~~Temporal segregation of individual and behavioral signatures in banded mongoose close calls~~ Segmental concatenation of individual signatures and context cues within the single syllable of the banded mongoose close call

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Abstract

Background Most animals are anatomically constrained in the number and variety of call types they can produce. Recent studies suggest that by combining existing calls into meaningful sequences, animals can increase the information content of their vocal repertoire despite these constraints. Additionally, signalers could use vocal signatures or cues to increase the information encoded in their vocalizations. However, encoding multiple vocal signatures and/or cues using the same components of vocalizations usually reduces signals' reliability. Segregation of information (e.g. temporally) could effectively circumvent this trade-off. ~~There currently exist no other studies that refer to this principle within a single call type.~~ Here, we investigate how banded mongooses ~~(Mungos mungo)~~(*Mungos mungo*) encode multiple vocal signatures and cues in their frequently emitted ~~close~~ graded close calls.

Methodology/Principal Findings The data for this study was collected on a wild, but habituated, population of banded mongooses. Using behavioral observations and detailed acoustical analysis we found that close calls contain temporally separated signatures and cues, encoding information regarding both an individual's identity and its current behavioral context as a discrete unit. Indeed, close calls possess individual specific marks and differ whether the individual is digging, searching or moving. We therefore provide the first evidence of Marler's segregation of information within a single ~~call type~~ syllable. Additionally our work also represents the first example of an identity cue integrated as a discrete element within a single call that is independent from context. This likely functions to avoid ambiguity between individuals or receivers having to keep track of several context-specific identity cues.

Conclusions/Significance Our study provides the first evidence of segmental concatenation of information ~~temporal segregation of information in a mammalian~~ non-human vocalization. By reviewing descriptions of call structures in the literature, we suggest a general application of these mechanisms in birds, frogs and humans. Our study suggests that temporal segregation and segmental concatenation of vocal signatures and cues is a new and wholly unexplored dimension of information coding in animal vocal communication. We argue that temporal segregation of vocal signatures and cues evolves in species where communication of multiple unambiguous signals is crucial, but is limited by the number of call types produced.

Keywords: vocal signature, vocal cue, close call, segregation of information, graded calls, banded mongoose, segmental concatenation

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Background

Nonhuman-animals have finite vocal repertoires and are anatomically constrained in the number of different call types they can produce [1,2]. These constraints limit the variation of a species' vocal repertoire and may have played an important role in the evolution of meaningful combinations of calls [3,4]. Another possible way to encode sender related information in vocalizations is through vocal signatures and/or cues. [5–8]. Although individual identity is the most commonly reported vocal signature [8], animal vocalizations have also been shown to contain signatures for group identity [7–11] or cues for male quality (hereafter we refered to both signatures and cues as vocal cues) [12–14], sex [15,16], and reproductive state [17].

Animals can encode ~~signature~~ vocal cue information using two general sets of acoustic properties. Firstly, spectral features, such as fundamental frequency or harmonic-to-noise ratio, can differ between individuals to encode for instance individuality [8]. Secondly, ~~signature~~ vocal cue information can be encoded in vocalizations through temporal features. Individual signatures encoded by variance in the temporal aspects, such as duration or temporal arrangement of frequency elements have been reported for species such as the big brown bats (*Eptesicus fuscus*), pallid bats (*Antrozous pallidus*) or cricket species (*Gryllidae spp.*) [8]. ~~Signatures potentially provide useful information to the receiver whenever the within-category variation is smaller than the between-category.~~ Vocal cues potentially provide useful information to the receiver whenever variation exists between categories and this variation between categories is larger than the within-category variation (stereotypic within). Furthermore, previous research has shown that calls can contain combinations of different ~~signature~~ vocal cues [8]. However because acoustic space is limited and many acoustic parameters are correlated with one another, the amount of variation that can be used by signalers to encode different ~~signature~~ vocal cue types is ultimately constrained. This conflict can result in a trade-off between the various kinds of information, and typically reduces reliability of at least one of the ~~signatures~~ vocal cues [13,18]. For instance the use by signalers of variation for individual recognition conflicts with the need for stereotypic characteristics for group recognition in bird song [18]. Briefer et al [13] showed a similar trade-off between the ~~signatures~~ vocal cues for identity (stable over time) and male quality (variable over time) in fallow deer (*Dama dama*). ~~Temporal segregation of information could partially resolve this trade-off, by using different acoustic features, which are separated in time to encode functionally different signatures~~ Segregation of information could partially resolve this trade-off, by using different acoustic features, which are separated in time (temporal separation) or different ranges in some feature (e.g. frequencies; spectral separation) to encode functionally different signatures [13,18]. In the

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white-crowned sparrow (*Zonotrichia leucophrys pugetensis*), for example, individual identity and group membership are segregated into the note complex and trill phrases of its song respectively, avoiding a trade-off in reliability between the vocal ~~signatures~~ vocal cues [19]. Although, this principle was already proposed by Marler in 1960 [18], there currently exist no studies that refer to it within a ~~single call type~~ a single (short) syllable call type. Such within-syllable encoding would have anologues with 'phonological' or segmental concatenation used in human language. .

