Acoustic cues to individuality in free-ranging 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 analysing the acoustic parameters of social rumbles recorded over several years from wild, mature, male African savanna elephants (*Loxodonta africana*) we expand current knowledge about the information encoded within these vocalisations 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 a wide range of frequency parameters all contribute to individual differences creating a unique vocal signature.

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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 behaviours related to mating, parental care, predator-prey interactions, group cohesion, and foraging (Bradbury and Vehrencamp 2011). However, for many of these interactions to be successful, animals must possess the ability to recognize others. Recognition can vary in specificity, from ~~animals distinguishing~~ discrimination of a species, to ~~recognizing~~ recognition of sex, kin, mates, rivals or even specific individuals (Tibbetts and Dale 2007). It is particularly important when repeated interactions occur ~~among~~ within a group of conspecifics ~~given animals~~ as it allows individuals to adjust their behavioural response based on previous encounters with conspecifics (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). The presence of individual discrimination has been shown for a wide variety of taxa, and while ~~it is used~~ discrimination is vital in ~~different~~ multiple contexts, prior research has focused primarily on competition, territoriality, reproduction and parental care, ~~with many gaps in knowledge existing about individual recognition in contexts other than reproduction.~~

Recognition can be achieved through many sensory modalities, ~~yet different~~ Communication signals ~~cues~~ are subject to ~~various~~ limitations resulting from the physical properties of ~~cues~~ signal and the anatomical restrictions of the animal~~s~~, and these limitations determine~~determining~~ which sensory ~~channel~~ modality is most effective ~~is used~~ in a given context (Bradbury and Vehrencamp 2011, Higham and Hebets 2013). Acoustic cues tend to be exploited by animals as sound usually overcomes obstacles better than visual cues, propagates better than olfactory cues and ~~is relatively fast~~ and communicates and immediate state (Yorzinski 2017). 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 (Moss et al. 2011). Vocal communication and recognition have been extensively studied for this species ~~in the past~~, with rumbles shown to encode sex (Baotic and Stoeger 2017), age (Stoeger et al. 2014), reproductive (Soltis et al. 2005), as well as emotional (Soltis et al. 2005), ~~reproductive (Soltis et al. 2005)~~ and affective state (Soltis et al. 2009). ~~Animals~~ Male African elephants have been shown to

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recognize rumbles of familiar females ~~use rumbles for the recognition of familiar~~ (Stoeger and Baotic 2017) and family/bond group members ~~(McComb et al. 2000),~~ 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. 2005). While ~~there seems to be an abundance of information about~~ African elephant rumbles and the information they convey has been extensively studied, a vast majority of this research focused on females and there is ~~a dearth~~ relatively little ~~of~~ information about acoustic cues produced by males. This is a result of the characteristics of the elephant social structure. Female~~s~~ African elephants live in stable, matrilineal groups and repeated interactions among individuals are easily observed, with their social structure and association patterns well explored (Moss et al. 2011). As a result, the communication basis that allows for complex social bonds to be developed has also been studied in detail.

Males disperse from their natal groups (Moss et al. 2011) and have been previously thought to live mostly solitary lives. ~~There was not much information available about~~ Studies on male-male interactions have focused primarily on males ~~, other than those~~ in musth, ~~(~~a state of heightened sexual activity, during which animals are highly aggressive (~~;~~ Poole 1987). However, recent studies have shown that mature males outside of the sexually active period are a lot more social than previously thought (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. 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) in some contexts. Acoustic cues allow 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 would allow for the evaluation of risk at a distance, and an adjustment of behaviour, potentially limiting direct aggressive encounters and decreasing the risk of injury. For this process to be successful, acoustic cues would have to allow for individual recognition across a variety of contexts, physiological states and social scenarios.

Recent research has shown that information about ~~maturity~~ age and individuality can be conveyed in male African elephant rumbles (Stoeger and Baotic 2016). The study provided much needed insight into male vocalisations, yet it was conducted in captivity, in a controlled and consistent setting and over a short period of time. While this was necessary for obtaining initial information, it is now important to investigate information encoded in vocalisations and the stability of acoustic cues produced by ~~wild~~ free-ranging male elephants ~~in a natural setting~~. This will allow us to better evaluate their potential for conveying identity information and usefulness

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Commented [SG17]: Kate Evans has contributed significantly to our knowledge of male sociality.

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To evaluate risk, the receive may assess from the signal:
That is Joe and I know Joe is big; or that is a big male.

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in a biological context. Factors such as social context, behavioural state or physiological changes (influenced by hormone fluctuations) can affect the vocalisations produced by animals. Therefore, it is important to ~~incorporate such variation in data,~~account for these factors when investigating the basis for recognition. For individual recognition to be successful in a natural setting, the sound produced by the caller ~~s~~ should be robust enough to be individually distinctive despite ~~such potential~~ variability influenced by intrinsic and extrinsic factors, and the receiver must have the capability to distinguish differentiating acousttic parameters. In this study, ~~using a long-term dataset and not limiting the data to a specific social context,~~ we investigated rumbles produced by wild male African elephants, to determine whether they are individually distinct and stable over time, and evaluated 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 in most directions.

