Acoustic cues to identity and predator context in meerkat barks

Simon W. Townsend [a, b] , Benjamin D. Charlton [c], Marta B. Manser [a, b, d]

a Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Switzerland
b Kalahari Meerkat Project, Kuruman River Reserve, South Africa
c School of Psychology, University of Sussex, Brighton, U.K.
d Mammal Research Institute, Pretoria University, Pretoria, South Africa

ABSTRACT

Formants – the resonance frequencies of the vocal tract - are the key acoustic parameters underlying vowel identity in human speech. However, recent work on non-human animal communication systems has shown that formant variation provides potentially important information to receivers about static and dynamic attributes of callers. Meerkats (*Suricata suricatta*) produce broadband noisy bark vocalizations, lacking a clear fundamental frequency and harmonic structure, when they detect aerial or terrestrial predators. Here we investigated whether formants in meerkat barks have the potential to provide reliable information on caller identity and the predator context (aerial versus terrestrial predator) that they are delivered in. Acoustic analyses of naturally occurring barks and measurements of this species vocal tract length were used to confirm that the six clear frequency bands below 15 kHz in meerkat barks represent formants. Discriminant Function Analyses subsequently demonstrated significant inter-individual variation in the formant pattern of meerkat barks, suggesting that formants could be used by meerkats to identify conspecifics. In addition, Mixed-effects Models indicated that the frequency of the first formant was lower in barks produced in aerial versus terrestrial predation contexts. These data add to a growing body of literature on the potential function of formants in non-human animal vocal communication systems, and also imply that signaling external and referential information through such resonance frequencies, as in human language, might be more widespread in animals than previously thought.

Keywords: Formants, Barks, Meerkats, Individuality, Functional Reference

The information content of animal vocalizations has been at the forefront of empirical work addressing the diversity and complexity of animal communication systems and the function of specific vocal signals (Hauser 1996, Bradbury and Vehrencamp 2011). Early research correlating phenotypic or behavioural context information with acoustic features of mammalian calls focused primarily on variation in amplitude, duration and the vibration rate of the vocal folds which determines the pitch or fundamental frequency of a vocalization (Lieberman et al. 1969, Titze 1994, see also Taylor and Reby 2010). Subsequent studies have attempted to deconstruct the acoustically encoded information based on whether it is related to the source (the larynx) or whether it is independently derived as the sound wave is shaped by the vocal tract resonances (so called filter-related characteristics) (Briefer et al. 2010, Charlton et al. 2010, see also Taylor and Reby 2010 for a review). As with any tube of air, the supralaryngeal vocal tract has resonant modes that can generate vocal tract resonances, or formant frequencies, by amplification or dampening of specific frequencies originating from the source (Fitch and Hauser 1995, Fitch 1997, Riede and Zuberbuhler 2003). Utilising this well-established source-filter framework, several mammal studies have now shown that formants are reliable cues to the caller’s body size (e.g. Fitch 2000, Fitch and Reby 2001, Charlton et al. 2012) because of a close relationship between formant spacing, vocal tract length and overall body size. In addition, because formant frequency values are also affected by the shape of the vocal tract, which will vary between individuals, these spectral components of mammal vocalizations are often found to be reliable cues to individual identity (Rendall 2003, Solstis et al. 2005, Reby et al. 2006, Charlton et al. 2009, Charlton et al. 2012).

Research from human speech and primate vocal communication has demonstrated that the first two formants can be modulated more readily than the upper formants (which are more affected by vocal tract length) (Riede and Zuberbuhler 2003). For example, during human vowel and Diana monkey (*Cercopithecus diana*) alarm call production articulatory movements in the frontal oral cavity, specifically the tongue and lip positions, can result in dramatic shifts in the first two formant frequencies (Peterson and Barney 1952, Story et al. 1996, Riede and Zuberbuhler 2003). Such flexibility highlights the possibility that dynamic contextual information, in addition to static cues to anatomical features (e.g. body size or identity), is potentially encoded within the formant structure of animal vocalisations.

Cooperatively breeding meerkats (*Suricata suricatta*) possess a diverse and complex communication system characterized by over 30 different vocalization types, including a range of specific and general alarm calls, vocalizations used to maintain group cohesion (close calls, lead calls), and mediate social interactions (aggression calls within food competition, grooming calls (Manser 1998)). Such acoustic complexity is likely to have evolved due to their foraging technique, where their visual system is directly compromised during food acquisition, their need to coordinate activities and the habitat they occupy with open areas and a high predation risk (Clutton-Brock et al. 1998). Thus, vocal communication is essential for meerkats to keep track of changes in both their social and ecological environment (Manser 1999, Manser 2001, Townsend et al. 2011, 2012b). Observational and experimental data have demonstrated that considerable information is encoded within meerkat alarm and close-range contact calls, including referential and urgency-based information (Manser 2001, Manser et al. 2001) as well as information on predation probability and group membership (Townsend et al. 2010, Townsend et al. 2011). Further research on meerkat terrestrial alarm calls and close-range vocalisations has also shown that these call-types are individually distinctive (Schibler and Manser 2007, Townsend et al. 2010). However, because individuality in these calls was quantified using temporal and source-related acoustic parameters (e.g. duration and fundamental frequency variation), the potential for formants in meerkat vocalisations to cue identity and external contextual events remains unknown.