Contact calls are among the most common vocalizations produced by both, mammalian and bird species. In a wide variety of species, contact calls seem to function to coordinate movements and cohesion of individuals on a range of spatial scales, concurrently with various behaviors and in a variety of social systems [20, 21]. Contact calls have been shown to contain individual ~~signatures~~ vocal cues [5, 7, 8, 22] and group membership ~~signatures~~ vocal cues [7, 9, 11, 23]. Contact calls can also contain multiple ~~signatures~~ vocal cues (e.g., for group and individuality in meerkats, *Suricata suricatta*) [7]. While some species' contact calls seem to function on mid- to long-distances, in others contact calls play a more important role on short-distances. It has therefore been suggested that these calls, often low in amplitude and pitch, are better described as close calls [7, 24]. Such close calls have the potential to provide constant information about the individual characteristics of the caller and individuals likely use the calls to monitor changes in behavior and relative spatial positioning of members in social groups [7, 20, 21, 25, 26].

Cooperatively breeding banded mongooses (*Mungos mungo*) are small ($\leq$ 2kg) social carnivores that show high group cohesion. They live in mixed sex groups, with an average of around 20 individuals, but groups occasionally grow to more than 70 individuals [27]. They forage together as cohesive units and cooperate in pup care, predator avoidance and territory defense [27–29]. During foraging banded mongooses move in and out of dense vegetation with many position shifts, both in distance to nearest neighbor and in relative position within the group. They regularly dig for food items in the soil with their head down. Besides digging they also search for food on the surface, but this is predominantly done in the thickets (see Table 1 for details). They are often visually constrained during foraging and therefore vocalizations play a critical role in keeping individuals regularly informed of changes in the social and ecological environment. Banded mongoose use a range of graded vocalizations to coordinate behaviors and to maintain group cohesion [30, 31]. One of the most commonly emitted call types is the close call and previous work has already demonstrated the presence of an individual ~~signature~~ vocal cue within the call [32]. Subsequent field observations suggested additional graded variation in the close calls, which appears to be related to the behavioral context the caller experiences (personal observations DJ). We therefore investigated whether

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banded mongooses close calls contain multiple vocal ~~signatures~~ vocal cues ~~in their close calls~~, and how these are encoded in the temporal and spectral related aspects of ~~a~~ this graded call.

Results

The close call in banded mongoose varied significantly between individuals and behavioral contexts. Specifically, the initial noisy part of the call remained stable within an individual in all of the quantified behavioral contexts, while a gradation was detected in the subsequent harmonic tonal element (Figure 1, S1-S3). Close calls could be distinguished statistically on the basis of the individual in all four groups (total number of individuals = 36, range per group 7 to 14). Correct cross validation probabilities varied between 40 and 61% for the initial noisy part and the whole call, and bootstrapping showed that all classification probabilities were much higher than that expected by chance (7 to 14%). The cross-validation values for the harmonic part of the call were considerably lower at 11 to 25% and were not significantly different than expected by chance (Table 2). A group-specific ~~signature~~ vocal cue was found in the noisy part of the call (number of correctly cross-classified elements ($ncce$) = 44.47, $p = 0.038$, $n = 36$), but not for the whole call ($ncce = 38.08$, $p = 0.27$), nor the harmonic element ($ncce = 44.47$, $p = 0.038$, $n = 36$). No evidence for a sex-specific ~~signature~~ vocal cue was found in ~~either~~ the whole call ($ncce = 60.35$, $p = 0.54$, $n = 36$), ~~nor~~ the initial noisy part ($ncce = 64.23$, $p = 0.19$, $n = 36$). A cross-classified permutated discriminant function analysis (pDFA) showed that, overall, close calls were correctly classified to the appropriate behavioral context (Table 1) based on their acoustic structure ($ncce = 44.22$, $p < 0.001$, $n = 20$). Specifically, the harmonic extension of the close calls varied significantly and could be correctly classified according to the behavioral context ($ncce = 78.04$, $p = 0.009$, $n = 18$), whereas the initial noisy part of the call did not ($ncce = 19.87$, $p = 0.79$, $n = 20$). Thereby, the harmonic element was either not present or of a very short duration in the digging context ($mean \pm sd$; 0.01s $\pm$ 0.02), while its duration increased in the searching context (0.05s $\pm$ 0.03). The longest and most pronounced harmonic elements were observed in the moving context (0.08s $\pm$ 0.03). For pairwise comparisons between behavioral contexts see Table 3.

