

Wild African elephants (*Loxodonta africana*) discriminate between familiar and unfamiliar conspecific seismic alarm calls

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The ability to discriminate between call types and callers as well as more subtle information about the importance of a call has been documented in a range of species. This type of discrimination is also important in the vibrotactile environment for species that communicate via vibrations. It has recently been shown that African elephants (*Loxodonta africana*) can detect seismic cues, but it is not known whether they discriminate seismic information from noise. In a series of experiments, familiar and unfamiliar alarm calls were transmitted seismically to wild African elephant family groups. Elephants respond significantly to the alarm calls of familiar herds ($p=0.004$) but not to the unfamiliar calls and two different controls, thus demonstrating the ability of elephants to discriminate subtle differences between seismic calls given in the same context. If elephants use the seismic environment to detect and discriminate between conspecific calls, based on the familiarity of the caller or some other physical property, they may be using the ground as a very sophisticated sounding board. © 2007 Acoustical Society of America. [DOI: 10.1121/1.2747161]

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I. INTRODUCTION

Animals assess their acoustic environment based on frequency, amplitude and temporal properties of sounds. These parameters have a different level of importance for different species, depending on the limitations of the ear, the importance of the acoustic environment to survival, the social organization of the species and the context of the sound. A variety of species are able to use the acoustic properties of their calls to detect differences within conspecific vocalizations that distinguish call types as illustrated in Barbary macaques (Fischer, 1998) and elephants (Langbauer *et al.*, 1991; Poole, 1999), as well as familiar versus unfamiliar callers in the spear-nosed bat (Boughman and Wilkinson, 1998), sheep (Ligout *et al.*, 2004), lions (McComb *et al.*, 1993), bottlenose dolphins (Sayigh *et al.*, 1999) and elephants (McComb *et al.*, 2001), or even body size (Cheney and Seyfarth, 1991).

Research on suricate vocalizations has also shown that information about the level of danger presented by the prox-

imity of a predator can also be discerned, based on the severity of the call (Manser, 2001). Information about the type of predator is even encoded in vervet monkey vocalizations (Seyfarth *et al.*, 1980). In addition, subtle frequency differences that distinguish the individual caller have been found in marmots (Blumstein *et al.*, 2004). The ability to detect subtle changes in frequency has been demonstrated in such species as the squirrel monkey (Weinicke *et al.*, 2001), where this species is able to detect frequency differences as small as 20–40 Hz in the range of 4–8 kHz, and an especially keen discrimination ability above 10 kHz, followed by the bottlenose dolphin (Thompson and Herman, 1975) and the lesser spear-nosed bat (Esser and Keifer, 1996). But in the lower frequency range, in the hundreds of hertz, the squirrel monkey has poor frequency discrimination ability. Frogs that vocalize in the range of 350–400 Hz assess the size of the caller based on frequency (Bee *et al.*, 2000), where frequency discrimination is on the order of 12–14%; some frogs discriminating as little as a 5.7% difference (Wagner, 1992).

Frequency sensitive touch receptors have been described in humans in the ranges of 5–15, 10–65 and 65–400 Hz (Makous *et al.*, 1995). Such vibrotactile sensory structures have been found in primates and other large mammals, in-

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TABLE I. Elephant group sizes and composition for each trial (where subadults are three quarters the size of a full size adult at the shoulder and back, half being half the size of an adult, and one quarter is a range between greater than one year old to less than half the size of an adult. A baby fits under the stomach of a full size elephant and ranges up to one year.

Adult	Sub-adult	Half	Quarter	Baby	Total No.	Playback
						Unfamiliar alarm
7	5	7	5	1	25	1
8	4	4	2	0	18	2
7	4	8	2	2	23	3
4	4	5	6	2	21	4
9	0	8	3	2	22	5
3	2	4	2	1	12	6
3	1	3	3	0	10	7
8	2	2	5	4	21	Control 1
5	4	4	2	1	16	2
4	2	4	3	0	13	3
6	1	5	4	3	19	4
3	4	4	4	0	15	5
8	4	8	3	2	25	6
4	4	6	3	1	18	7
7	5	4	2	2	20	8
11	8	9	2	5	35	9
1	1	4	3	1	10	Familiar alarm 1
5	4	3	6	2	20	2
7	3	4	5	3	22	3
9	5	6	4	3	27	4
3	1	3	1	2	10	5
5	2	3	1	1	12	6
8	2	7	4	1	22	7
6	3	6	3	2	20	8

cluding elephants (Rasmussen and Munger, 1996). The ability of these touch receptors to discriminate very small changes in frequency (2 Hz) has been demonstrated in humans and other primates (Recanzone *et al.*, 1992). For those species that communicate seismically (see O'Connell-Rodwell *et al.*, 2000a for review), the ability to distinguish call type and individual callers has been demonstrated in the kangaroo rat (Randall, 2001).