Meerkat bark vocalizations are short (e.g. 0.1s), rapidly produced, harsh or “noisy” calls (see Figure 2 and Supplementary Files 1 and 2) that should be particularly good for revealing formants because the sound source has a very broad frequency spectrum and no harmonics (multiple integers of the fundamental frequency) that could potentially be confused with formants (Fitch and Hauser 1995, Charlton et al. 2013). Bark-like vocalisations are produced in a number of mammal species from sea lions (Charrier et al. 2011) and dogs (*Canis familiaris*) (Yin and McCowan 2004) to chimpanzees (*Pan troglodytes*) (Goodall 1986) and are commonly associated with social disturbance (e.g. threats from conspecifics (Slocombe 2005, Charrier et al. 2011)) or heterospecific predators (Manser 2001, Slocombe 2005). There is some evidence to suggest that, within species, barks are produced in subtly different behavioural contexts and also differ in their spectral profiles (Yin and McCowan 2004) and potentially convey information regarding these contextual changes. For example, dogs produce barks in disturbance and isolation contexts and detailed acoustic and statistical analysis could demonstrate that these barks, previously classed as similar, are in fact subtypes (Yin and McCowan 2004). Meerkats produce barks when they are at a safe-sheltered location and have detected either a perched aerial or a terrestrial predator (Manser 2001, Townsend et al. 2012b). As with other alarm calls they likely function to inform foraging conspecifics of a potential threat, but given their relative heightened amplitude it is possible that they also play a role in predator deterrence (Manser 1998, Manser 2001, Townsend et al. 2012b). Meerkats also produce barks outside of predation contexts when isolated or lost from their home group (Manser 1998), but these barks are less frequent compared to those elicited by predation events.

In the current study we first investigated whether meerkat barks have the potential to encode information about the individual identity of callers. Since vocal tract morphology is likely to be individually specific we predicted that the formant pattern of meerkat barks will vary consistently according to the identity of the caller. Our second aim was to determine whether barks produced in different predator alarm contexts consistently vary in their formant structure. Following findings in non-human primates (Riede and Zuberbuhler 2003), we investigated whether the less anatomically constrained first and second formants of barks varied in different predator alarm contexts (aerial vs. terrestrial predators) and hence, have the potential to signal referential information regarding the current external situation (Seyfarth et al. 1980, Manser 2013).

METHODS

Study site and subjects

Barks were recorded from a wild, but habituated population of meerkats at the Kalahari Meerkat Project (KMP), Kuruman River Reserve (KRR) in South Africa. The study site is situated in the southern Kalahari Desert, 30km west of Van Zylsrus, South Africa (26°58’S, 21°49’E) (Clutton-Brock et al. 1998). Recordings were taken from 12 different groups of meerkats between 1995 and 2011 (longterm Kalahari Meerkat Project audio recordings). All meerkats were habituated to close observation and handling, enabling detailed recordings of behavioural and acoustic interactions. Additionally, all meerkats were dye-marked and had a microchip transponder for individual identification. One individual in each group was fitted with a radio collar (Sirtrack®) to track the group at any time of the day (Jordan et al. 2007). The study population has been observed since 1993 and the life history of all individuals is known since birth. The study was conducted under the permission of the ethical committee of Pretoria University and the Northern Cape Conservation Service, South Africa (Permit number: EC011-10).

Recording of meerkat barks

Barks were recorded at a distance of between 1 and 2 m from the caller with a directional Sennheiser microphone (ME66 with K6 power module and a MZW66 pro windscreen, frequency response 20 kHz, 2.5 dB, Old Lyme, CO, U.S.A.) connected to a Sony digital audiotape recorder DAT-TCD D100 (frequency response: 20 kHz, 1 dB, 16 bit, 44.1 kHz) or a Marantz PMD-660/670. We uploaded the calls on to a PC notebook and digitized them with either a U24 waveterminal USB audio interface (Ego-sys, Seoul, Korea) or transferred the calls directly from micro HD to a laptop.

Acoustic analysis

We used automated programs in Praat 5.1.03 DSP package (www.praat.org, Boersma and Weenink 2014) to perform the acoustic analysis. Before conducting the acoustic analysis narrow-band spectrograms were used to inspect the overall spectral structure of each bark, so that poor quality recordings with excessive background noise and/or unclear frequency components could be excluded. A total of 138 barks were excluded based on these criteria, leaving us with a total of 143 calls from 11 individuals (range calls/individual=10-25; N calls produced in terrestrial predation events=24 (from 4 events contributed by 3 individuals), N calls produced in aerial predation events=119 (from 7 events contributed by 9 individuals)).

