Acoustic cues to individuality in wild male African savannah elephants (*Loxodonta africana*) (#52158)

First revision

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Acoustic cues to individuality in wild male African savannah elephants (*Loxodonta africana*)

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The ability to recognise conspecifics plays a pivotal role in animal communication systems. It is especially important for establishing and maintaining associations among individuals of social, long-lived species, such as elephants. While research on female elephant sociality and communication is prevalent, until recently male elephants have been considered far less social than females. This resulted in a dearth of information about their communication and recognition abilities. With new knowledge about the intricacies of the male elephant social structure come questions regarding the communication basis that allows for social bonds to be established and maintained. By analyzing the acoustic parameters of social rumbles recorded over 1.5 years from wild, mature, male African savanna elephants (*Loxodonta africana*) we expand current knowledge about the information encoded within these vocalizations and their potential to facilitate individual recognition. We showed that social rumbles are individually distinct and stable over time and therefore provide an acoustic basis for individual recognition. Our results revealed that different frequency parameters contribute to individual differences creating a unique vocal signature.

Acoustic cues to individuality in wild male adult African savannah elephants (*Loxodonta africana*)

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Abstract

The ability to recognise conspecifics plays a pivotal role in animal communication systems. It is especially important for establishing and maintaining associations among individuals of social, long-lived species, such as elephants. While research on female elephant sociality and communication is prevalent, until recently male elephants have been considered far less social than females. This resulted in a dearth of information about their communication and recognition abilities. With new knowledge about the intricacies of the male elephant social structure come questions regarding the communication basis that allows for social bonds to be established and maintained. By analyzing the acoustic parameters of social rumbles recorded over 1.5 years from wild, mature, male African savanna elephants (*Loxodonta africana*) we expand current knowledge about the information encoded within these vocalizations and their potential to facilitate individual recognition. We showed that social rumbles are individually distinct and stable over time and therefore provide an acoustic basis for individual recognition. Our results revealed that different frequency parameters contribute to individual differences creating a unique vocal signature.

Introduction

Communication plays an important role in social interactions among animals (Enquist et al. 2010). It is an essential component of a wide variety of behaviors related to mating, parental care, predator-prey interactions, group cohesion, and foraging (Bradbury and Vehrencamp 2011). However, for many of these interactions to take place, animals must possess the ability to recognize others. Recognition can vary in specificity, from discrimination of a species, to recognition of sex, kin, mates, rivals or even specific individuals (Tibbetts and Dale 2007). It is particularly important when repeated interactions occur within a group of conspecifics as it allows individuals to adjust their behavioral response based on previous encounters (Yorzinski 2017). Individual recognition is one the most complex forms of recognition and takes place when individually distinctive characteristics encoded within signals or cues are used by animals for the identification of others (Tibbetts and Dale 2007, Carlson et al. 2020). In order to be useful, information encoded in an individually distinctive cue has to not only be unique to a specific individual and different from that of others, but must also be either stable over time, or the rate of change in a cue must be less than the frequency of interactions between individuals (Thom and Hurst 2004).

Recognition can be achieved through many sensory modalities, yet different cues are subject to limitations resulting from the physical properties of cues and the anatomical features of the animal, and these limitations determine which sensory modality is most effective in a given context (Bradbury and Vehrencamp 2011, Higham and Hebets 2013). Here, we focus on acoustic cues. Acoustic cues are used by many social species to regulate various behavioural processes, including recognition (Owings and Morton 1998; Tibbetts and Dale 2007). They usually communicate immediate states as they do not persist in the environment (Bradbury and Verencamp 2011). However, they have the ability to be used over long distances, with low frequency sound propagating further and not subject to scattering to the extent of high frequency sound (Bradbury and Verencamp 2011). Consequently, utilizing acoustic cues for individual discrimination is beneficial when there is a need to broadcast or perceive identity information at a distance. For example, when approaching other individuals is costly (e.g. Falls 1982; Wierucka et al. 2018a, b); or when the environment limits the use of other cues, such as in water (Caldwell and Caldwell 1965).

