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Vocal stress associated with a translocation of a family herd of African elephants (*Loxodonta africana*) in the Kruger National Park, South Africa

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We used vocal indicators to examine the effect of a translocation of an African elephant family herd within the Kruger National Park. These animals were moved 300 km from their home range, but returned unaided to this range within 23 days. We found that translocation resulted in a change in the mean fundamental frequency of low-frequency elephant vocalizations, known as rumbles. The rumbles increased significantly in pitch compared with pre-translocation levels during the 23 days the animals spent outside their normal home range. Mean fundamental frequency returned close to pre-translocation level by the time the animals had navigated their way back to their previous home range. Raised pitch is known to be an indicator of stress in humans and other animals. The observed acoustic results are consistent with a physiological measure of stress, faecal glucocorticoid metabolite levels, which were monitored from the same animals during the study and have already been reported elsewhere. To our knowledge, this is the first report of prolonged monitoring of vocal stress response in free-ranging animals. Measuring behavioural responses, such as vocalizations, may provide an objective non-invasive method for assessing stress. This could help in determining the effects that particular management actions might have on elephants.

Keywords: infrasound; elephant; *Loxodonta africana*; vocalization; stress

Introduction

The continent-wide population of African elephants has declined dramatically in the last 100 years, from a high estimation of 3–4 million in 1960 to approximately 500,000 today (IUCN 2012), primarily due to them being killed for their ivory (Douglas-Hamilton 2009). Despite this, there are areas where local wildlife managers feel there are too many elephants for the environment to sustain, mostly due to the purported adverse effect of elephants on the woody plant population (see Ahlers et al. 2012). In these areas, managers have used a combination of three techniques to reduce elephant numbers: (1) culling excess elephants, usually by killing the adult members of family groups and capturing and selling the young calves; (2) contraception; and (3) translocating elephants, usually as an entire family group, to areas that can better support them ecologically.

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This study looks at whether elephant vocalizations can be used as a measure of stress in translocated elephants, and is part of a larger project that studied the behaviour of a translocated family group of elephants in the Kruger National Park (KNP), South Africa.

Vocal indicators of stress

Although 'stress' has become an increasingly popular and widely applied term to use, it is still a challenging concept to define, probably because of its appearance and integration into various scientific disciplines such as biomedicine, psychology, ethology and animal welfare (Palme et al. 2005). Vocal indicators of stress have been reasonably well studied in humans (Protopapas and Lieberman 1997; Scherer et al. 2001). Prosodic and other vocal cues can allow the listener to evaluate the emotional state of a speaker (e.g. Scherer et al. 2001; Bänziger and Scherer 2005) and it has been proposed that decoding vocal expressions across different human cultures can serve as a universal mechanism for determining the level of emotion (Scherer et al. 2001). Moreover, recent empirical studies across several non-human species reveal stress-related variation of acoustic features (e.g. Rendall 2003; Bastian and Schmidt 2008; Zimmermann 2010). In domesticated animals, evidence was found that vocalizations can be useful in assessing physiological and psychological well-being and could therefore be utilized to improve management and welfare (Watts and Stookey 2000).

In non-human animals, determining a physiological response to stress can be challenging, as the animal's emotional state is still largely inaccessible. Elevated glucocorticoid levels, or changes in vocal parameters, may be more conservatively considered to indicate a change in emotion, level of excitement or both – whether or not that change is stressful depends on the context. Keeping in mind these caveats, in non-human mammals, various acoustic features vary according to arousal or stress level. Temporal and spectral characteristics were shown to indicate stress levels in baboons (*Papio hamadrayas*, Rendall 2003), red-fronted lemurs (*Eulemur rufifrons*, Fichtel and Hammerschmidt 2002), tree shrews (*Tupaia belangeri*, Schehka et al. 2007) and mouse lemurs (*Microcebus* ssp., Zimmermann 2010). In particular, increased and more variable fundamental frequencies are common acoustic features associated with increased emotional intensity in mammals (Boinski et al. 1999; Soltis et al. 2005, 2011; Coss et al. 2007; Li et al. 2007; Stoeger-Horwath et al. 2007; Stoeger et al. 2011). For example, the roar of infant African elephants (*Loxodonta africana*), which is higher in pitch than most other elephant calls, signifies primarily the caller's arousal state and therefore indicates the arousal-based physiological changes influencing acoustic features of vocalizations (Langbauer 2000; Stoeger et al. 2011). Soltis et al. (2005, 2009) demonstrated that structural variation in rumbles of captive female African elephants represents the individual identity and the emotional state of callers. The elephants produced rumbles with increased and more variable fundamental frequency during high-affect contexts.