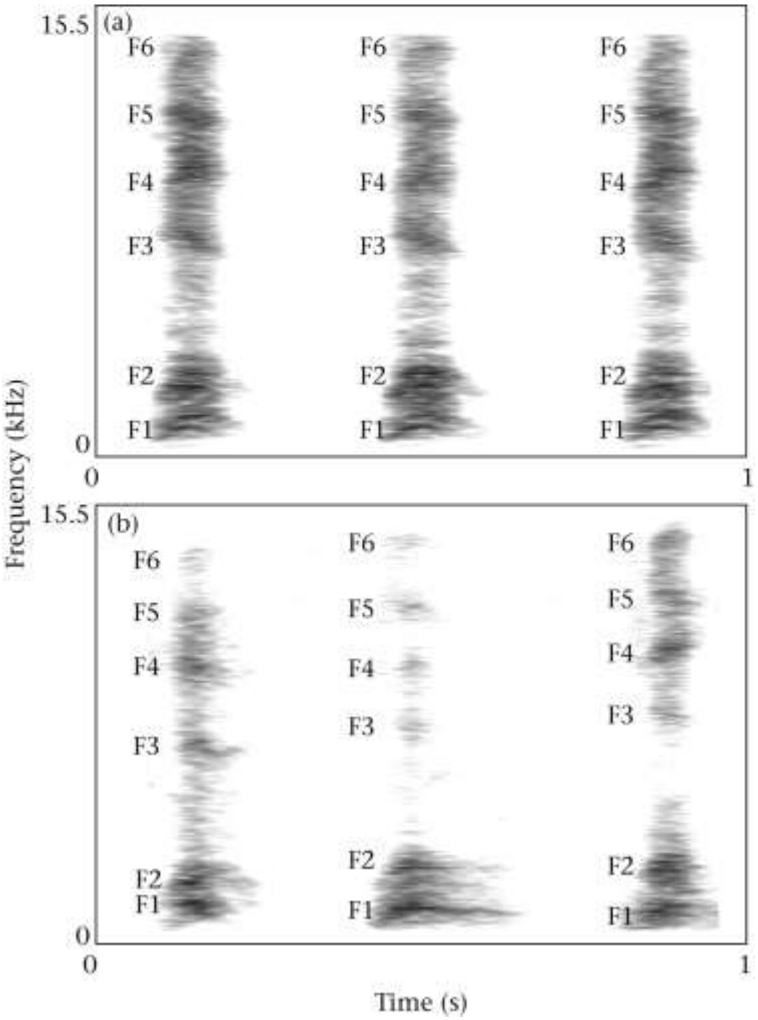

Figure 1: (a) Spectrograms showing barks from the same individual, illustrating the very low degree of intraindividual variability in bark acoustic structure. (b) Spectrograms showing barks from three different individuals, illustrating the interindividual variability in bark acoustic structure. Spectrogram settings: FFT method; window length: 0.05 s; time steps: 250; frequency steps: 1000; Gaussian window shape; dynamic range: 45 dB.

Before we conducted the acoustic analysis it was crucial to establish an approximate vocal tract length (VTL) for our study population at KMP, in order to make *a priori* predictions about the number of formants to expect in a given frequency range. We obtained x-rays from 25 deceased individuals kept frozen at -20 degrees on the reserve (13 males, 12 females) and measured the supra-laryngeal vocal tract (from glottis to lips) using a flexible ruler placed against the calibrated radiograph (see Figure 1). Individuals either died from natural causes or were euthanized due to injury or infection over the last 15 years (Drewe 2009). The average VTL measured in this way was 6.67 cm (range: 5.61-8.03cm, SD=0.65). Because meerkat barks are delivered with an open mouth (Manser pers. obsv.) the vocal tract could then be modelled as a 6.67 cm linear tube open at one end (the mouth) and closed at the other (the glottis).

Using this "open-one-end" tube model, the expected position of the first formant can be calculated using the following equation: $F1 = c/4*VTL$, in which c is the approximate speed of sound in the mammalian vocal tract (350 m/s) (Titze 1994). This gives us a predicted F1 value of = 1311.8 Hz. Formants F2-F6 are then predicted to occur at 3935.5 Hz ($F2 = 3*F1$), 6559 Hz ($F3 = 5*F1$), 9182.6 Hz ($F4 = 7*F1$), 11806.2 Hz ($F5 = 9*F1$), and 14429.8 Hz ($F6 = 11*F1$), respectively. Initial inspection of spectrograms also confirmed that six frequency bands exist below 15000 Hz that could represent formants (Figure 2). Accordingly, we set our automated programs in Praat to track and measure six formants in the frequency range 0-15000 Hz. To check if Praat was accurately tracking these frequency components we compared the outputs with visual inspections of each call's spectrogram and power spectrum (using cepstral smoothing: 500 Hz). Once we had confirmed that Praat was accurately tracking formants, the frequency values of the first six formants (F1-F6) were measured using Linear Predictive Coding and the following analysis parameters: time step: 0.01

seconds; window analysis: 0.03 seconds; maximum formant value: 15000 Hz; maximum number of formants: 6; pre-emphasis: 50 Hz.

It is worth noting that it can be difficult to measure formants in “noisy” calls such as meerkat barks because it is hard to differentiate between formants and harmonics of the fundamental frequency that could still remain in sections of deterministic chaos, so called “pseudo-formants” (Fitch, 2002). Nevertheless, because the formants we measured in meerkat barks were not harmonically related (Figure 2), and the number of formants we found in the frequency range 0-15 kHz corresponded to the number predicted using our “open-one-end” tube model, it seems unlikely that these frequency components could be harmonics of the fundamental frequency. Thus, they are very likely to represent supra-laryngeal resonances, or formants.

Figure 2: X-ray image of a meerkat illustrating the vocal tract length (A, estimated as 7.93 cm) and the position of the larynx, B.