We have previously demonstrated that elephant vocalizations propagate in the ground (O'Connell-Rodwell *et al.*, 2000a; Gunther *et al.*, 2004) and that elephants are capable of detecting seismic cues (O'Connell-Rodwell *et al.*, 2006), but it has not yet been established whether they have the ability to discriminate between various seismic signals. In this study, we test the ability of African elephant family groups to discriminate subtle differences between familiar and unfamiliar callers within the same call type.

II. METHODS

A. Experimental design

A series of seismic playback experiments were conducted by transmitting previously recorded acoustic vocalizations of known context into the ground to elephant family groups at a remote waterhole in Etosha National Park, Namibia between the hours of 4:00 P.M. and 2:00 A.M. Experiments were videotaped, and night vision used for experi-

ments occurring after sunset. Total numbers of individuals were counted in real time, or from the videotape and a herd composition breakdown compiled for each group (Table I) to confirm that groups were not being treated more than once within any one playback stimulus. Two different seismic stimuli were delivered to determine if elephants can distinguish subtle differences between meaningful biological signals made in the same context (alarm) but by familiar and unfamiliar callers. As controls, we played back a generated warble tone or no stimulus at all. Each trial began 2 min after the arrival of the elephants, to allow them to drink and settle down. Following this, 5 min of base line observations were made. Three minutes of playback stimuli was delivered, where 15 s of signals were played seismically at the beginning of each minute. A subsequent 5 min period was used to monitor any changes in behavior.

The playback stimuli were as follows. **Familiar alarm calls** consisted of three alarm calls emitted by the individuals of one family group while lions were hunting near them at this study site in Etosha National Park. These calls have been shown to elicit a vigilant response (O'Connell-Rodwell *et al.*, 2006). **Unfamiliar alarm calls** consisted of three alarm calls emitted by two different family groups in Amboseli National Park, Kenya while lions were hunting near them. Since these calls are rarely recorded by researchers, the familiar and unfamiliar calls used were the only ones available

for this playback study. All alarm signals (familiar and unfamiliar) were filtered with a Butterworth bandpass filter (low cut at 10 Hz and high cut between 50 and 60 Hz) such that only the fundamental and second harmonic were still present in the calls.

Controls consisted of either no seismic stimulus at all, or a series of three simulated warble tones. The warble tones were designed with frequency content and duration similar to an elephant rumble. Its base frequency of 30 Hz was modulated by 3 Hz at a rate of 1 Hz for 3 s, with 2 s of silence between the three signals.

All signals were played back seismically through two Guitammer Butticker LFE shakers (frequency range 5–200 Hz with 9 Hz resonant frequency), buried in the ground 20 m from the water hole. A TASCAM digital two-channel recorder provided the signal source for the transmitters. A 1000 W amplifier was used to raise the amplitude of the signals to a level resembling the power of an elephant vocalization at a distance of 20 m. See Figs. 1(a)–1(c) for spectrograms of playback signals.

Playback signals were recorded during the trials on a Geometrics Geode 24 channel seismic recorder through two, 4.5 Hz Mark Products vertical geophones 10 m from the source, one placed 10 m from the shaker toward the water hole and the other 10 m from the shaker in the opposite direction to measure the signal strength at the noisy waterhole versus a more quiet area away from the waterhole. These sensors were used to monitor the integrity of the playback signal. A Neumann KM131 low frequency microphone was used to record the trials in the acoustic environment, to record vocal responses to the different stimuli, as well as to ensure that no presentation signal coupled with the air. This microphone was placed directly above the geophone that was placed in the direction away from the water hole.

The order of trial type (familiar alarm, unfamiliar alarm, control) was randomized. Each trial was presented during separate waterhole visits by single family groups. Family groups were distinguished by herd size and composition and the data presented are representative of distinct groups within each playback treatment type.