Comparatively little work has been carried out on the subject of stress expression in vocalizations of free-ranging wild elephants (but see Poole et al. 1988; Langbauer 2000; Clemins et al. 2005; Wood et al. 2005; King et al. 2010; Soltis et al. 2011). In environments where elephant movement is unrestricted, elephant vocalizations provide insight into their reproduction, resource utilization, predator avoidance, coordinating movement and social interactions (Payne et al. 1986; Poole et al. 1988; McComb et al. 2000; Garstang 2004), all information useful to wildlife managers. Seasonal variability in quantity and quality of resources in the environment highlights the importance of elephant's capability of coordinating movements. Vocal communication further assists to uphold social bonds, cohesion in breeding herds, and in maintaining the population-genetic structure in fission–fusion societies where male elephants do not form permanent associations with breeding herds (Wittemyer and Getz 2007; Poole 2011). King et al. (2010) showed that free-ranging elephants in Kenya produced rumbles with increased and more variable fundamental frequency indicating increased emotional intensity in reaction to various playback sounds (the sound of disturbed African honey bees *Apis melifera scutellata* as well as to white noise). Rumbles produced in response to bees were further distinguished by formant (vocal tract resonance) structure.

The information contained in vocalizations of African elephants could be of interest to managers and researchers alike, and could contribute towards the conservation of the species (Langbauer 2000; McComb et al. 2003; Wood et al. 2005). In assessing the effect of translocation on elephant's behaviour, we analysed recordings of vocalizations as an empirical indicator of stress. In this paper, we investigated the stress-related response of a breeding herd of elephants to translocation by means of evaluating vocalizations.

Methods

Study area

This study was conducted in the KNP, South Africa (Figure 1) which covers an area of approximately 19,000 km^2. Data during the pre- and post-translocation phases were collected in the southern KNP around the Lower Sabie rest camp. During the translocation phase, data were collected in the northern KNP, north of the Letaba rest camp.

Study population and data collection

This study was part of a larger study that was designed as a controlled experiment to assist in the management of elephants (*L. africana*) and was conducted entirely within KNP over a period of 3.5 years (March 2002 to September 2005). The first breeding herd of elephants in the southern region of KNP spotted from a helicopter after take-off in a south-easterly direction towards Lower-Sabie from Skukuza was selected as our focal group.

The matriarch was fitted with a VHF radio collar and later replaced in August 2002 with a GPS satellite collar (both collars manufactured by African Wildlife Tracking, Pretoria, Gauteng, South Africa). We followed the breeding herds on foot and field crews always avoided being positioned upwind of the herd in an attempt to minimize disturbance and being detected. During each session, record was kept of the estimated distance to visible elephants, the gain settings of the recorder, the date, time and GPS coordinates, as well as of audible vocalizations from elephants or other animals. Typical recording distances while on foot ranged from 50 to 120 m and the few occurrences when family herds were sighted close to roads, recordings from the vehicle were made at distances ranging from 20 to 100 m. The period of vocal sampling for pre-, during and post-translocation was from March 2003 to August 2005. During this period, a total of 47 h of recordings over 61 appropriate condition days were made. The length of the recording sessions varied, with an average of 3 min per session. Most of the recordings were made between 06:00 and 11:00 h and include brief periods during the capture process and the time immediately after release. Due to the vegetation and the distance to elephants, it was not possible to accurately identify the calling individual, so the vocalizations of the group as a whole were recorded. We have general behavioural notes for the group during the overall period during which the recordings were taken, but as most elephant vocalizations were inaudible to humans, it was usually impossible to determine what the call elephant was doing at the exact time of the vocalization. Thus, we made no attempt to correlate recordings with specific behaviours.