Statistical analysis

We used Discriminant Function Analysis (DFA) to determine the classification probabilities of barks to individuals. Discriminant function analysis identifies linear combinations of predictor variables (e.g. acoustic parameters F1-F6) that best characterize the differences between groups and combines the variables into one or more discriminant functions, depending on the number of groups to be classified (Mundry and Sommer 2007). This analysis method provides a classification procedure that assigns each call to its appropriate class (correct assignment) or to another class (incorrect assignment). For external validation, we used a leave-one-out cross-validation procedure and to estimate the overall significance of the classification with DFA, we used two-tailed binomial tests with a corrected level of chance corresponding to the number of categories discriminated between (Mundry and Sommer 2007). To investigate the effect of external context (aerial vs. terrestrial) on formant structure we performed Linear Mixed-effects Models (LMMs). LMMs account for multiple contributions from the same individual by incorporating subject identity as a random factor in the model (Crawley 2002). To assess the significance of explanatory variables, we compared the full model (with fixed (e.g. external context) and random effects (e.g. subject)) with a reduced model comprising only the intercept and random effects (subject) using a likelihood ratio test (Faraway 2006). Because all individuals producing barks with a suitable acoustic structure for analysis within the terrestrial predator category were female, we also repeated the analysis but controlled for the sex of the caller by including this as an additional fixed explanatory variable in the model. We again used a likelihood ratio test to assess the significance of fixed effect (external context) by comparing a “full” model (with both fixed factors and random effects) against a reduced model containing only Sex (fixed factor) and random effects (e.g. subject). We also calculated 95% C.I.s to verify the reliability of our estimates. When C.I.s include zero, the null hypothesis (of no effect) cannot be rejected

(Nakagawa and Cuthill 2007). Furthermore we compared AIC values of the full and reduced model as an additional assessment of external context influence on first and second formant frequencies. Lower AIC values indicate improved support for each model (Akaike 1974, Golabek et al. 2012) with terms considered to improve the fit only if they inflated the AIC value by more than two units (Burnham and Anderson 2004). All analyses were performed in SPSS version 19.0 (SPSS inc, Chicago) or R version 2.12 (R core development team, 2013). Alpha values were set at 0.05.

RESULTS

Cues to identity

A Discriminant Function Analysis (DFA) correctly classified 76.9% of barks to 11 individuals. When applying a leave-one-out cross-validated DFA this value dropped to 67.1% (cross-validated) of barks to individual callers (Wilk's λ =0.016, Chi Square (60)= 552.4, *P*<0.000). A two-tailed binomial test demonstrated that this cross-validated classification level was still significantly higher than expected by chance (Chance level: 1/11= 9%, binomial test, *P*<0.001). Inspection of the DFA structure matrix and the accompanying eigenvalues shows that the upper formants F3-F6 contributed most to the observed variation between individuals (Correlation coefficients for Function 1 all above 0.3 see Table 1).

Table 1: DFA structure matrix

Structure matrix derived from the DFA of meerkat barks (based on formants 1-6) from 11 different individuals highlighting pooled within-groups correlations between discriminating variables and the first three standardized canonical discriminant functions with eigenvalues >1, explaining 89.5% of the total variance. Correlation coefficients above 0.3 (bold) indicate those acoustic variables that explained a substantial proportion of the variance in bark structure between individuals within the first three Discriminant Functions.

	Function		
Acoustic variable	1	2	3
F1	-0.01062938	**0.988680953**	-0.012597248
F2	0.182879953	**0.341162015**	0.298996144
F3	**0.507532407**	0.063813126	**-0.316882962**
F4	**0.565273305**	-0.03782931	-0.146703095
F5	**0.520212197**	0.114201165	**0.454673731**
F6	**0.734468659**	-0.235538029	-0.039221699
Eigenvalues	4.546196204	1.507715706	1.227096647

Cues to predator context

Linear Mixed-effects Models (LMMs) demonstrated that predator type had a significant effect on the mean frequency of the first formant (LMM; N=143, LR test: Chi Square= 9.879, df=1, *P*= 0.002, see Figure 3 and 4, Table 2 for CI's and AIC values). This significant effect remained when controlling for the sex of the caller (LMM; N=143, LR test: Chi Square= 11.6, df=1, *P*<0.001). Specifically, model estimates controlling for pseudoreplication show that barks produced in the presence of a terrestrial predator had a higher F1 than those produced in aerial contexts (Figure 3 and 4). Predator context, however, did not influence the frequency of the second formant (LMM; N=143, LR test: Chi Square= 2.28, df=1, *P*= 0.137, see Table 2 for CIs and AIC values) or upper formants 3-6 (see Table 3).

Table 2: Lower formant differences between predator classes

Effect sizes, confidence intervals and change in AIC values for Likelihood ratio tests on F1 and F2 (when excluding explanatory variable, predator context, from the final Linear Mixed-effects Model). Note that the C.I.s for F1 do not include zero and the delta AIC is greater than two units verifying the significant effect detected for context on F1 frequency.

Acoustic variable	Effect size	CI's	Delta AIC
F1	253.82	120.22, 387.42	7.9
F2	161.31	-44.8, 367.42	0.3

Table 3: Upper formant differences between predator classes

Results of the LMMs investigating the effect of predatory context on remaining formant frequencies 3-6. Chi square and p-values correspond to the likelihood ratio tests.

Acoustic variable	Chi Square	P value
F3	0.2	0.64
F4	0.02	0.8
F5	0.05	0.8
F6	0.5	*0.4*