African savanna elephants (*Loxodonta africana*) produce a range of vocalisations, including low frequency calls, called rumbles, that are used in various social contexts (summarized in Moss et al. 2011; Morris-Drake and Mumby 2017). Vocal communication and recognition have been extensively studied for this species, with rumbles shown to encode sex (Baotic and Stoeger 2017), age (Stoeger et al. 2014), and reproductive (Soltis et al. 2005b) as well as emotional state (Soltis et al. 2005b, Soltis et al. 2009, Wesolek et al. 2009). African savanna elephants use rumbles for the recognition of familiar (Stoeger and Baotic 2017) and family/bond group members (McComb et al. 2000) and to mediate inter-partner distance (Leighty et al. 2008; Soltis et al. 2005a). The species has been shown to retain long-term memory of conspecifics' calls

(McComb et al. 2000), and have been shown to produce individually distinct calls (McComb et al. 2003, Soltis et al. 2005b, Clemins et al. 2005). While African elephant rumbles and the information they convey has been extensively studied, a vast majority of this research focused on females and there is relatively little information about acoustic cues produced by males, with only one study investigating non-musth vocal communication (Stoeger and Baotic 2016). This is a result of the characteristics of the elephant social structure. African savanna elephants live in stable, matrilineal groups and repeated interactions among females are easily observed, with their social structure and association patterns well explored (as summarized in Moss et al. 2011). As a result, the communication basis that allows for complex social bonds among females to be developed has also been studied in detail.

African savanna elephant males disperse from their natal groups (as summarized in Moss et al. 2011) and mature males have been previously thought to live mostly solitary lives. Studies on male-male interactions have focused primarily on males in musth – a state of heightened sexual activity, during which animals are highly aggressive (Poole 1987; e.g. Hollister-Smith et al. 2008, Ganswindt et al. 2005). However, recent studies have shown that mature males outside of the sexually active period are a lot more social than previously assumed (Chiyo et al. 2011, Goldenberg et al. 2014), with stable, long-term relationships occurring over time (Murphy et al. 2019). The centrality of animals within a network does not seem to be affected by the age (and thus size) of the animals (Murphy et al. 2019), meaning that they are likely established on an individual basis. If males interact with each other regularly, the ability to identify conspecifics based on individually distinct acoustic cues, would be beneficial for the maintenance of long-term associations and hierarchy.

Previous research has shown that information about individuality can be conveyed in male African elephant rumbles (Stoeger and Baotic 2016). This study provided much needed insight into male vocalisations, yet it was conducted on animals living under human care and over a relatively short period of time. While this was necessary for obtaining initial information, it is now important to investigate whether calls are individually distinct for wild individuals and over longer timeframes. This will allow for a better evaluation their potential for conveying identity information. In this study, we aimed to expand on earlier research by investigating rumbles produced by wild male African elephants recorded over 1.5 years, to determine whether patterns of individual distinctiveness are stable over time and to confirm their potential to facilitate individual recognition in a natural setting.

Materials & Methods

Data collection

The data were collected between June 2016 and October 2017 in the Associated Private Nature Reserves (APNR) in South Africa (24°18′S, 31°18′E). The APNR is an area of approximately

20,800 km2, adjacent to Kruger National Park, encompassing multiple privately-owned nature reserves. Although the western border is fenced, the individual reserves to the east are unfenced, as is the boundary to Kruger National Park, allowing for unrestricted movement of animals.

Rumbles of adult male elephants were recorded at a sampling frequency of 44.1 kHz on a Marantz PMD661 MKI recorder connected to an Earthworks QTC50 omnidirectional microphone (with a 3Hz – 50kHz flat frequency response), while the animals were 23.5m (mean, SD=14.4) away from the microphone. Rumbles are very distinct, low frequency calls that cannot be confused with other types of vocalisations produced by elephants (Soltis et al. 2010). Individual identity of males was established visually during recording sessions assessing the pattern of ear tears and holes and markers of age and sex, then confirmed based on photo-identification methods ~~after returning to field base~~ (following Black et al. 2019). The elephants in this study were collared (as a part of a different, ongoing long-term project), allowing us to maximize the number of sightings and rumble recordings. To eliminate the influence of age and sex on acoustic parameters (Stoeger and Baotic 2016) and focus on individual differences, we recorded vocalisations of only mature males (over 35 years of age; age was determined following Black et al. 2019). Furthermore, to test for individual differences in a general social context we focused our efforts only on non-musth males. During musth males produce distinct musth-rumbles encoding their sexual state (Poole 1987) that are quantitatively different from rumbles produced during inter-musth periods (Poole 1999). Therefore, animals that were acoustically sampled ~~did not present with~~ typical signs of musth (urine-dribbling, urine staining on back legs, temporal gland secretions or temporal gland swelling; Poole 1987) at the time of recording. All sampled animals inhabit the same area, therefore regional differences were not a relevant factor. As our aim was to evaluate the distinctiveness of rumbles across naturally occurring conditions we did not attempt to limit the recordings to a specific behavioral or social contexts. Therefore, elephants were sampled at random, with rumbles recorded from animals exhibiting a variety of behaviors (foraging, resting, socializing, traveling, combination). However, to avoid rumbles that may have been produced in a reproductive context, we limited the data to vocalisations produced by males when no females were within sight.