Elephant behaviors were monitored for adult members of each of the family group tested. Individual behaviors were scored, including freezing/leaning, scanning, lifting one foot, smelling, head shakes and vocalizing, each as a measure of vigilance, or heightened wariness in the context of a potentially threatening situation. Herd spacing was scored separately (similar to O'Connell-Rodwell *et al.*, 2006; McComb *et al.*, 2001; Poole, 1999; Langbauer *et al.*, 1991), where individuals were noted as being within a body length, at one body length, or greater than one body length apart. One experienced elephant behavior observer (naïve to the trial types and timing of the trials) recorded individual behaviors while another documented herd spacing. The occurrence of the vigilant behaviors listed above was noted every 15 s during the trials, then summed (equal weighting) for the pre and postplayback periods, then divided by the duration of that period and the number of elephants present to give us a measure of vigilant behavior. Herd spacing was also noted every 15 s during trials and then averaged for the pre and postplay-

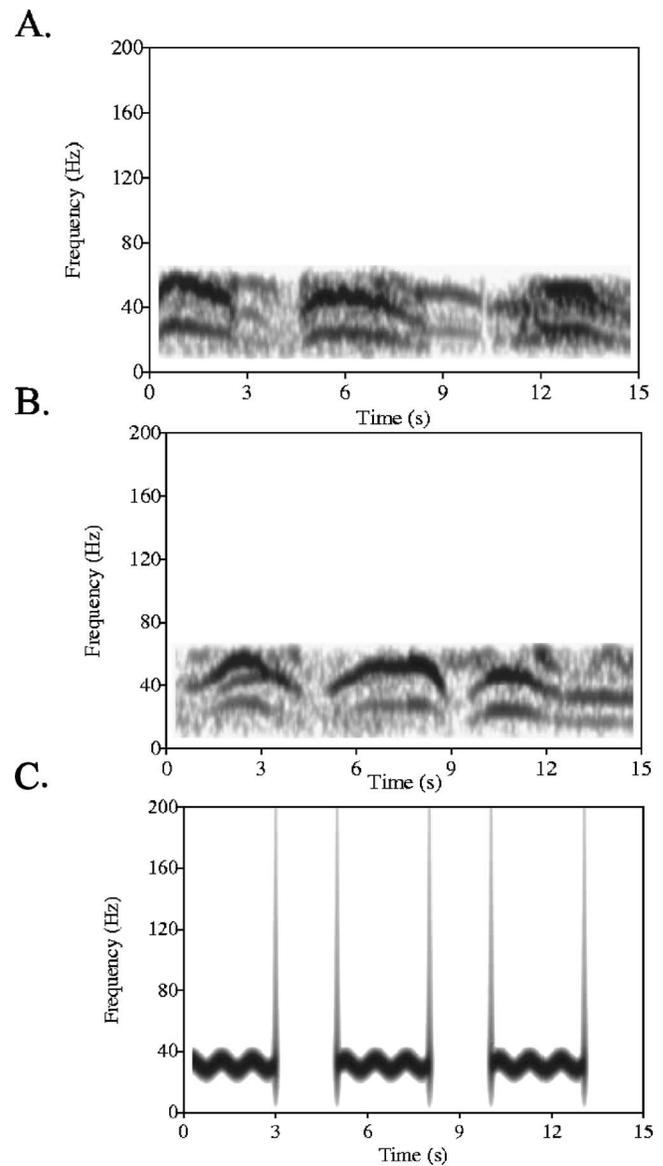


FIG. 1. Spectrograms of the playbacks that were used. A: Unfamiliar Alarm Call Rumbles B: Familiar Alarm Call Rumbles C: Warble tones. Each spectrogram was band pass filtered to remove higher frequencies that tend to couple with the air when played seismically as well as very low frequency noise (filter used was a 20th order Butterworth band pass with low cut at 10 Hz and high cut between 50 and 60 Hz). Spectrograms generated in Praat software V4.1 (Institute of Phonetic Sciences, University of Amsterdam) with the following settings: sampling rate 16 000 Hz, window length 0.3 s, max freq 200 Hz, Gaussian window (equivalent to an FFT size of 4800 and resultant frequency resolution of 3.33 Hz).

back periods. All playback sessions were video recorded by a third observer who also documented herd size and composition. All observations were made from a tower and two platforms, 100 m from the water hole.