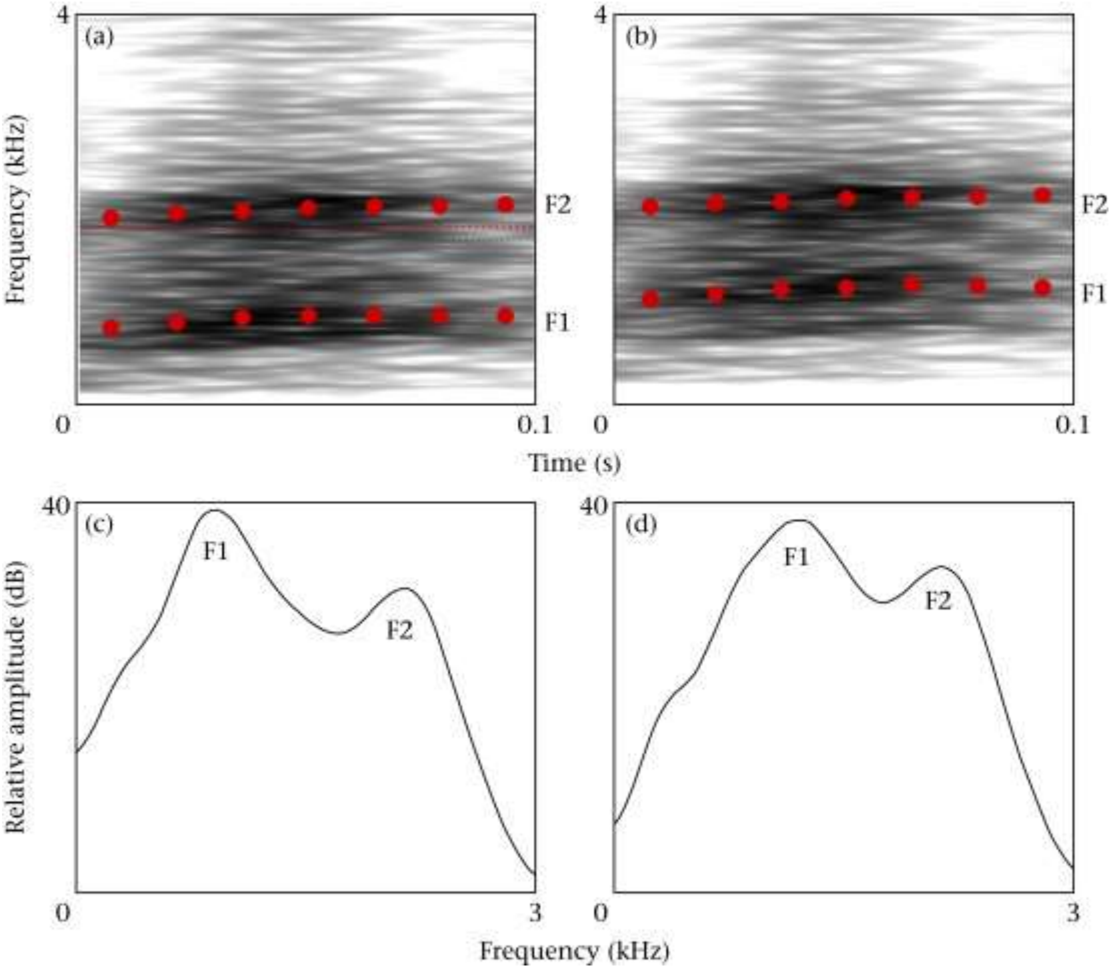

Figure 3: The spectral acoustic structure of (a) an aerial and (b) a terrestrial bark given by the same individual. Spectrogram settings: FFT method; window length: 0.05 s; time steps: 250; frequency steps: 1000; Gaussian window shape; dynamic range: 45 dB. (c, d) The corresponding 800 Hz cepstral-smoothed LPC spectra from (c) the aerial and (d) the terrestrial barks. The formants are labelled F1 and F2. The red dots on the spectrograms illustrate the formant tracking facility in Praat. Note that F1 is higher in the terrestrial bark.

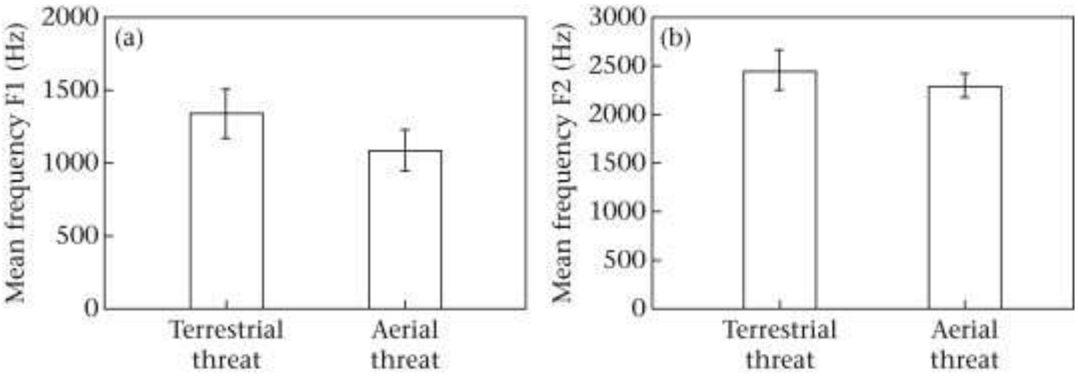

Figure 4: Influence of external threat type on the mean frequency of (a) the first formant (Hz) and (b) the second formant (Hz). Bars represent model predictions and 95% confidence intervals.

DISCUSSION

Our results demonstrate that the formant structure of meerkat barks has the potential to provide static cues to individual identity and dynamic cues to the current external context experienced by the signaler, specifically whether an aerial or terrestrial predator is present. These findings add to a growing body of literature on the potential function of formants in non-human animal vocal communication systems (see Taylor and Reby 2010). Formants have been shown to vary consistently according to caller identity in several other mammal species (Rendall 2003, Soltis et al. 2005), and we also found that the upper formants (F3-F6) of meerkat barks contributed the most to individual distinctiveness. This is in line with similar findings in other species such as African elephants (*Loxodonta Africanis*) (Soltis et al. 2005), koalas (*Phascolarctos cinereus*) (Charlton et al. 2012), red deer (*Cervus elaphus*) (Reby et al. 2006) and chacma baboons (*Papio ursinus*, Rendall 2003).