All recordings were collected as part of field surveys by the South African non-profit Elephants Alive in line with their agreements with the management of the Associated Private Nature Reserves. The research forms part of a registered and approved SANParks project, in association with the Kruger National Park and Scientific Services and the Associated Private Nature Reserves (Project ID: judith1547.22). We thank the private landowners and Wardens of the Associate Private Nature Reserve for the permission to work on their land.

Data processing and statistical analysis

Rumbles were processed in Raven Pro 1.5. The spectrogram settings were set to a Hann window size of 600 ms, with a hop size of 300 ms and an overlap of 50%. We only selected rumbles that were of good quality (clearly visible on the spectrogram, with no overlapping vocalisations). Rumbles were identified manually by selecting an area encompassing the entire rumble on the spectrogram (Fig. 1). We focused on parameters describing the frequencies and duration of the acoustic cue as frequency values (including the fundamental frequency) have been previously determined to be likely most important to encode information on individual identity in African elephants (McComb et al. 2001, Stoeger and Baotic 2016). We did not include formant frequencies, as these are correlated to the maturity (age and size) of elephants (Stoeger and Baotic 2016). Our aim was to investigate true individual differences (*sensu* Tibbetts and Dale 2007) and therefore limited our study animals to one age group (>35 years of age) and similar size. To keep spectral measurements unbiased and consistent as possible, ~~we only took~~ robust measurements of each rumble ~~into consideration~~ (Table 1). These measurements consider the energy that is stored in the selection rather than time and frequency endpoints, making them ~~not observer/selection biased~~ (Charif et al. 2010). We measured the Center Frequency, Frequency 5%, Frequency 95%, Bandwidth, and Duration 90% (Charif et al. 2010; Table 1; Fig. 1). While Frequency 5% is by definition “the frequency that divides the selection into two frequency intervals containing 5% and 95% of the energy in the selection” (Sharif et al. 2010), in practice, in the case of elephant rumbles, Frequency 5% is equivalent to the fundamental frequency.

Following the standardization of each variable to a range of 0-1 (to avoid abundance bias in our results), we used a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001; using the vegan package; Oksanen et al. 2019), incorporating Euclidean distances in the matrix, to test whether differences in frequency parameters exist among individuals. This non-parametric method allows for considering multiple variables at low sample sizes to identify overall differences (across individuals) and is appropriate for unbalanced data. To confirm that observed differences are in fact a result of differences across individuals and not an artefact of large differences in within-individual variability, we conducted an analysis of multivariate homogeneity (‘betadisper’; Anderson 2001) combined with an ANOVA. We used a SIMPER analysis (Clarke 1993) to determine which variables contributed most to the observed differences.

Results

The final database included 81 rumbles from five identified, mature males, over a long time period (an average of 402.8 days between the first and last recording; Table 2). Rumbles had a mean Duration 90% of 4.19s (SD=1.05) and mean Center Frequency of 28.37 Hz (SD=6.87; Table 2). Mean Frequency 5% for elephant rumbles used in our study was 11.65 Hz, which is consistent with the average fundamental frequency of 9.91-13.81 Hz reported for African elephant male rumbles for a similar maturity group (and therefore similar size; Stoeger et al. 2016), confirming that this measurement is, in practice, equivalent to the fundamental frequency (Figure 1). We found significant individual differences in measured spectral features of wild male social rumbles (R2=0.22, p=0.0001). Results of the multivariate homogeneity analysis were not significant (F=1.6, df=4, p=0.173), indicating that the assumption of homogeneity of variances was met by our data and differences across individuals could not be attributed to differences in within-individual variability. SIMPER analyses indicated that the overall contribution of measured spectral parameters to the observed differences was relatively even, ranging from 12.3-24.2% (Table 3).