B. Signal calibration and acoustic coupling

We used a matched filter technique to confirm that there was no evidence of the seismic signal in the acoustic environment (acoustic coupling) during our seismic playback trials. We modified the following matched filter from <http://cnx.rice.edu/content/m10757/latest/>

$$\text{Matched Filter} = \frac{|\langle f, g_i \rangle|}{\|g_i\|}$$

to

$$\text{Matched Filter} = \frac{|\langle f, g_i \rangle|}{\|f\| \|g_i\|}$$

by adding the norm of f so that the matched filter would vary between 0 and 1; f is the signal while g_i is the recording at time i . The numerator is the absolute value of the inner products of f and g_i . The denominator in the modified equation is the norm of f multiplied by the norm of g_i . As one moves the matched filter along the recording the output varies between 0 and 1, with 1 being a perfect match. To determine a threshold above which acoustic coupling would occur, we calculated the relationship between the matched filter output and a biological criterion. For this study, we calculated the relationship between the matched filter output and the signal to noise ratio (SNR) in order to throw out any trials with a matched filter equivalent to -2 dB SNR in our microphone recordings during the playbacks. We chose this as our cutoff point because, to date, the most comparable hearing pattern to that of the elephant, in terms of frequency range where data are available to serve as a reference point, is that of the human which has a signal detection threshold at -2 dB SNR (Zwicker and Feldtkeller, 1999).

Because the matched filter output varies depending on the noise in which the signal is embedded, we felt it was most appropriate to utilize noise from each of the trials. Therefore a 15 s segment of noise was extracted from the microphone recording for each trial. The playback signal was then added to this noise so as to achieve a SNR of -2 dB for each trial. We focused on the second harmonic of the alarm call playback as the second harmonics were of a larger amplitude and higher frequency and therefore more likely to couple with the air. For the control (warble) playbacks there were no harmonics, and so we focused on the fundamental frequency.

SNR was measured before adding the signal to the noise by calculating the spectrum of the highest amplitude 1 s segment of the signal and the spectrum of the same 1 s of noise in the microphone recording. We then integrated the energy across the signal width of the rumble and integrated the noise energy across the estimated critical bandwidth for elephants at the center frequency of the signal. To estimate critical bandwidth, we followed Günther *et al.*, 2004 and Greenwood, 1961. The bandwidth for each call is different due to the difference in frequencies of each call. We used the following estimates in Hz: (frequency: critical bandwidth) familiar alarm: 52:19, unfamiliar alarm: 49:18, control warble tone: 33:15.

Once we had inserted the signal into the microphone noise of each trial at a -2 dB SNR, we ran the matched filter on these files. The output of the matched filter for each trial was used as the cutoff point for our seismic playback trials (i.e., the matched filter equivalent of -2 dB SNR). We then ran the matched filter on the microphone recording of each seismic playback trial. Any trial that had a matched filter