When comparing the influence of external predator context on formant structure we found that, even with a small sample size, the average frequency of the first formant, but not the second, varied significantly between aerial and terrestrial predator contexts. Specifically, statistical model predictions suggested barks produced in the presence of a terrestrial predator had, on average, a higher first formant frequency value than those produced in aerial contexts. Because the first formant alone (and not F2-6) varied between different predator contexts, size-related differences (which would shift the entire formant pattern up or down) are very unlikely to have generated these contextual differences in the acoustic structure of barks. Furthermore, we are confident that the frequency components we have measured in meerkat barks are formants because they were not harmonically related (i.e., they are not multiple integers), and the number of formants we found in the frequency range 0-15 kHz corresponded to the number predicted using our vocal tract model derived from 25 individuals.

In humans, articulation of the lower formants (F1, F2) is critical for vowel production and hence represents one of the primary anatomical mechanisms for meaning encoding in speech (Titze 1994, Fitch 2010). In comparison to humans, meerkat articulation is unlikely to be actively controlled, but more passively modulated by the underlying arousal state of the signaller. One mechanistic explanation for contextual based variation in F1 may be that aerial predators eliciting barks are often perched at considerable distances (range >100 m to >1 km away). Barks to terrestrial predators on the other hand are primarily produced when such predators are in close proximity (range 20 to 200 m away) (Manser 2001) and hence terrestrial predators, in this context, may be perceived by signallers as a more imminent danger. Such heightened arousal in meerkats is often associated with posture changes in the head and neck (Manser, unpub. data), which ultimately can have downstream effects on the shape of the oral cavity or lip positions and subsequent modulation of the frequency of the first formant. Further detailed investigation into variation in vocal anatomy between barks produced in different contexts will verify from a proximate perspective how and why such acoustic differences arise.

Similar findings where potentially “external”, referential information has consistently varied with average F1 or F2 frequency have been demonstrated in species more phylogentically proximate to humans, such as baboons (Rendall et al. 1999) and Diana monkeys (Riede and Zuberbuhler 2003). Both in Diana monkeys and meerkats the frequency of the first formant varies with regard to predator type, though the direction of change seems to differ between species, as in Diana monkeys F1 decreases in the presence of terrestrial predators, whereas in meerkats F1 increases. However, as in meerkats, this may still map onto urgency levels, given that in arboreal monkeys aerial predators are often more threatening than terrestrial predators. Irrespective of the directionality and the exact production mechanisms underlying F1 articulation, our findings represent the first evidence for similar externally induced variation in formant structure in a non-primate mammal. Given the phylogenetic distance between humans and meerkats (circa 50 million years, Eizirik et al. 2010) these data may shed important additional light on the conservative nature of vocal production mechanisms. Specifically, our results imply that signaling referential information through the articulation of lower formants, which are less constrained by anatomy than upper formants, might be more widespread in animals than previously thought. As formant articulation is common in human language (e.g. during vowel production), this may represent an example of “deep homology” for the encoding of meaning in vocalizations.

Whether meerkats can perceive relevant variation in identity and context-related formant information remains to be tested. Previous research on the anti-predator behaviour of meerkats has demonstrated different escape responses are employed based on whether predators are aerially or terrestrially located (Manser 1998, 2001, Manser et al. 2001). Being able to determine predator type from the formant structure of barks would provide meerkats with important referential information that could be used to inform future foraging decisions based on potential threat levels (i.e. to remain in a safe position or continue to forage). For example, in the presence of a perched aerial predator, meerkats may be able to return to foraging more quickly than when exposed to a potentially more imminent threat such as a terrestrial predator. Barks may be one communicative medium through which such information can be acquired. If the potential confounding effects of the urgency of the event (e.g. terrestrial predators are more dangerous) can be excluded from the processing of calls, to our knowledge such discriminatory abilities would represent some of the clearest evidence for referential signaling within a single call type and thus shed important light on pervasiveness of referential communication in animals (see Townsend and Manser 2013).

In terms of individual recognition, recent experimental work employing a novel violation of expectation paradigm has demonstrated individual discrimination via meerkat social close call vocalisations, which likely is important in coordinating spacing between certain conspecifics (Townsend et al. 2012a, Reber et al. 2013). Regarding alarm calls, however, habituation-discrimination playbacks have indicated the absence of individual recognition and this is likely linked to the costs associated with not responding to alarm calls (Schibler and Manser 2007). Whilst bark vocalizations are indeed alarm calls, they are primarily given when meerkats gather together at a burrow or a bolt hole. Receivers may therefore be under less pressure to respond consistently when they are already sheltered and hence, in comparison to other alarm call types, barks may be more suitable to test for individual recognition. Given the highly cooperative nature of meerkat societies, the ability to recognize individuals using barks may facilitate behavioural coordination allowing group members to keep track of cooperative anti-predator contributions (Mulder and Langmoore 1993). Moreover, it may also be that the ability to discriminate individuals from their barks would confer fitness advantages, potentially in detecting less reliable signalers (Seyfarth and Cheney 1990). Previous experiments in primates and non-primate mammals has shown that the alarm calls of individuals experimentally manipulated to be unreliable (through habituation and exposure to new alarm calls from the same individual) are less evocative than the calls of reliable individuals (Seyfarth and Cheney 1990, Blumstein et al. 2004). This suggests that recognition of individuals from alarm calls may be beneficial by allowing receivers to respond flexibly and adaptively to alarm calls based on the past calling behaviour of signallers. The highly repetitive serial nature of bark production also provides an excellent opportunity for the employment of habituation discrimination experiments testing for recognition of identity and external predator-type cues, in addition to ruling out more parsimonious explanations such as urgency related effects in explaining behavioural responses to bark types. Furthermore to systematically disentangle the influence of the first formant for discrimination between terrestrial and aerial barks, manipulation of the first formant could be undertaken to “create” terrestrial barks from aerial barks (by synthetically raising F1). Such playback perception experiments are crucial if we are to fully understand the adaptive significance of formant variation in meerkat vocal communication.