Discussion

Banded mongoose close calls were not only individually distinct, but also differed in their acoustic structure depending on the current behavior of the signaler. This acoustic variation related to the behavioral context was encoded within a harmonic extension of the basic noisy part of a close call. To our

knowledge this is the first example of such ~~temporal segregation described within a call type , where two~~

~~different sets of acoustical properties are used to encode multiple signatures~~vocal cues ~~in the same call.~~ a

temporally-segmented fashion of encoding multiple types of information withing a single short syllable.

Variation in spectral aspects (e.g. fundamental frequency) of the more noisy call element verify previous

findings demonstrating encoding of individuality in close calls of banded mongoose [32]. Specifically Müller

and Manser [32] showed, with playback experiments, that pups are able to discriminate between close calls

of their escorting adult and of other adults. These results suggest that individual ~~signatures~~vocal cues of

these close calls are meaningful to receivers. Additionally, we provide evidence for group specific

~~signatures~~ vocal cues. Such group identity is likely to arise, as the physical characteristics that determine

vocal characteristics of an individual (e.g. larynx length) are, on average, more similar to its group

members than its non-group members. Another mechanism that can arise in species with vocal flexibility

and were individuals change groups is group convergence [33,34]. At present it is unknow with of these two

processes is applicable for the banded mongoose. In contrast, temporal features (e.g. duration) of the tonal

harmonic second element of the call seem to encode the behavioral ~~signatures~~vocal cues. Future research

using playback experiments will need to be conducted to investigate if behavioral context vocal cues are

used by receivers.

While many animal signaling systems like human speech use concatenation of acoustically-separate

syllables to enrich and extend the signaling space (e.g. birdsong [19,35], rock hyraxes (*Procavia*

capensis) [36] or cetacean spp. [37,38]), human speech also encodes information into individual syllables.

By combining stop consonants with different vowels at a phonological level syllables are created that have

different meanings. Thus a stop consonant like /b/ versus /p/ can be combined with a vowel like /a/ or

/o/ to create a richer signaling unit than either class (i.e. stop consonants or vowel) alone could provide.

Such combinations (versus "syntactic" concatenation of syllables and words) are a core component of the

phonological component of human spoken language [39]. The temporally segmented fashion in which

banded mongoose encode multiple cues into the single syllable close call mimics this system. Moreover, our

study provides the first example of a discrete individual 'element' in a graded call containing information

regarding individuality. The noisy, yet stable, part of the close call, explained almost as much individual

variation as the whole call. This implies that, despite the graded nature of the close call, individual

identity is encoded in a discrete way. The functional aspect of the discrete identity cue in combination with

a graded behavioral cue seems most analogous to human communicative contexts, when sender and

receiver do not see each other. For example, in the drum or whistle languages of tribes in the remote and

isolated conditions of mountainous or densely forested areas, discrete signals are used to announce identity

and other information to avoid ambiguity [40, 41]. ~~Similar~~Similarly, in radio conversations in aviation

between pilots and control towers, identity and additional information are shared in a highly standardized

order (i.e. You Me Where What With; chapter 5) [42]. Signals in these 'conversations' are intentionally

selected for their ~~unambiguity~~clarity to the receivers [43, 44]. In particular in species that are constantly

moving as a cohesive unit, in their search for food or shelter, and where the identification of an individual

cannot be based on its spatial position, acoustic individual identity may be a crucial aspect for the

successful operation of the system. This is true for banded mongooses where coordination of who is doing

what and when facilitates the successful functioning of the overall social system.

Temporal segregation of vocal signatures may enable banded mongooses to reliably encode dual

information sets regarding an individual's identity and its current behavioral context. The close calls of the

banded mongoose represent the first example of such segregation within a single ~~call type~~ syllable call type.

However, reviewing spectrograms of other species' calls, available in the literature, reveals that our findings

are not unique for banded mongooses. For example, the well-known 'whine-chuck' advertisement call of the

~~tungara~~túngara frog (*Physalaemus pustulosus*) provides another example of segregation of information

within a single syllable, where whines encode the species identity and the chucks refer to male

quality [45, 46]. Such a system is highly advantageous in providing detailed reliable information in an

otherwise ambiguous graded system regarding ongoing contexts.

Human speech [44, 47–49], and elements of some other species' vocal repertoires such as Barbary macaque

(*Macaca sylvanus*) [50, 51], chimpanzee (*Pan troglodytes*) [52, 53] and Japanese macaque (*Macaca*

fuscata) [44] are, from the production side, classified as a graded system, yet perceived by the receivers as

discrete [49–52, 54]. Graded signals have the potential to convey subtle and complex information, but

potentially suffer from heightened ambiguity [44, 55]. This ambiguity can partly be resolved by meaningful

within-category classification of a graded signal into perceptually discrete signals [55, 56]. It has been

hypothesized that this perception of a graded continuum as a series of discrete units was a crucial stage in

the evolution of human language [54, 55]. This analogous ability in banded mongoose demonstrates that

animal communication systems also have the potential to convey a rich set of information in an

acoustically sophisticated way.