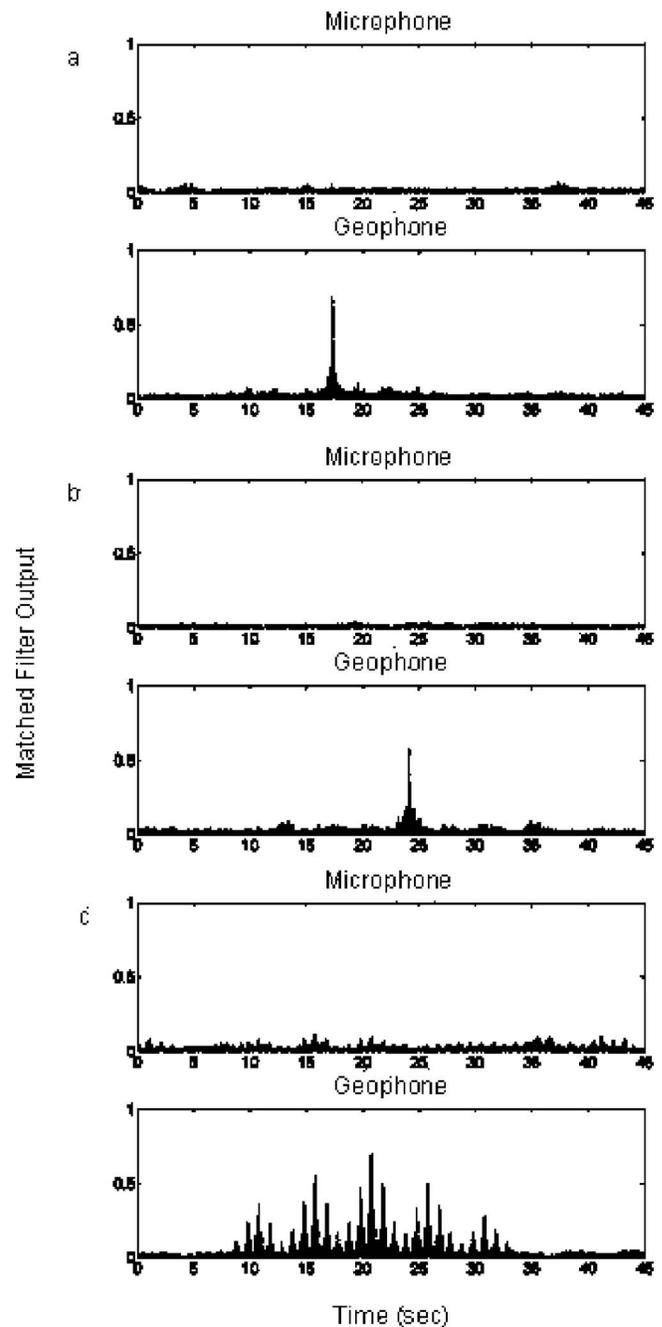


FIG. 2. Typical examples of the matched filter output in the microphone recording (top graph of each pair) and the geophone recordings (bottom graph of each pair). The playback peak is clearly visible in the geophone graph, but not in the microphone graph. (a) Result of a familiar alarm call seismic playback. Playback occurred at ~ 17 s. (b) Result of an unfamiliar alarm call seismic playback. Playback occurred at ~ 24 s. (c) Result of warble seismic playback. Playback occurred at ~ 20 s. Multiple peaks are evident because the same signal was repeated three times and because there is a repetitive pattern within each signal. The highest peak though occurs at the playback time.

output greater than the -2 dB SNR equivalent that was within 100 ms of our playbacks was not included in our further analyses. See Figs. 2(a)–2(c) for matched filter output in the microphone/geophone pairs for each playback type showing the signal present in the ground but not in the air at a level greater than -2 dB SNR.

C. Statistical analysis

To test if our various seismic stimuli had an effect on vigilant behavior and herd spacing, we ran a series of repeated measures multivariate analysis of variance (MANOVA) tests. This allowed us to test vigilant behavior and herd spacing at the same time, while controlling for any correlation between these two dependent variables. All statistical tests were conducted in MINTAB (v 13) (MINITAB Inc., State College, PA).

After excluding trials that had evidence of acoustic coupling, we had the following sample sizes of individual family groups treated for each of our three stimulus types: Unfamiliar Alarm Calls: $N=7$, Control: $N=9$, Familiar Alarm Calls: $N=8$. As a test to ensure that combining our control stimuli (warble and no stimulus) was appropriate, we ran two sample t tests comparing vigilant behavior or herd spacing in the postplayback periods for these two control stimuli. Since we found no significant difference we felt it justified to combine these into a single control stimulus in order to simplify our experimental design and increase our sample size [Warble $N=4$, No stimulus $N=5$, Spacing ($t=1.56$, $P=0.162$, $DF=7$), Behavior ($t=-0.78$, $P=0.459$, $DF=7$)]. Our original MANOVA tested if there was a difference in vigilant behavior and herd spacing before versus after our seismic playbacks. The Wilks' lambda criterion found a significant difference ($F_{2,20}=18.649$, $P<0.001$). Given this result we tested each stimulus type separately using a repeated measures MANOVA to determine which stimulus type resulted in significant differences before and after the seismic playback.

D. Call type differences

In order to assess whether there were any quantitative differences between the playback signals used in these experiments, a script was written for MATLAB (Mathworks Inc., Natick, MA) to extract the rumble frequency contour of all six alarm calls used in the seismic playbacks as well as the generated warble noise tone. This script was similar to the one used by McCowan (1995) and Wood *et al.* (2005) in that it extracted the rumble frequency at 40 evenly spaced points along the duration of each rumble. This was done by calculating the spectrum at each of these 40 points and recording the peak frequency. The sampling rate of the signals was 1000 Hz while the fast Fourier transform (FFT) length was set at 2048 making the frequency resolution 0.5 Hz.