Discussion

For individual recognition to occur, animals must produce individually unique and stable cues, which their conspecifics will remember and use as a template for recognition during subsequent encounters. In this study, we demonstrate that wild male African savanna elephants produce individually distinct vocalisations that are stable over time and context and thus have the potential to be used for individual identification providing a basis for complex social associations to be established and maintained. We showed that rumbles produced by male African savanna elephants were characteristic to a given animal and significantly different from that of other individuals. Vocalisations were distinct despite the animals being of the same sex and age category, and inhabiting the same area, pointing to true individual differences (differentiating each individual) rather than those resulting from other factors such as sex, age, or geographical region. All measured frequency parameters contributed relatively evenly to these differences, suggesting that it is the overall characteristics of the vocalisations rather than just one or several spectral parameters that encode identity.

Previous research explored the distinctiveness of male African elephant rumbles in captivity (Stoeger and Baotic 2016). The authors focused on age and size differences among males and also showed that individuality can be encoded in rumbles. While providing important information about the call structure, the recordings were collected over a short period of time (average of 12 days per location) and thus the within-individual similarity could have potentially resulted from context- or state- dependent factors and the evaluation of the stability of the cues was not possible. Furthermore, the elephants were housed in four different institutions, and thus the observed differences among individuals could have been confounded by population or regional differences resulting from different origins or influence of associating conspecifics (as is the case in some other mammals; Laimera et al. 2010). Our study allowed for testing wild animals over a long time period (mean of 402.8 days between the first and last recording of the same individual) to confirm the presence of individually distinct vocalisations while concurrently indicating the robustness of male vocalisations over time and various behavioral contexts. Rumbles are used by African elephants in many different contexts (Moss et al. 2011) and the vocalisations used in our analysis were recorded while elephants were displaying various behaviors. Despite the contextual differences, the individual differences were still pronounced, suggesting that vocal signatures can provide reliable identification information across a variety of contexts. Furthermore, while elephants ~~were not in~~ musth when recorded, there exists a possibility that some individuals could have been in a state of pre-musth or post-musth, which was not visible, but could have resulted in fluctuations in hormone levels. Testosterone has been shown to influence male vocalisations in mammalian species (e.g. Pasch et al. 2011; Dabbs and Mallinger 1999; Fedurek et al. 2016) and androgen fluctuations could potentially influence elephant rumbles. If this is the case, and we recorded animals that were influenced by increased circulating testosterone and cortisol concentrations, our results become even more robust than initially anticipated. As samples were collected on multiple occasions and elephants undergo musth once a year (summarized in Schulte and Rasmussen 1999), we would have sampled animals producing varied androgen amounts. Despite this, the individual distinctiveness in the overall rumble characteristics are still significant.

Male-male interactions are often competitive as they are frequently related to resource acquisition (van Hooff and van Schaik 1994). This is the case for elephants, where males compete for females and resources, with high aggression rates occurring among adults (Lee et al. 2011), particularly during reproduction. In the context of these behaviors, acoustic cues (allowing for the transmission of information over large distances; Bradbury and Vehrencamp 2011) combined with knowledge about the outcomes of previous encounters, the identification of individuals through acoustic cues allows for the evaluation of risk at a distance, and an adjustment of behavior, potentially limiting direct aggressive encounters and decreasing the risk of injury. Because of this, studies of intra-sexual, male-male recognition have often focused on competition and rival assessment (e.g. Casey et al. 2015, Charlton et al. Kitchen et al. 2003, Pitcher et al. 2015, Reby et al. 2005). While this is a likely explanation for recognition to exist, “true” (*sensu* Tibbetts and Dale 2007) individual recognition (defined as animals being able to recognize multiple individuals, as opposed to distinguishing groups of individuals – e.g. determined by age or sexual status) in context of intra-sexual interactions has been not studied ~~frequently~~ (Carlson et al. 2020). Therefore, there still remains ambiguity as to the recognition abilities of many studied species. If certain variables, such as size are not adjusted for, yet vary among the tested individuals, class-level recognition (e.g. age or size) could be interpreted as individual recognition. By controlling for age and size in our study, we eliminated that possibility and found that cues were individually distinct, indicating that recognition in males could be used not only for rival assessment, but also for maintaining long-term affiliative associations during non-competitive periods.