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). Rumbles are very distinct, low frequency calls that cannot be confused with other types of vocalisations produced by elephants. Individual identity of males was established visually during recording sessions ~~in the field~~ by assessing the pattern of ear tears and holes and ~~, as well as~~ markers of age and sex, then confirmed ~~and further confirmed after returning to the field base,~~ based on photo-identification methods (following Black et al. 2019) after returning to field base. The elephants ~~used~~ 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. ~~As we were interested in the individual distinctiveness of rumbles, t~~To minimize ~~other factors~~ the influence of age and sex on acoustic parameters ~~that could influence our results (e.g. sex, age; (~~Stoeger and Baotic 2016) we ~~only~~ recorded vocalisations only of 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 ~~(that occurs throughout a majority of the year),~~ we focused our efforts only on non-musth males, as they are more social during inter-musth periods ~~animals (when males are a lot more social;~~ Chiyo et al. 2011, Goldenberg et al. 2014). During musth, males produce distinct musth-rumbles encoding their sexual state (Poole 1987) that are quantitatively different from rumbles produced

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~~throughout the rest of the year~~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 ~~we wanted to test~~ to evaluate the distinctiveness of rumbles across naturally occurring conditions ~~despite natural variability of elephant activities and states,~~ we did not attempt to limit the recordings to a specific behavioural context or social scenario. Therefore, elephants were sampled at random, with rumbles recorded from animals exhibiting a variety of behaviours (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 ~~recorded~~ within the sight~~ing.~~

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).

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, and no excessive background noise). Rumbles were identified manually~~,~~ by selecting an area ~~closely~~ encompassing the ~~whole~~ entire rumble on the spectrogram (Supplemental Methods S1). To keep spectral measurements unbiased and consistent as possible, we only took robust frequency 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% and duration 90% (Charif et al. 2010; Table 1; Supplemental Methods S1). We did not include formant frequencies or fundamental frequency, as these have been shown to correlate to the maturity 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 focused on parameters describing the acoustic cue more broadly.

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

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overall differences ~~among groups (~~ across individuals~~)~~ and is appropriate for unbalanced data. To confirm that observed differences are in fact a result of differences ~~among~~ across individuals and now an artefact of large differences in within-individual variability, we conducted an analysis of multivariate homogeneity ('betadisper'; Anderson 2001) combined with an ANOVA. We then performed a pairwise comparison (RVAideMemoire package (Hervé 2019); using a Wilk's test, and false discovery rate method for p-value adjustment) along with a SIMPER analysis (Clarke 1993) to determine which individual pairs showed strongest differences and which variables contributed most to the observed differences.

Results

The final database included 81 good quality rumbles from five identified, mature males, over a ~~long~~ 15 month time period (an average of 402.8 days between the first and last recording; Table 2). Rumbles were long (mean 90% duration (±SD): 4.19s (± 1.05)) and low frequency (mean center frequency: 28.37 Hz (± 6.87; Fig. 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 ~~among~~ across individuals could not be attributed to differences in within-individual variability. Pairwise comparisons showed that even after the adjustment of p values for multiple comparisons, the differences between acoustic characteristics of calls was significant for a majority of pairs of individuals (Table ~~2~~3). These differences were not centred or clustered around specific individuals (no one individual was significantly different than others; Table 3), but rather reflected a random variation of individual differences.

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 4).

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,

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pointing to true individual differences (differentiating each individual) rather than those resulting from other factors such as sex, ~~maturity~~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. Pairwise comparisons further confirmed the robustness of individual differences in male vocalisations. The overall individual distinctiveness of acoustic cues was not driven by one or two individuals being very different from the rest, but were a result of strong differences between a majority of elephants, reflecting natural variation of vocalisations between individuals.

Previous research explored the distinctiveness of male African elephant rumbles in captivity (Stoeger and Baotic 2016). The authors focused on maturity 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, captive environments can potentially limit the variety of behavioural contexts an animal can experience and influence communication and produced sounds. Finally, 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.

Our study allowed for testing wild animals, in a natural environment and 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 behavioural 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 behaviours. 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~~hormone levels~~ [cite], 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.

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Our recordings were collected from wild and free ranging male elephants. This context presents logistic challenges in recording vocalisations, particularly given the low frequency of rumbles, which overlaps substantially with disturbance such as wind and engine noise. However, we considered data from wild elephants, which determine their own movement and social patterns, to be required to understand communication in male elephants. Much information that can be communicated by animals using vocalisations may be context specific, and the structure may be influenced by factors such as reproductive state, or emotional state. As musth is associated with specific vocalisations, we chose to avoid recording the males during musth, for safety and consistency reasons. However, allowing the possibility for state and behaviour-associated variation enabled for the residual individual variation to be incorporated into our data.

Conclusions

We extend earlier studies of acoustic communication in elephants to investigate the structure 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 ~~are~~ 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 male savannah elephants were considered to be primarily solitary, this is not the case (Chiyo et al. 2011; Goldenberg et.al. 2014). 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 behaviourally 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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Acknowledgements

We thank Amy Morris Drake for beginning the collection of vocal samples under the guidance of HSM. We are grateful to Christin Winter, Jessica Wilmot and Tammy Eggeling from Elephants Alive for many hours of sound recordings. The Private landowners and Wardens of the Associate Private Nature Reserves are thanked for the permission to work on their land.

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