Since the second harmonic was of a higher amplitude than the fundamental in our playbacks, we concentrated on it by filtering the calls and sampling the second harmonic at 40

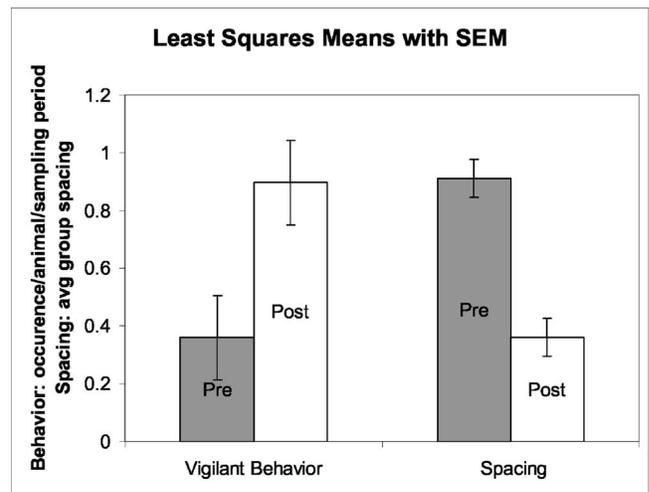


FIG. 3. Least squares means and standard error of the means from the MANOVA test comparing pre and postperiod vigilant behavior and spacing for the familiar alarm call playbacks. Behavior is measured as number of occurrences per animal per sampling period. Spacing is measured in body lengths.

points. Wood *et al.* (2005) found ten acoustic parameters that differed significantly between the elephant rumble types they analyzed. We calculated these same ten parameters from our rumble contours to see if there were noticeable differences between our playback calls. We did not, however, run any statistical tests on these parameters, as the sample size was too small.

III. RESULTS

We found no significant change in vigilant behavior and herd spacing when comparing the pre and postseismic playback periods for the control, or unfamiliar alarm calls using the Wilk's lambda criterion for the MANOVA; Control: $F_{2,7}=4.328$, $P=0.060$, Unfamiliar Alarm Call: $F_{2,5}=3.572$, $P=0.109$. We did, however, find a significant change in vigilant behavior and herd spacing when comparing the pre and postseismic playback periods for the familiar alarm calls (MANOVA: $F_{2,6}=15.720$, $P=0.004$). Vigilant behavior increased after the playbacks while spacing decreased (Fig. 3). See Table II for the least squares means and standard error of the means.

A. Call type differences

Figure 4 depicts the frequency contours extracted from the six alarm call and warble tone playbacks, while Table III

TABLE II. Least squares means and the standard errors of the means from the MANOVA tests on vigilant behavior and spacing.

Stimulus	Period	LSM behavior	SEM behavior	LSM spacing	SEM spacing
Control	Pre	0.36	0.13	0.91	0.09
Control	Post	0.69	0.13	0.53	0.09
Unfamiliar alarm	Pre	0.45	0.08	1.00	0.11
Unfamiliar alarm	Post	0.54	0.08	0.55	0.11
Familiar alarm	Pre	0.36	0.15	0.91	0.07
Familiar alarm	Post	0.90	0.15	0.36	0.07