To conclude, we have demonstrated that the formant pattern of meerkat anti-predator barks systematically varies according to caller identity and external predator contexts, and hence can potentially provide cues to receivers regarding both. Exactly whether such information is salient to receivers still remains to be shown, but habituation/discrimination playback experiments provide a rigorous opportunity to test this. These results support previous findings suggesting additional dimensions of information may be encoded within the layers of the vocalization modulated by the supra-laryngeal vocal tract and hence that parameters, other than source-related features, should be investigated when attempting to understand the form and function of mammalian vocalisations.

References

Akaike, H. 1974. New look at statistical-model identification. *LEEE Transactions on Automatic Control AC, 19*, 716-723.

Blumstein, D.T., Verenyre, L. & Daniel, J.C. 2004. Reliability and the adaptive utility of discrimination among alarm callers. *Proceedings of the Royal Society, London B*, 27,1851-1857.

Boersma, P. & Weenink, D. 2014. Praat: doing phonetics by computer [Computer program]. Version 5.3.66.

Bradbury, J.W. & Vehrencamp, S.L. 2011. Principles of Animal Communication (2nd edition). Sunderland MA: Sinauer Associates.

Briefer, E., Vannoni, E. & McElligott, A. G. 2010. Quality prevails over identity in the sexually selected vocalisations of an ageing mammal. *BMC Biology*, 8, 35.

Burnham, K.P. & Anderson, D.R. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research,* 33, 261-304.

Charlton, B.D., Zhihe, Z. & Snyder, R. J. 2009. The information content of giant panda, *Ailuropoda melanoleuca,* bleats: acoustic cues to sex, age and size*. Animal Behaviour,* 78, 893-898.

Charlton, B. D., Zhihe, Z. & Snyder, R. J. 2010. Giant pandas perceive and attend to formant frequency variation in male bleats. *Animal Behaviour,* 79, 1221-1227.

Charlton, B.D., Ellis, W. A. H., Brumm, J., Nilsson, K. & Fitch, W. T. 2012. Female koalas prefer bellows in which lower formants indicate larger males. *Animal Behaviour,* 84, 1565-1571.

Charlton, B. D., Taylor, A. M. & Reby, D. 2013. Are men better than women at acoustic size judgements? *Biology Letters,* 9, 20130270.

Charrier, I., Ahonen, H. & Harcourt, R.G. 2011. What makes an australian sea lion (*Neophoca cinerea*) males bark threatening? *Journal of Comparative Psychology,* 125, 385-392.

Clutton-Brock, T.H., Gaynor, D., Kansky, R., MacColl, A.D.C., McIlrath, G., Chadwick, P., Brotherton, P.N.M., O'Riain, J.M., Manser, M. & Skinner, J.D. 1998. Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proceedings of the Royal Society, London B,* 265, 185-190.

Crawley, M.J. 2002. Statistical computing: an introduction to data analysis using S-Plus. Wiley, Chichester.

Drewe, J.A. 2009. Social networks and infectious disease transmission: Epidemiology of tuberculosis in wild meerkats. PhD thesis, University of Cambridge.

Eizirik, E., Murphy, W.J., Koepfli, K.P., Johnson, W.E., Dragoo, J.W., Wayne, R.K. & Obrien, S.J. 2010. Pattern and timing of diversification of the mammalian order Carnivora inferred from multiple nuclear gene sequences. *Molecular Phylogenetics and Evolution,* 56, 49–63.

Faraway, J.J. 2006. Linear Models with R. Chapman & Hall/CRC, Boca Raton, FL

Fitch, W. T. 1997. Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *Journal of the Acoustical Society of America,* 102, 1213-1222.

Fitch, W. T. 2000. Skull dimensions in relation to body size in nonhuman mammals: the causal bases for acoustic allometry. *Zoology,* 103, 40-58.

Fitch, W. T. 2002. Primate vocal production and its implications for auditory research., in Primate Audition: Ethology and Neurobiology., edited by A. A. Ghazanfar (CRC press, Boca Raton,
FL), 87-108.

Fitch, W.T. 2010. The evolution of language. Cambridge University Press.

Fitch, W. T. & Hauser, M. D. 1995. Vocal production in nonhuman-primates-acoustics, physiology, and functional constraints on honest advertisement. *American Journal of Primatology,* 37, 191-219.

Fitch, W. T. & Reby, D. 2001. The descended larynx is not uniquely human. *Proceedings of the Royal Society, London B*, 268, 1669-1675.

Golabek, K.A., Ridley, A.R. & Radford, A.N. 2012. Food availability affects strength of seasonal territorial behaviour in a cooperatively breeding bird. *Animal Behaviour,* 83, 613-619.