The focal group was composed of 11 animals on 7 October 2004 when they were captured in the Lower Sabie section. Immediately after capture, this group was loaded into a SANparks Elephant family group mass transport unit. The elephants were transported for approximately 300 km and offloaded north of the Letaba Rest Camp after 4 h of travel (Figure 1). The age of the captured animals was categorized according to shoulder heights measured on the day of capture (Shrader et al. 2006). The family herd consisted of three adult females (≥ 28 years), five sub-adult females (8–10 years), one juvenile female (2–3 years) and two male calves (1–2 years). They were immobilized with a combination of M99 and Azaperone (at a dosage of 3–12 mg depending on the size and age of the

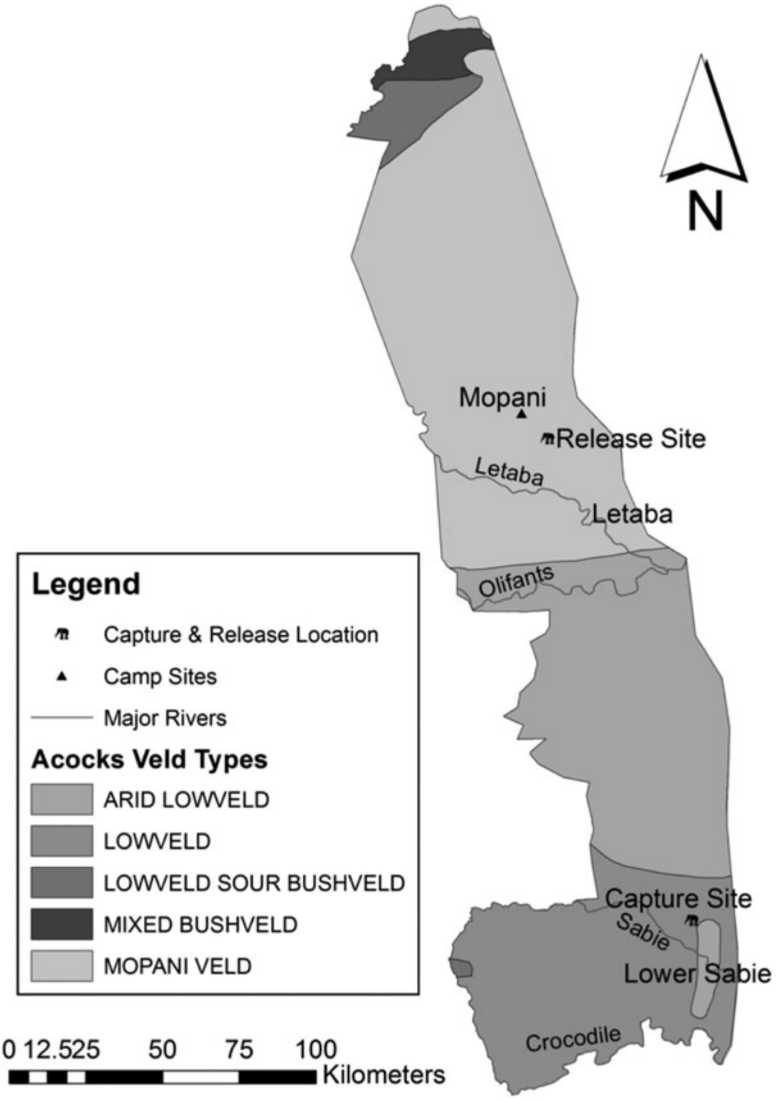

Figure 1. Study area with capture and release site.

individual). The antidote (M5050 and Naltrexone, at dosages of 12–36 mg of M5050 and 25–100 mg of Naltrexone according to the age of the elephant) was administered intravenously as soon as the individual was loaded into the transport crate. Capture drugs were Etorphine (M99, Novartis, Kempton Park, 1619, South Africa), Diprenorphine (M5050, Novartis, Kempton Park, 1619, South Africa) and Naltrexone (Naltrexone, Kyron Laboratories, Benrose, 2011, South Africa).

The elephants then navigated their way back and re-entered their pre-translocation home range 23 days later. The post-translocation monitoring phase (30 October 2004 to 31 August 2005) was defined as starting the day the experimental group re-entered the pre-translocation home range (i.e. was south of the northern-most sighting of the pre-translocation phase).