Recent studies have shown that some free ranging primates use meaningful call- and element-combinations

to vastly increase the range of information that can be decoded by listeners [3, 3, 4, 57–62]. This may be

particularly important for forest species living in dense vegetation, where no visual cues can be used to

verify the information content or context of the signal [3,4]. In the same way, we suggest species that use vocal ~~signatures~~vocal cues ultimately benefit from an increased informational repertoire, and therefore similar species demonstrating combinatorial calling behavior could be expected to make use of multiple vocal ~~signatures~~vocal cues and therefore benefit from temporal segregation of information. ~~Vocal signature~~Vocal cues predominantly encode individual related cues of the sender (e.g. identity or male quality) and we therefore predict temporal segregation to evolve when signalers could benefit from unambiguous multiple ~~signatures~~vocal cues. Call combinations have been hypothesized to occur in response to discrete external events (e.g. alarm calls) or behavioral contexts, but not directly related to characteristics of the signaler [3,62]. Species with graded vocal systems would especially benefit from the use of unambiguous vocal signatures, since these would; i) avoid the ~~lack of~~ ambiguity that generally occurs in graded vocalizations, and ii) potentially enhance the reliability of categorization by receivers of graded signals into discrete units.

Conclusion

In summary, our results show that considerable variation underlies the close calls of banded mongooses with specific information in segregated ~~vocal signatures~~vocal cues. Through the segregation of acoustic information the potential trade-off in reliability between vocal signatures can be avoided. Many nonhuman-animals have small vocal repertoires [3,4,63] and call combinations are one way animals can get around the limited information content of a finite vocal repertoire size. Here we demonstrate for the first time that reliable~~vocal signatures~~vocal cues provide an equally effective solution to this problem and represent an additional dimension to the complexity underlying information coding in animal vocal communication. To what extent these are used throughout the animal kingdom is an important question to be addressed in the future, as it helps us to identify the selective pressures that gave rise to these kind of abilities in ~~animals, and in humans~~human and non-human animals.

Methods
Study population

The study site was located in Uganda, in the Queen Elisabeth National park (0°12S; 29°54E). The study site and the habituated population have been described in detail elsewhere [27,64]. During the period of data collection (February 2009 - July 2011), the study population consisted of six habituated groups and three semi-habituated groups, with group sizes ranging from 6 to 50+ individuals. In five groups, most

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¹ individuals were habituated to a level that allowed us to follow them with a microphone and to do detailed

² focal watches. As part of the Banded Mongoose Research Project long term data collection protocol, all

³ animals were tagged with subcutaneous transponders (TAG-P-122GL, Wyre Micro Design Ltd,, UK),

⁴ whereas for field identification individuals were given small hair cuts or, for less habituated fully grown

⁵ adults, color-coded plastic collar (weight $\leq$ 1.5 g, regularly checked to ensure a loose fit) [64].

Recording methods

⁷ All close calls used in the acoustic analysis were recorded from well habituated adult (~~less then~~$\geq$ 1 year)

⁸ banded mongooses at a distance of approximately 1-2 m, using a Sennheiser directional microphone

⁹ (ME66/K6 and a MZW66 pro windscreen, frequency response 40-20000 Hz $\pm$ 2.5 dB, Old Lyme,

¹⁰ Connecticut, U.S.A.) connected to a Marantz PMD-660 solid state (Marantz Japan Inc.), or a M-Audio

¹¹ Microtrack II (Avid Technology USA Inc). Calls were recorded in wav format with 16 bits and 44.1 kHz.

¹² Calls were recorded as part of detailed behavioral focal watches or during Ad Libitum sampling recording

¹³ sessions. In 2009, audio recordings were made at the same time as video focal watches to record behavior

¹⁴ (Canon HF100); in 2010/11, commentaries on behavior were added to the audio recording. It was noted

¹⁵ whether the individual was a.) digging, b.) searching, or c.) moving within the foraging patch of the group

¹⁶ (Table 1 and for details of behavior see [65]). For the acoustic analysis, calls with high signal-to-noise ratio

¹⁷ were selected, using Avisoft SASLab Pro 5.18 (R. Specht, Berlin, Germany) [66]. Only individuals for

¹⁸ which we had at least five calls for at least two of the behavioral contexts were included in the analysis.

¹⁹ For individuals for which more than five calls were available, we randomly selected five calls [67].