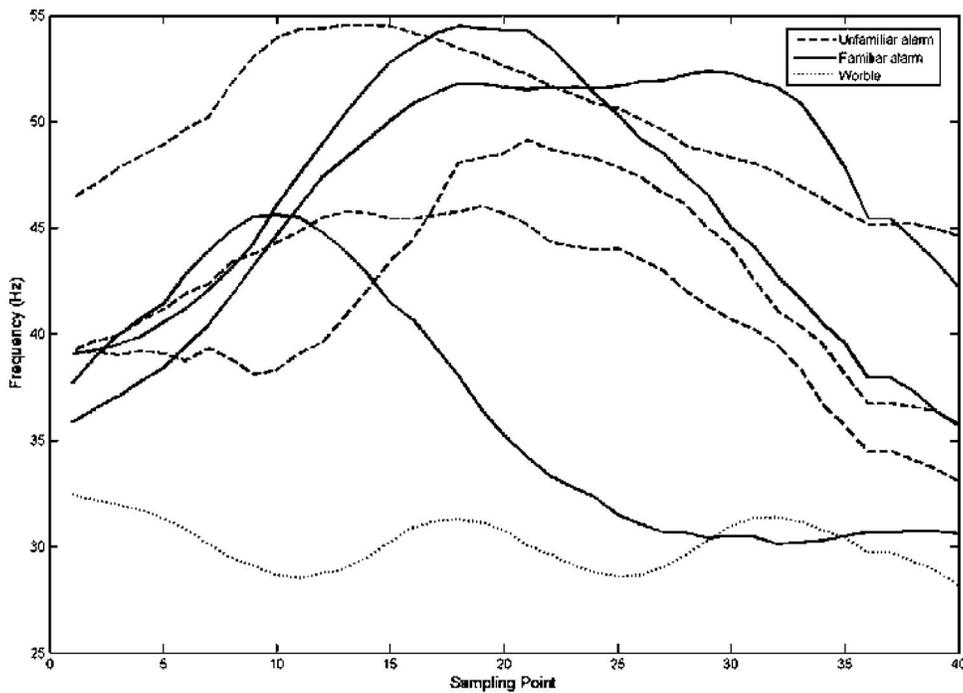


FIG. 4. Graphic of rumble contour differences between the unfamiliar alarm call rumbles recorded in Amboseli (dashed line), the familiar alarm call rumbles recorded in Etosha (solid line), and the generated warble tone (dotted line). All contours depict the second harmonic, other than for the warble tone, which is the fundamental.

lists the ten acoustic parameters extracted from these frequency contours. The warble tone is easily differentiated in the figure and table by its lower frequency (min, max, mean), smaller frequency modulation (FR), and the way in which the frequency is modulated (CV). The variables with the most consistent differences between unfamiliar and familiar alarm calls are frequency variability (CV), which is measuring the magnitude of the frequency modulation across the rumbles, and frequency range (FR). Familiar alarm call rumbles have a larger amount of frequency modulation and a larger frequency range (Table III).

IV. DISCUSSION

In this study, we played familiar and unfamiliar seismic alarm call signals to elephant family groups while they visited a water hole, as well as a warble tone which served as a seismic control stimulus. Only one of these signals (familiar alarm calls) was found to cause a significant change in behavior. Vigilant behaviors increased while spacing decreased. This leads us to draw two main conclusions.

First, because there was a significant change in behavior after the familiar alarm calls, but not during control trials, we are able corroborate our earlier findings that elephants are able to detect a seismic signal of biological importance in the absence of its acoustic counterpart (O'Connell-Rodwell *et al.*, 2006). Second, there was a significant change in behavior after the familiar alarm calls, but not after the unfamiliar alarm calls. This suggests a very fine ability to discriminate between biological seismic signals given in the same context. Either the familiar alarm was a more intense call (in terms of frequency modulation), thus inducing a more dramatic response, or it is also possible that alarms made from unfamiliar callers may not be perceived as being a reliable source of information.

A. Call recognition

The familiar alarm calls had a slightly higher frequency modulation, which could code for a more severe threat as the relative change in frequency is somewhat analogous to motivation-structural rules (Morton, 1977). If the herd ex-

TABLE III. Parameters used to quantify differences between the anti-predator alarm calls recorded at two different sites ($n=3$ for each site) and the generated warble tone. CV is the frequency variability index calculated as the variance in frequency divided by the square of the mean frequency, and then multiplying by 10. IF is the inflection factor calculated as the percentage of points showing a reversal in slope. PAF is the peak amplitude frequency. FF is the final frequency. FR is the frequency range. Duration is in seconds.

Recording	CV	IF	PAF	FF	MIN	MAX	MEAN	FR	MAX/MEAN	DUR
Unfamiliar alarm 1	0.042	0.077	48.01	44.60	44.60	54.53	49.94	9.93	1.09	2.49
Unfamiliar alarm 2	0.089	0.128	41.99	33.04	33.04	46.01	41.58	12.97	1.11	3.61
Unfamiliar alarm 3	0.106	0.154	46.60	35.65	35.65	49.10	42.10	13.45	1.17	4.44
Familiar alarm 1	0.176	0.026	49.15	35.73	35.73	54.47	45.72	18.74	1.19	3.73
Familiar alarm 2	0.128	0.128	45.41	42.16	35.84	52.36	47.10	16.52	1.11	3.97
Familiar alarm 3	0.251	0.128	45.57	30.60	30.11	45.57	36.28	15.46	1.26	5.16
Warble	0.015	0.103	^a	28.16	28.16	32.42	30.10	4.26	1.08	3.00

^aThere was no amplitude modulation during warble tone

posed to the familiar alarm calls interpreted the higher frequency modulation as a warning of more imminent threat, their reactions of increased vigilance and decreased herd spacing would be entirely appropriate. On the other hand, if threatening calls contain enough geographic variation such that the Kenyan elephant alarm calls were unrecognizable to Namibian herds, this could explain the lack of response to the unfamiliar call. This seems unlikely however, as the physical properties of the alarm calls are very similar and it seems likely that this type of call would be fairly universal. And in a previous study, we showed that elephants responded with different levels of intensity to the same alarm call played back in different areas of the same park (O'Connell-Rodwell *et al.*, 2000b).