Equipment

For our acoustic recordings, we used a Sennheiser MKH 20-P48 condenser microphone, with a manufacturer-specified frequency response of 12 Hz to 20 kHz (at the 3 dB downpoint). We covered the microphone with a Rycote windshield (open cell foam with a fur cover) in order to reduce wind noise. The microphone was connected to a Marantz PMD670 solid-state recorder, and recordings were saved as ".wav" files. The nominal frequency response of this recorder is 20 Hz to 20 kHz, but bench tests confirmed that the response was flat down to 5 Hz. We recorded at a sample rate of 16 kHz, so the overall frequency response of the system was 12 Hz to 8 kHz, which encompasses the known range of elephant calls, from infrasonic calls to trumpets (12 Hz to 2 kHz: Berg 1986; Langbauer 2000). A handheld Garmin III was used for the recording of GPS coordinates.

We recorded at a sample size of 16 bits which corresponds to a dynamic range of 96 dB SPL. The signal from the microphone was split into the right and left channels of the recorder, and the gain of the channels was adjusted to a difference of 20 dB, to improve the dynamic range of the system to 116 dB SPL.

Selection of analysis parameters

The overall amplitude, harmonic structure, shimmer and jitter of a vocalization, along with the pitch and variability of its fundamental frequency, are all potential indicators of arousal level in mammals. However, the measurement of many of these parameters can be unreliable even in laboratory settings (Heman-Ackah and Batory 2003). The habitat type and density of the vegetation can also affect sound propagation and the harmonic structure of recorded animal vocalizations (Ey et al. 2009). Attenuation and other acoustic phenomena can thus affect the structure of detected elephant vocalizations, in particular the higher frequency components. Therefore, the fundamental frequency and the second harmonic are the most reliable acoustic features to measure (yet, fundamental frequency in particular is also sometimes masked by environmental noise). The fundamental frequency is also relatively easier to measure in a noisy environment compared with other parameters, such as jitter (Figure 2). We thus selected the fundamental frequency of the elephant vocalization as the most robust parameter to measure under field conditions.

Analysis protocol

The recordings were analysed using the Raven 1.3 software, developed by the Cornell Bioacoustics Research Program. We played back each file at 10 times the recorded speed,

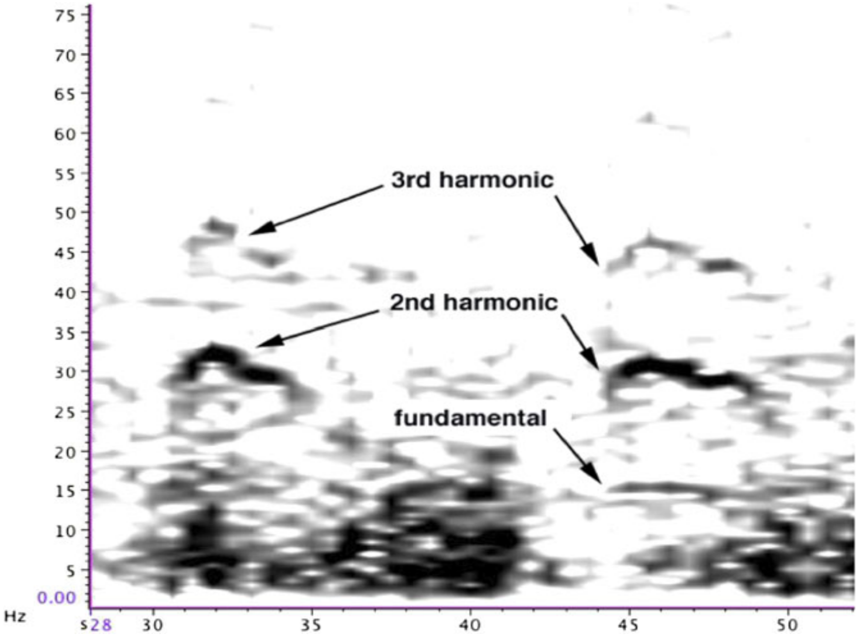

Figure 2. Field recording of two elephant vocalizations. Both vocalizations have fundamental frequencies of 15 Hz at the start of the call. While the fundamental frequency of the first vocalization is hidden in noise, it can be inferred from the difference in frequency (15 Hz) between the second and third harmonics of the call. While there was usually enough information to measure fundamental frequency, noisy field conditions made other measurements, such as jitter, unreliable.