Acoustic analysis

²¹ ~~To increase the quality of measurements and reduce low pitched background noise (e.g. wind disturbance)~~

²² ~~a high-pass FIR filter was used. This removed noise below 200 Hz.~~ A 1024-point fast Fourier

²³ transformation (Hamming window; time step: 0.07 ms; overlap: 96.87%; frequency range: 44.1 kHz;

²⁴ frequency resolution: 43 Hz) was conducted for all calls, using Avisoft. We manually assigned labels to the

²⁵ whole call, the noisy base of the call and, if present, the harmonic part of the call (Figure 1). We then used

²⁶ a batch processing option to obtain automatic measurements for ~~16~~12 parameters (Table 4). The minimum

²⁷ frequency is the lowest frequency having an amplitude exceeding the threshold (-20dB), whilst the

²⁸ maximum frequency is the highest frequency having an amplitude exceeding threshold. The bandwidth is

²⁹ the difference between minimum and maximum frequency. These quartile variables characterize the

1 distribution of energy across the spectrum and indicate the below which frequency at respectively 25, 50 or

2 75% of the energy can be found. The distance between quartile 75% and quartile 25% is a measure of the

3 pureness of the sound. The 50% quartile also indicated the mean frequency. All mean frequency measures

4 were obtained from the mean spectrum of each call or call component, while the 3 quartiles were also

5 measured from the point within the call or call component that had the maximum amplitude [66]. We also

6 calculated the transition onset (frequency of fundamental frequency (F0) at the onset of call minus

7 frequency of F0 at the middle of the call) and offset (frequency of F0 at the middle of the call minus

8 frequency of F0 at the end of the call) [7]. The automatic measurements were checked by visual inspection

9 of the graphic results of the measurements in the spectrograms. ~~Besides spectrographic measurements, we~~

10 ~~performed a pulse-train analysis to obtain temporal measurements of the waveform. We used a~~

11 ~~Rectification + Exponential decay method to calculate the amplitude envelope (time constant 1 ms,~~

12 ~~threshold 0.15 V and hysteresis 8 dB). Thereafter, a Peak Search with Hysteresis method was used to~~

13 ~~detect the pulses in the envelope (hysteresis 8 dB and start/end threshold -3 dB). By using the group~~

14 ~~analysis option, we could use the same labeled sections as used in the pulse-train analysis.~~

15 **Statistical analysis**

16 We conducted all ~~analyzes~~ analyses in R, version 2.14 (R Development Core Team 2010), using the

17 software packages 'car' [68], 'kla' [69], 'lme4' [70] and 'MASS' [71]. The ~~analyzes~~analyses described below

18 were done on the whole call, on the 'noisy' base of the call and, and if present, on the 'harmonic part' of

19 the call (Figure 1). ~~To determine whether close calls differed in their acoustic structure between the~~

20 ~~behavioral contexts,~~ We performed linear mixed effect models on the acoustic variables to calculating

21 variance inflation factors and obtaining a subset of acoustic parameters that was free from multicollinearity

22 as this is essential for the proper functioning of the Discriminant Function Analysis (DFA). It has been

23 argued that conventional DFA provides grossly inflated levels of overall significance of discriminability

24 when using multiple samples of the same individual [67] and that in such cases a permuted Discriminant

25 Function Analysis (pDFA) should be used). We controlled for repeated sampling of groups and individuals

26 by fitting 'individual' nested in 'group' as a random factor [72]. We used an adapted form of the variance

27 inflation factors (VIF) analysis that worked directly on predictors in lmer models (Austin Frank, pers.

28 comm.) to detect multicollinearity in the acoustic parameters. Only parameters with a VIF ≤ 2.5 were

29 included in the ~~analyzes~~analyses. The remaining parameters were entered into a ~~Discriminant Function~~

30 ~~Analysis (DFA)~~ DFA to determine the correct classification probabilities of close calls to a) behavior while

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controlling for individual and b) for individuals while controlling for behavior. DFA identifies linear combinations of predictor variables that best characterize the differences among groups and combines the variables into one or more discriminant functions, depending on the number of groups to be classified [69, 71]. This method of ~~analyzes~~analyses provides a classification procedure that assigns each call to its appropriate class (correct assignment) or to another class (incorrect assignment). A stepwise variable selection was performed for the DFA. The initial model consisted of the parameters that remained after the selection with the linear effect model and the VIF analysis; in subsequent steps new models were generated by either including or excluding single variables in the model. This resulted in a performance measure for these models that were estimated by cross-validation, and if the maximum value of the chosen criterion was better than the previous model, the corresponding variable was included or excluded. This procedure was stopped once the new best value, after including or excluding any variable, did not exceed a 5% improvement. The number and type of variables included in the analysis different per analysis and sub-analysis. Duration was included in all behavioral context specific tests. The number of variables included was smaller than the number of individuals included in the test [67]. For external validation, we used a leave-one-out cross-validation procedure and estimated the significance levels for correct statistical assignment of calls using post hoc 'bootstrapping' ~~analyzes~~ analyses. This method determined the probability that a cross-validated correct assignment value was achieved by chance [32].outIt has been argued that conventional DFA provides grossly inflated levels of overall significance of discriminability when using multiple samples of the same individual [67]. Our data for behavioral, group and sex ~~signatures~~vocal cues were two factorial (test factor and individual) and contained five call examples per individual, we therefore used a crossed pDFA (Mundry, pers. comm.). Furthermore, to ensure no differences resulted from variation in sex or group, we also performed pDFA's whilst keeping these two additional variables constant. We performed 4 pDFA to test for overall and the pairwise comparison between behavioral contexts. In addition we performed 2 additional pDFA to test for the group signature (while controlling for individual) and for sex cue (again while controlling for individual). From one of the groups, we did not have calls from a large enough number of individuals to perform a classification analysis, and therefore the group ~~signature~~ vocal cue analysis was done on four groups only.