Goodall, J. 1986. The Chimpanzees of Gombe: Patterns of Behaviour. Cambridge: Harvard University Press.

Hauser, M. 1996. MIT Press; The evolution of communication Cambridge, MA.

Jordan, N.R., Cherry, M.I. & Manser, M.B. 2007. Latrine distribution and patterns of use by wild meerkats: implications for territory and mate defence. *Animal Behaviour*, 73, 613-622.

Lieberman, P., Klatt, D. H. & Wilson, W. H. 1969. Vocal tract limitations on the vowel repertoires of rhesus monkeys and other nonhuman primates. *Science,* 164, 1185-1187.

Manser, M.B. 1998. The evolution of auditory communication in suricates *Suricata suricatta*. PhD thesis, University of Cambridge.

Manser, M.B. 1999. Response of foraging group members to sentinel calls in suricates (*Suricata suricatta*). *Proceedings of the Royal Society, London B,* 266,1013-1019.

Manser, M.B. 2001. The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society, London B,* 268, 2315-2324.

Manser, M.B., Bell, M.B. & Fletcher, L.B. 2001. The information that receivers extract from alarm calls in suricates. *Proceedings of the Royal Society, London B,* 268, 2485-2491.

Manser, M.B. 2013. Semantic communication in vervet monkeys and other animals.
Animal Behaviour, 86, 491-496

Mulder, R. A. & Langmore, N. E. 1993. Dominant males punish helpers for temporary defection in superb fairy-wrens. *Animal Behaviour,* 45, 830-833.

Mundry, R. & Sommer, C. 2007. Discriminant function analysis with nonindependent data: consequences and an alternative. *Animal Behaviour,* 74, 965-976.

Nakagawa, S. & Cuthill, I. C. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews,* 82, 591–605.

Peterson, G.E. & Barney, H.L. 1952. Control methods used in the study of vowels. *Journal of the Acoustical Society of America,* 24, 175-184.

R Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Reber, S.R., Townsend, S.W. & Manser, M.B. 2013. Social monitoring via close calls in meerkats. *Proceedings of the Royal Society, London B,* 280, 1765.

Reby, D., Andre-Obrecht, R., Galinier, A., Farinas, J. & Cargnelutti, B. 2006. Cepstral coefficients and hidden Markov models reveal idiosyncratic voice characteristics in red deer (*Cervus elaphus*) stags. *Journal of the Acoustical Society of America,* 120, 4080-4089.

Rendall, D. 2003. Acoustic correlates of caller identity and affect intensity in the vowel-like grunt vocalizations of baboons. *Journal of the Acoustical Society of America*, 113, 3390-3402.

Rendall, D., Seyfarth, R.M., Cheney, D.L. & Owren, M.J. 1999. The meaning and function of grunt variants in baboons. *Animal Behaviour,* 57, 583-592.

Riede, T. & Zuberbuhler, K. 2003. The relationship between acoustic structure and semantic information in Diana monkey alarm vocalizations. *Journal of the Acoustical Society of America,* 114, 1132–1142

Schibler, F. & Manser, M.B. 2007. The irrelevance of individual discrimination in meerkat alarm calls. *Animal Behaviour,* 74, 1259-1268.

Seyfarth, R.M., Cheney, D.L. & Marler, P. 1980. Monkey responses to three different alarm calls: Evidence for predator classification and semantic communication. *Science,* 210, 801-

803.

Seyfarth, R.M. & Cheney, D.L. 1990. The assessment by vervet monkeys of their own and another species' alarm calls. *Animal Behaviour,* 40, 754-764.

Slocombe, K. 2005. Vocal communication in chimpanzees (*Pan troglodytes*). PhD thesis, St Andrews University, UK.

Soltis, J., Leong, K. & Savage, A. 2005. African elephant vocal communication II: rumble variation reflects the individual identity and emotional state of callers. *Animal Behaviour*, 70, 589-599.

Story, B. H., Titze, I. R. & Hoffman, E. A. 1996. Vocal tract area functions from magnetic resonance imaging. *Journal of the Acoustical Society of America,* 100, 537–554.

Taylor, A. & Reby, D. 2010. The contribution of source-filter theory to mammal vocal communication research*. Journal of Zoology,* 280, 221-236.

Titze, I. R. 1994. Principles of Voice Production. Englewood Cliffs, New Jersey: Prentice Hall.

Townsend, S.W., Hollen, L.I. & Manser, M.B. 2010. Meerkat close calls encode group-specific signatures, but receivers fail to discriminate. *Animal Behaviour,* 80, 133-138.

Townsend, S.W., Zottl, M. & Manser, M.B. 2011. All clear? Meerkats attend to contextual information in close calls to coordinate vigilance. *Behavioural Ecology and Sociobiology,* 65, 1927-1934.

Townsend, S.W., Allen, C. & Manser, M.B. 2012a. A simple test for vocal individual recognition in wild meerkats. *Biology Letters,* 8, 179-182.

Townsend, S.W., Rasmussen, M., Clutton-Brock, T. & Manser, M.B. 2012b. Flexible alarm calling in meerkats: the role of the social environment and predation urgency. *Behavioural Ecology*, 23, 1360–1364.

Townsend, S.W. & Manser, M.B. 2013. Functionally referential communication in mammals: the past, present and the future. *Ethology,* 118, 1-11.

Yin, S. & McCowan, B. 2004. Barking in domestic dogs: context specificity and individual identification. *Animal Behaviour,* 68, 343–355.