and identified elephant vocalizations by ear and by examination of a spectrogram of the entire file. Spectrograms used for measurement were calculated using fast Fourier transformation (FFT length 2048 samples), a Hamming window and a 50% overlap, resulting in a frequency resolution of 0.781 Hz. We measured 306 calls pre-translocation (March 2003 to October 2004), 68 calls while the elephants were in the translocated area (23 days during October 2004) and 421 calls post-translocation (October 2004 to August 2005). Statistical analysis was carried out using SPSS 20.0. We first conducted a Kruskal–Wallis *H*-test across all conditions, to see whether there was a significant variation in the data. We then applied the Mann–Whitney *U*-test to compare the fundamental frequencies in each condition (pre-translocation, translocation and post-translocation) against the others.

To control for observer bias, the recording files were given a code number and the order randomized for analysis, so that the person doing the analysis was blind as to whether any given recording was made before, during or after translocation.

Many low-frequency elephant vocalizations are frequency modulated, with their spectrogram resembling an upside-down U shape. For this reason, to insure a consistent measure, we measured the fundamental frequency averaged over the initial second of the call.

Determination of faecal glucocorticoid metabolite levels

Faecal samples were also collected for determining respective faecal glucocorticoid metabolite (FGM) levels during the study period (Viljoen, Ganswindt, Palme, et al. 2008;

Viljoen, Ganswindt, du Toit, et al. 2008). Due to wind conditions and safety concerns, acoustic recordings were not always taken when faecal samples of the herd were collected. Hormone values were determined according to the procedure described by Viljoen, Ganswindt, Palme, et al. (2008). FGM levels of samples collected during the translocation phase were significantly higher than FGM concentrations of samples collected during the pre- and post-translocation phases (Figure 3, Viljoen, Ganswindt, du Toit, et al. 2008).

Results and discussion

There was a significant difference in the variation of the data over all conditions (Kruskal–Wallis *H*-test). The distribution of the fundamental frequency of rumbles recorded during translocation was significantly different from both pre-translocation ($p < 0.001$, Mann–Whitney *U*-test) and post-translocation ($p < 0.001$, Mann–Whitney *U*-test) samples during the 23 days the animals spent outside their normal home range, with the mean frequency of rumbles during translocation being higher than those in the other two conditions (Table 1, Figures 3 and 4).

The mean fundamental frequency dropped after the elephants returned to their home range, but was still significantly higher than pre-translocation levels. This may be due to either residual stress response of the translocation or excitement at being back to the pre-translocation range.

Vocalizations can be affected by many things – immediate behavioural events (e.g. interruption of suckling), group composition and so on. Any bias due to short-term behavioural effects is more likely to occur with very short sampling periods – with the long sampling periods, both in the experimental condition (translocation) and in the