Ethical note

This research was carried out under license from the Uganda National Council for Science and Technology, and all procedures were approved by the Uganda Wildlife Authority. Trapping and marking procedures,

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which are part of the long term research program, followed the guidelines of the Association for the Study of Animal behavior [29, 64].

Abbreviations

DFA: discriminant function analysis; F0: fundamental frequency; ncce: number of correctly cross-classified elements; pDFA: permutated discriminant function analysis; VIF: variance inflation factors;

Author's contributions

DJ designed the study, collected data in the field, analyzed the data and wrote manuscript. MC assisted in writing the manuscript and provided logistical support in the field. MM designed research and wrote paper. All authors read and approved the final manuscript.

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References

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

2. Hammerschmidt K, Fischer J: **Constraints in primate vocal production**. In *The evolution of communicative creativity: From fixed signals to contextual flexibility.*. Edited by Griebel U, K O, The MIT Press, Cambridge. MA, pp 2008:93–119.

3. Arnold K, Zuberbühler K: **The alarm-calling system of adult male putty-nosed monkeys, *Cercopithecus nictitans martini***. *Animal Behaviour* 2006, **72**(3):643–653.

4. Arnold K, Zuberbühler K: **Meaningful call combinations in a non-human primate**. *Current Biology* 2008, **18**(5):R202–R203.

5. Janik V, Dehnhardt G, Todt D: **Signature whistle variation in a bottlenosed dolphin, *Tursiops truncatus***. *Behavioral Ecology and Sociobiology* 1994, **35**:243–248.

6. Sayigh LS, Tyack PL, Wells RS, Solow AR, Scott MD, Irvine AB: **Individual recognition in wild bottlenose dolphins: a field test using playback experiments**. *Animal Behaviour* 1999, **57**:41–50.

7. Townsend SW, Hollen LI, Manser MB: **Meerkat close calls encode group-specific signatures, but receivers fail to discriminate**. *Animal Behaviour* 2010, **80**:133–138.

8. Shapiro A: **Recognition of individuals withing social group: signature vocalizations**. In *Handbook of mammalian vocalization*. Edited by Brudzynski S, Elsevier 2010:495–503.

9. Briefer E, Aubin T, Lehongre K, Rybak F: **How to identify dear enemies: the group signature in the complex song of the skylark *Alauda arvensis***. *Journal of Experimental Biology* 2008, **211**(3):317–326.

10. Crockford C, Herbinger I, Vigilant L, Boesch C: **Wild chimpanzees produce group-specific calls: a case for vocal learning?** *Ethology* 2004, **110**(3):221–243.

11. Boughman JW, Wilkinson GS: **Greater spear-nosed bats discriminate group mates by vocalizations**. *Animal Behaviour* 1998, **55**(6):1717–1732.

12. Fischer J, Kitchen D, Seyfarth R, Cheney D: **Baboon loud calls advertise male quality: acoustic features and relation to rank, age, and exhaustion.** *Behavioral Ecology and Sociobiology* 2004, **56**:140–148.

13. Briefer E, Vannoni E, McElligott AG: **Quality prevails over identity in the sexually selected vocalisations of an ageing mammal**. *BMC Biology* 2010, **8**(35):1–15.

14. Bradbury J, Vehrencamp SL: *Principles of animal communication*. Cornell University 1998.

15. Charlton BD, Zhang Z, Snyder RJ: **Vocal cues to identity and relatedness in giant pandas (*Ailuropoda melanoleuca*)**. *Journal of the Acoustical Society of America* 2009, **126**(5):2721–2732.

16. Mathevon N, Koralek A, Weldele M, Glickman SE, Theunissen FE: **What the hyena's laugh tells: Sex, age, dominance and individual signature in the giggling call of *Crocuta crocuta***. *BMC Ecology* 2010, **10**:9.

17. Charlton BD, Keating JL, Li R, Yan H, Swaisgood RR: **Female giant panda (*Ailuropoda melanoleuca*) chirps advertise the caller's fertile phase**. *Proceedings of the Royal Society of London Series B-biological Sciences* 2010, **277**(1684):1101–1106.

18. Marler P: **Bird song and mate selection**. In *Animal sounds and communication*. Edited by Lanyon W, Tavalga W 1960:348–367.

19. Nelson DA, Poesel A: **Segregation of information in a complex acoustic signal: individual and dialect identity in white-crowned sparrow song**. *Animal Behaviour* 2007, **74**:1073–1084.

20. Kondo N, Watanabe S: **Contact calls: Information and social function**. *Japanese Psychological Research* 2009, **51**(3):197–208.