A more likely explanation for the difference in reaction to these alarm calls is that the elephant herds differentiated the alarm calls as being familiar and unfamiliar. Given that the local herds would have interacted with the herd that originally made the familiar alarm calls, they would be in a much better position to evaluate the reliability of those calls. They would know from prior experience whether or not the signaling herd was likely to be correct in its assessment of the level of danger. Given that McComb *et al.* (2001, 2003) found that elephant herds could distinguish the contact calls of other herds as being part of their bond group, or outside their bond group, it seems plausible that the elephants in our playback studies are capable of doing the same.

B. Call structure, detection pathways and frequency discrimination

The analysis of the physical parameters of our seismic playback calls provides some insight into how these elephants might be distinguishing between seismic signals. The control warble is easily distinguishable from the other signals by a number of variables (mean frequency, frequency variability (CV) and frequency range (FR); see Table III), and also by the fact that only the fundamental is present in the signal, while both the fundamental and second harmonic are present in the alarm call presentations. The alarm calls, however, are more similar to each other, but most distinguishable from each other by their frequency variability and range (CV and FR). Since these elephants discriminated between these two sets of calls, they may be relying on the differences in frequency modulation for this discrimination.

The frequency range of the second harmonic of the alarm signals varied from about 10–19 Hz and should be within the range of vibrotactile frequency discrimination ability of elephants. No one has measured this directly in the African elephant, but we can make estimates based on work in other species, using similar sensory structures. The frequency discrimination ability of seismic signals in these elephants would depend on which pathway of detection is used. Two pathways have been proposed, bone conduction from the feet to the ear (Reuter *et al.*, 1998), or somatosensory (O'Connell *et al.*, 1999) via vibrotactile corpuscles in the feet (Weissengruber *et al.*, 2006; Bouley *et al.*, *in press*).

If the pathway of detection of seismic signals is via bone conduction to the ear, then the frequency discrimination ability will be reliant on the acoustic frequency discrimination

ability of this species. As noted above, we estimated the acoustic critical bandwidth in the frequency range of our playback calls to be around 15–19 Hz. Fletcher (1940) found that the minimum perceptible frequency change (Δf) was related to the critical bandwidth (CBW) in the following way: $CBW = \Delta f^* 20$. Therefore, if this equation holds true for elephants as well, we would estimate a Δf of 0.75–0.95 Hz, which would allow them the ability to detect very small changes in frequency modulation across these calls.

If the seismic detection pathway is via vibrotactile corpuscles, then elephants should still be able to discriminate fine frequency differences. Recanzone *et al.* (1992) tested the tactile frequency discrimination ability of adult owl monkeys, using 20 Hz as the reference tone. They found that the monkeys' ability to discriminate frequency differences improved from an initial 6 Hz down to 2 Hz. They report that their final threshold was similar to those found in humans and macaques (Goff, 1967; LaMotte *et al.*, 1975; Mountcastle *et al.*, 1969, 1990). Given that primates have not been shown to use seismic signaling, while our data support the idea of elephants using this modality, it is likely that elephants have at least the same vibrotactile frequency discrimination abilities as primates, if not better. Elephants could be using the Pacinian corpuscles found in their trunks (Rasmussen and Munger, 1996) and possibly in their feet to distinguish the frequency modulation between familiar and unfamiliar alarm calls.

The ability to tap into the seismic channel to discriminate biologically relevant information from background noise and to discriminate subtle differences between calls of familiar versus unfamiliar groups indicates that elephants may be using the ground as a sounding board for much more subtle cues than previously thought. Given the ability to detect subtle frequency differences, they most probably could also distinguish larger events such as an approaching vehicle, helicopters, airplanes, weather (thunderstorms) or earthquakes, providing the elephant with a sophisticated ability to exploit the seismic modality for many different purposes. Having previously shown that elephants produce and detect seismic cues and now demonstrating that elephants respond to and discriminate between seismic cues, we present the full complement of signal and receiver assessment components necessary from signal detection theory to state that elephants may indeed be communicating seismically.

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