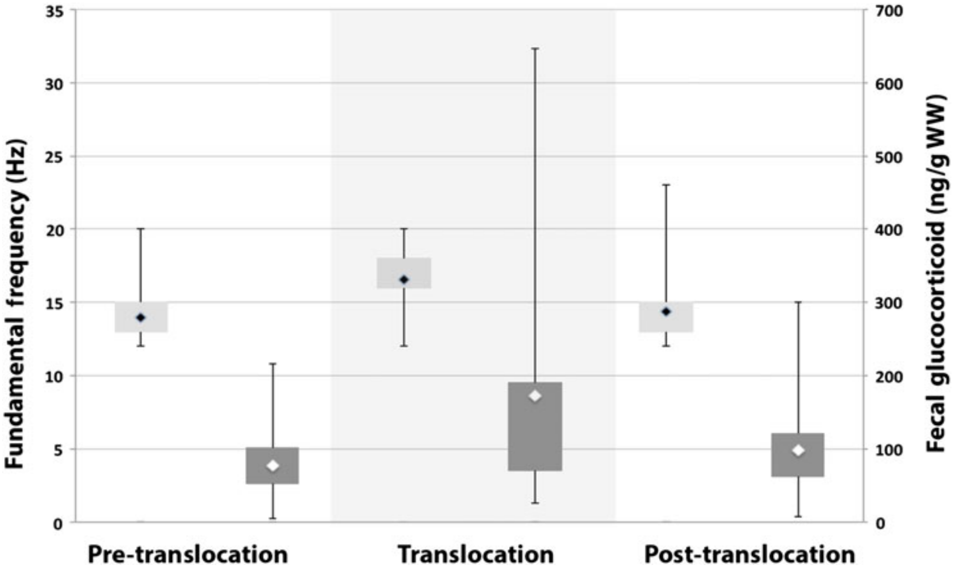

Figure 3. Box plot of fundamental frequencies (light grey) and FGM levels (dark grey) in the pre-translocation, translocation and post-translocation phases of the study. The boxes extend from the first to the third quartiles, the diamonds are the mean values and the whiskers extend from the minimum to maximum values. All pairwise comparisons are significant at the 0.001 level, except the pre-translocation to post-translocation comparison of glucocorticoid levels, which is not significant.

Table 1. The mean fundamental frequency and the variance of the rumbles recorded during the translocation, with the results of statistical tests.

			Fundamental frequency	
Groups	Count	Sum	Mean (Hz)	Variance (Hz)
Pre-translocation	306	967	14.2	1.13
Translocation	68	1124	16.5	3.66
Post-translocation	421	1038	15.3	3.36

Statistical tests

Test	Null hypothesis	Groups compared	Probability (p)
Kruskal–Wallis *H*-test (asymptotic differences)	The distribution of fundamental frequencies is the same across all groups	All	0.000
Mann–Whitney *U*-test	The distribution of fundamental frequencies is the same in both groups	Pre-translocation to translocation	0.000
		Translocation to post-translocation	0.000
		Pre-translocation to post-translocation	0.001

Note: All null hypotheses are rejected at the $p < 0.05$ level.

pre- and post-translocation situations, the short-term behavioural events that occur in daily life should have tended to occur fairly equally, and the same core group of 11 animals was almost always present during recordings.

These results are consistent with the physiological changes found, in terms of elevated FGM levels, previously reported for the same translocation event (Viljoen, Ganswindt, du Toit, et al. 2008). FGM levels returned to pre-translocation values by the time the translocated animals returned to their previous home range. The fact that FGM levels peaked during and immediately after translocation in the experimental group, whereas no corresponding spike was seen in the control groups indicate that factors excluding capture and translocation can be barred as causal stimuli for the observed FGM response (Viljoen, Ganswindt, du Toit, et al. 2008).

Stress as a physiological mechanism is not innately harmful (Moberg 2000), but extended periods of high concentrations of glucocorticoids, as a result of prolonged periods of subjected stress, might compromise fitness (Munck et al. 1984) as well as reproductive success (Liptrap 1993) of an individual, and can also permanently alter behaviour.

As mentioned previously, elevated cortisol levels or changes in vocalizations do not, in and of themselves, prove that the animals are stressed. However, given the larger context – a group of highly social animals being drugged and abruptly moved from familiar surroundings to an unfamiliar location – the most parsimonious interpretation of our results is that both the increase in faecal glucocorticoid metabolites and the increase in the fundamental frequency of vocalizations indicate a stress response by the translocated