21. DaCunha RGT, Byrne R: **The use of vocal communication in keeping the spatial cohesion of groups: intentionality and specific functions**. In *South American primates: comparative perspectives in the study of behavior, ecology, and conservation.*. Edited by Garber PA, Estrada A, Bicca-Marques JC, Heymann E, K S, Springer Press. 2008:341–363.

22. Arnold BD, Wilkinson GS: **Individual specific contact calls of pallid bats (*Antrozous pallidus*) attract conspecifics at roosting sites**. *Behavioral Ecology and Sociobiology* 2011, **65**(8):1581–1593.

23. Jameson J, Hare J: **Group-Specific Signatures in the Echolocation Calls of Female Little Brown Bats (*Myotis lucifugus*) are Not an Artefact of Clutter at the Roost Entrance**. *Acta Chiropterologica 2009* 2009, **11**:163–172.

24. Harcourt A, Stewart K, Hauser M: **Functions of Wild Gorilla 'Close' Calls. 1. Repertoire, Context, and Interspecific Comparison**. *Behaviour* 1993, **124**(1-2):89–112.

25. Townsend SW, Zoettl M, Manser MB: **All clear? Meerkats attend to contextual information in close calls to coordinate vigilance**. *Behavioral Ecology and Sociobiology* 2011, **65**(10):1927–1934.

26. Townsend SW, Allen C, Manser: **A simple test of vocal individual recognition in wild meerkats**. *Biology Letters* 2012, **8**(2):179–182.

27. Cant MA: **Communal breeding in banded mongooses and the theory of reproductive skew**. *PhD thesis*, University of Cambridge, Cambridge 1998.

28. Rood AP: **Population dynamics and food habits of the banded mongoose**. *East Africa Wildlife Journal* 1975, **13**:89–111.

29. Cant MA: **Social control of reproduction in banded mongooses**. *Animal Behaviour* 2000, **59**:147–158.

30. Messeri P, Masi E, Piayya R, Dessifulgheri F: **A study of the vocal repetoire of the banded mongoose (Mungos mungo)**. *Monitore Zoologico Italiano-Italian Journal of Zoology* 1987, **Suppl. 22**:341–73.

31. Furrer R: **Leadership and Group-Decision-Making in Banded Mongooses (Mungos mungo)**. *PhD thesis*, Zurich University, Zurich 2009.

32. Müller CA, Manser MB: **Mutual recognition of pups and providers in the cooperatively breeding banded mongoose**. *Animal Behaviour* 2008, **75**(5):1683–1692.

33. Briefer M E: **Social effects on vocal ontogeny in an ungulate, the goat (*Capra hircus*)**. *Animal Behaviour* 2012, **83**:991–1000.

34. Candiotti ZKL A: **Convergence and divergence in Diana monkey vocalizations.** *Biology Letters* 2012, **8**(3):382–385.

35. Elfstörm ST: **Responses of Territorial Meadow Pipits To Strange and Familiar Song Phrases In Playback Experiments**. *Animal Behaviour* 1990, **40**(4):786–788.

36. Koren L, Geffen E: **Complex call in male rock hyrax: a multi-information distributing channel.** *Behavioral Ecology and Sociobiology* 2009, **63**:581–590.

37. Payne R, McVay S: **Songs of humpback whales**. *Science* 1971, **173**:57–64.

38. Ford J: **Acoustic behavior of resident killer whales (Orcinus orca) off Vancouver Island, British Columbia**. *Canadian Journal of Zoology* 1989, **67**:727–745.

39. Hauser M, Tecumseh F: **What Are the Uniquely Human Components of the Language Faculty? Marc D. Hauser and W. Tecumseh Fitch**. In *Language Evolution: The States of the Art*. Edited by Christiansen M, Kirby S, Oxford University Press. 2003.

40. Stern T: **Drum and Whistle "Languages": An Analysis of Speech Surrogates**. *American Anthropologist* 1957, **59**(3):487–506.

41. Meyer J, Gautheron B: **(2006), Whistled Speech and Whistled Languages.** In *Encyclopedia of Language and Linguistics, Volume 13*. Edited by Brown K, Elsevier 2006:573–576.

42. Todd S: *The pilot's handbook*. Pilot Handbook Publishing, LLC 2009.

43. Ong W: **African Talking Drums and Oral Noetics**. *New Literary History* 1977, **8**(3):411–429.

44. Green S: **Variation of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): A field study.** *Primate Behavior, Developments in Field and Laboratory Research* 1975, **2**:1–102.

45. Ryan M: **Frequency modulated calls and species recognition in a Neotropical frog.** *Journal of Comparative Physiology* 1983, **150**:217–221.

46. Ryan M: **Sexual selection and communication in a Neotropical frog, *Physalaemus pustulosus*.** *Evolution* 1983, **39**:261–272.

47. Nelson D, Marler: **Categorical perception of natural stimulus continuum; birdsong**. *Science* 1990, **244**:976–979.

