portas, R.; Melzheimer, J.; Fritsch, G.; Gerlach, C.; von Dörnberg, K. (2020) Savannah roars: The vocal anatomy and the impressive rutting calls of male impala (*Aepyceros melampus*) – highlighting the acoustic correlates of a mobile larynx. *Journal of Anatomy*, 236(3): 398-424. doi: 10.1111/joa.13114
18. Harrison, D. F. N. (1995) Detailed morphology. In The anatomy and physiology of the mammalian larynx. 48-184. Cambridge: Cambridge University Press. doi:10.1017/CBO9780511525766.005
19. Hastings, BE. (1991) The veterinary management of a laryngeal air sac infection in a free-ranging mountain gorilla. *Journal of Medical Primatology*, 20(7): 361-364.
20. Hewitt, G.; MacLarnon, A.; Jones, K. E. (2002) The functions of laryngeal air sacs in primates: A new hypothesis. *Folia Primatologica*, 73: 70-94. doi:10.1159/000064786
21. Knott, C. D. (1999) Orangutan Behavior and Ecology. In The Nonhuman Primates, edited by: P. Dolhinow and A. Fuentes. Mayfield Press: Mountain View, CA, 50–57
22. Kumar, S.; Fox, B.; Owston, M.; Hubbard, G. B.; Dick Jr., E. J. (2012) Pathology of spontaneous air sacculitis in 37 baboons and seven chimpanzees and a brief review of the literature. *Journal of Medical Primatology*, 41(4): 266-277. doi:10.1111/j.1600-0684.2012.00547

23. Lameira A.R.; Wich S.A. (2008) Orangutan Long Call Degradation and Individuality Over Distance: A Playback Approach. *International Journal of Primatology* 29:615–625 doi:10.1007/s10764-008-9253-x
24. Lawson, B.; Garriga, R.; Galdikas, B.M. (2006) Airsacculitis in fourteen juvenile southern Bornean orangutans (*Pongo pygmaeus wurmbii*). *Journal of Medical Primatology*, 35(3): 149-154. doi:10.1111/j.1600-0684.2006.00153.x
25. Maciej, P.; Fischer, J.; Hammerschmidt, K. (2011) Transmission Characteristics of Primate Vocalizations: Implications for Acoustic Analyses. *PLoS ONE* 6(8): e23015. doi:10.1371/journal.pone.0023015
26. Mennill, D. J.; Battiston, M.; Wilson, D. R.; Foote, J. R.; Doucet, S. M. (2012) Field test of an affordable, portable, wireless microphone array for spatial monitoring of animal ecology and behaviour. *Methods in Ecology and Evolution* 3(4): 704–712 doi:10.1111/j.2041-210X.2012.00209.x
27. Negus V.E. (1949) The Comparative Anatomy and Physiology of the Larynx. London, W. Heinemann Medical Books.
28. Nishimura, T.; Mikami, A.; Suzuki, J.; Matsuzawa, T. (2007) Development of the laryngeal air sac in chimpanzees. *International Journal of Primatology*, 28: 483-492. doi:10.1007/s10764-007-9127-7
29. Porter, P.W.; Vilensky, J.A. (2012) The Laryngeal Sacculae: Clinical Significance. *Clinical Anatomy* 25:647–649 doi:10.1002/ca.22015
30. Reeb, D. and Best, P. B. (1999) Anatomy of the Laryngeal Apparatus of the Pygmy Right Whale. *Journal Of Morphology*, 242:67–81 doi:10.1002/(SICI)1097-4687(199910)242:1<67::AID-JMOR5>3.0.CO;2-#
31. Riede, T.; Tokuda, I. T.; Munger, J. B.; Thomson, S. L. (2008) Mammalian laryngeal air sacs add variability to the vocal tract impedance: Physical and computational modeling. *The Journal of the Acoustical Society of America*, 124(1): 634-647. doi:10.1121/1.2924125
32. Schindelin, J. et al. (2012) Fiji: an open-source platform for biological-image analysis. *Nature methods* 9(7): 676-682. doi:10.1038/nmeth.2019

33. Steele, J.; Clegg, M.; Martelli, S. (2013) Comparative morphology of the hominin and African ape hyoid bone, a possible marker of the evolution of speech. *Human Biology*, 85(5): 639-672. doi:10.3378/027.085.0501
34. Tomar, S. (2006) Converting video formats with FFmpeg. *Linux Journal*, 146: 10.
35. Zihlman, A. L. and Bolter, D. R. (2015) Body composition in *Pan paniscus* compared with *Homo sapiens* has implications for changes during human evolution. *Proceedings of the National Academy of Sciences of the United States of America*, 112(24): 7466-7471. doi: 10.1073/pnas.1505071112