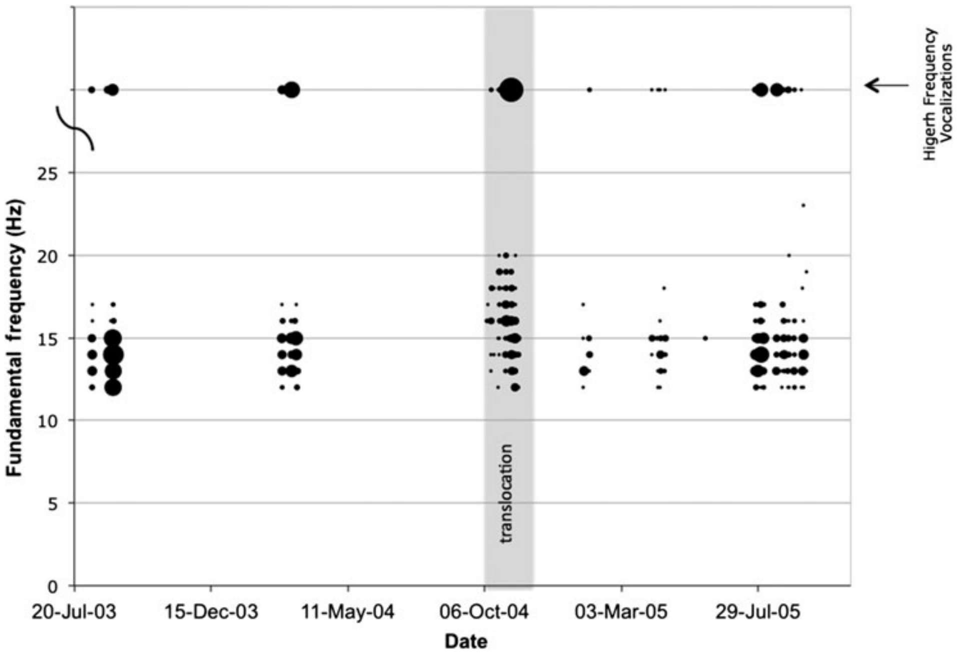

Figure 4. The fundamental frequencies of the elephant rumbles recorded during the translocation of the family herd of African elephants in the KNP, South Africa. The area of each point is proportional to the number of calls at that frequency on a given day. Calls with fundamental frequencies above 30 Hz were lumped into a single category ('higher frequency calls') and not included in the analysis of low-frequency vocalizations.

elephants. Other explanations cannot be discounted, and would be fertile ground for future research. For example, the elephants may have been calling more loudly when translocated, in an effort to find local conspecifics, with consequent increases in subglottal pressure which could also have resulted in increases in pitch (although anecdotal evidence suggests that elephants know when they are in unsafe areas; e.g. crop raiding elephants are usually silent – Ferrel Osborn, personal communication), and elephants are known to move faster when moving through unsafe areas (Douglas-Hamilton et al. 2005). It might further be possible that we recorded more calf-vocalizations after the translocation, which would result in an overall increase in the detected fundamental frequency. Stressed females might have been focusing on moving away from the unknown area (and spend less time browsing and resting) and therefore are not as patient as usual during suckling, which could have led to an increase in calf-protest calls. Alternatively, the elephants might have been using slightly different call types with increased fundamental frequency. Apart from all these theoretical possibilities, we document the simple fact that the vocal behaviour of the group changed significantly during the translocation period, and the definite reason for this warrants further research.

At the very least, in a transformed and fragmented South African landscape where elephant movements are restricted, remote monitoring of vocalizations can provide records of continuous tracks of the emotional changes. Utilizing this non-invasive technique of recording vocalizations can aid in the early detection of stress and appropriate action can be taken timely, contributing towards improving the welfare of the animals.

Elephants use the same general group of vocalization to express different things. For example, rumbles are used to keep vocal contact with other elephants and to coordinate movements (Berg 1983; Poole et al. 1988). Family herds of elephants have demonstrated defensive behaviour by aggregating in denser groups, freezing and/or scanning the air in response to seismic playbacks of low-frequency alarm calls and low-frequency conspecific calls (Langbauer et al. 1991; O'Connell-Rodwell et al. 2006). The presence of lions brought about a trumpeting response (Langbauer 2000) and elephants produced warning vocalizations and were joined in their flight by other elephants set off by the sound of troubled African honeybees (King et al. 2007, 2010). Although only a few studies have been carried out to link elephant vocalizations with particular emotional states such as fear or a response to the presence of predators, it seems clear that specific types of elephant vocalizations serve as acoustic deterrents in certain situations.

From the above discussion, it is clear that, in theory, African elephant acoustic communication and behavioural responses can serve as a departure point in devising techniques to solve problems and as a management tool to measure the outcomes of human interventions. The practical problem with many aspects of elephant vocal communication is that deciphering the meaning of a particular call, especially when the vocalization is inaudible to humans, is often time-consuming and uncertain. In contrast, measuring a physical parameter (the fundamental frequency) across all animals in a group is relatively unambiguous and uncomplicated. It is thus a much easier technique to implement for a conservation biologist, as it does not require making fine differentiations between calls and specific meanings.

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Notes

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