Conclusions

We extend earlier studies of acoustic communication in elephants to investigate the structure and stability of social rumbles recorded from wild, free-ranging male elephants and evaluate their potential for conveying individual identity information. For individual recognition to occur, animals must not only produce individually distinct cues, but these cues must also be stable (Thom and Hurst 2004). We demonstrated that both these conditions were met and thus, an acoustic basis for individual recognition of male African elephants exists, is stable, robust and seems to be encoded in the overall rumble spectrum. Therefore, acoustic individual recognition is likely to occur in male African elephants. While mature male savannah elephants were previously considered to be primarily solitary, we now know that this is not the case (Chiyo et al. 2011; Goldenberg et al. 2014; Murphy et al. 2019). Instead, they exhibit a fission-fusion social structure, which sits against a backdrop of seasonally fluctuating resource availability and cyclic reproductive state. Adult male elephants in the studied population maintain some stability in social relationships over time (Murphy et al. 2019), however, these relationships are disrupted by musth (Goldenberg et al. 2014). Therefore, the ability to recognize long-term associates over time could be central to the stability of male elephant social strategies. Future research should focus on experimentally confirming through bioassays whether acoustic cues are used by animals for individual recognition. There is also scope for behaviorally evaluating whether all measured parameters are used by the animals or whether elephants only rely on certain spectral features of the rumbles for recognition.

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Table 1(on next page)

Definitions of acoustic measurements collected for African elephant male rumbles (for accuracy, definitions are reproduced from Charif et al. 2010).

Measurement	Definition
Center Frequency	The frequency that divides the selection into two frequency intervals of equal energy. It is the smallest discrete frequency in which the left side of the formula exceeds 50% of the total energy in the selection.
Frequency 5%	The frequency that divides the selection into two frequency intervals containing 5% and 95% of the energy in the selection. The computation of this measurement is similar to that of Center Frequency, except that the summed energy has to exceed 5% of the total energy instead of 50%.
Frequency 95%	The frequency that divides the selection into two frequency intervals containing 95% and 5% of the energy in the selection. The computation of this measurement is similar to that of Center Frequency, except that the summed energy has to exceed 95% of the total energy instead of 50%.
Bandwidth 90%	Bandwidth 90% is the difference between the 5% and 95% Frequencies.
Duration 90%	The 5% Time and 95% Time are the points in time at which the selection is divided into two time intervals containing 5% and 95% or 95% and 5% of the energy in the selection, respectively. Therefore the 5% and 95% Time is the smallest discrete time in which the left side of the formula exceeds 5/95% of the total energy in the selection. Duration 90% is the difference between the 5% and 95% Times.

Table 2(on next page)

Sample size, range of dates, mean acoustic parameters (±SE) of recorded vocalizations of each African savanna elephant male (A-E).

	A	B	C	D	E
First recording	10/08/2016	16/12/2016	27/06/2016	16/08/2016	02/09/2016
Last recording	04/10/2017	04/10/2017	12/09/2017	26/10/2017	26/10/2017
Median recording	26/10/2016	15/06/2017	24/01/2017	22/06/2017	28/11/2016
Range of days	421	293	443	437	420
Sample size	24	6	10	35	6
Duration 90% [s]	4.06 (±0.19)	3.33 (±0.26)	3.81 (±0.26)	4.75 (±0.15)	2.98 (±0.49)
Bandwidth [Hz]	28.16 (±1.08)	23.43 (±2.34)	32.53 (±4.8)	28.38 (±0.29)	27.1 (±3.96)
Frequency 95% [Hz]	11.22 (±0.56)	10.5 (±0.95)	17.3 (±2.99)	11.14 (±0.34)	8.32 (±1.11)
Center Frequency [Hz]	85.04 (±2.71)	75.2 (±6.93)	69.73 (±4.79)	75.71 (±1.74)	74.95 (±3.68)
Frequency 5% [Hz]	73.83 (±2.61)	64.7 (±6.8)	52.45 (±2.96)	64.59 (±1.66)	66.67 (±3.7)

Table 3(on next page)

The average contribution of each measured spectral parameter to the overall observed difference between African elephant male rumbles.

Measured parameter	Average contribution [%]
Duration 90% [s]	24.22
Bandwidth [Hz]	24.19
Frequency 95% [Hz]	22.57
Center Frequency [Hz]	16.43
Frequency 5% [Hz]	12.29

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Figure 1

Example of a non-musth, mature African elephant male social rumble, with measurements that were used for analysis indicated on the spectrogram. Hann window size of 600 ms, with a hop size of 300 ms and an overlap of 50%.