48. Dooling R: **Hearing in Birds**. In *The Evolutionary Biology of Hearing*. Edited by Webster D, Fay R, Popper A 1992:545–560.

49. Hauser M: *The evolution of communication*. Cambridge: MIT Press 1996.

50. Fischer J, Hammerschmidt K, Todt D: **Factors affecting acoustic variation in Barbary-macaque (Macaca sylvanus) disturbance calls**. *Ethology* 1995, **101**:51–66.

51. Fischer J, Hammerschmidt K: **Functional referents and acoustic similarity revisited: the case of Barbary macaque alarm calls**. *Animal Cognition* 2001, **4**:29–35.

52. Slocombe KE, Townsend SW, Zuberbühler K: **Wild chimpanzees (Pan troglodytes schweinfurthii) distinguish between different scream types: Evidence from a playback study**. *Animal cognition* 2009, **12**:441–449.

53. Marler P, Mundinger P: **Vocalizations, social-organization and breeding biology of twite Acanthus flavirostris**. *Ibis* 1975, **117**:1 − 6.

54. Marler P: **Social organization, communication and graded signals: the chimpanzee and the gorilla**. In *Growing points in ethology*. Edited by Bateson P, Hinde R 1976:239–281.

55. Marler P: **The role of Speech language**. In *The role of Speech language.*. Edited by Kavanagh J, Cambridge, MA. USA: Cambridge University Press, MA 1975:11–37.

56. Harnad S: *Categorical perception : the groundwork of cognition*. Cambridge University Press 1987.

57. Crockford C, Boesch C: **Call combinations in wild chimpanzees**. *Behaviour* 2005, **142**:397–421.

58. Clarke E, Reichard UH, Zuberbühler K: **The Syntax and Meaning of Wild Gibbon Songs**. *PLoS ONE* 2006, **1**:e73.

59. Schel AM, Tranquilli S, Zuberbühler K: **The Alarm Call System of Two Species of Black-and-White Colobus Monkeys (*Colobus polykomos* and *Colobus guereza*)**. *Journal of Comparative Psychology* 2009, **123**(2):136–150.

60. Endress AD, Cahill D, Block S, Watumull J, Hauser MD: **Evidence of an evolutionary precursor to human language affixation in a non-human primate**. *Biology Letters* 2009, **5**(6):749–751.

61. Ouattara K, Lemasson A, Zuberbühler K: **Anti-predator strategies of free-ranging Campbell's monkeys**. *Behaviour* 2009, **146**:1687–1708.

62. Ouattara K, Lemasson A, Zuberbühler K: **Campbell's monkeys concatenate vocalizations into context-specific call sequences**. *Proceedings of the National Academy of Sciences of the United States of America* 2009, **106**(51):22026–22031.

63. Zuberbühler K: **Referential signaling in non-human primates: Cognitive precursors and limitations for the evolution of language**. *Advances in the Study of Behavior* 2003, **33**:265–307.

64. Jordan NR, Mwanguhya F, Kyabulima S, Rueedi P, Cant MA: **Scent marking within and between groups of wild banded mongooses**. *Journal of Zoology* 2010, **280**:72–83.

65. Bousquet C, Sumpter D, MB M: **Moving calls: a vocal mechanism underlying quorum decisions in cohesive groups.** *Proceedings of the Royal Society of London Series B-biological Sciences* 2011, **287**:1482–1488.

66. Specht R: *Avisoft SASLab Pro. User's Guide for version 5.1*. Avisoft Bioacoustics 2011.

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

68. Fox S John Weisberg: *An R Companion to Applied Regression*. Sage Publications, 2nd edition 2011.

69. Weihs C, Ligges U, Luebhe K, Raabem N: **klaR Analyzing German Business Cycles**. In *Data analysis and decision support*. Edited by Baier D, Decker R, Schmidt-Thieme L, Berlin 2005:335–343.

70. Bates D: *lme4: Mixed-effects modeling with R*. Springer 2011.

71. Venables B W N Ripley: *Modern Applied Statistics with S*. Springer Berlin Heidelberg, 4th edition 2002.

72. Crawley M: *The R book*. John Wiley 2007.

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Figures

Figure 1 - Spectrograms of banded mongoose close calls

Spectrograms of close calls of the same female associated with the three different behavioral contexts: a)
digging; b) searching; c) moving between foraging patches. The solid black arrow indicates the individually
stable foundation of the call, while the dashed arrow indicates the harmonic tonal element (Hamming,
FTT=1024, overlap=97.87%, frequency resolution=43h)

Tables

Table 1 - Definitions of the different behavioral context used for the acoustical analysis.

Context	Definition
Digging	The caller was digging for or eating food, animal was not moving and head was faced downward.
Searching	The caller was searching for food in and around the same foraging patch, head was predominately faced downward.
Moving	The caller was moving between foraging patches but within the spatial cohesion of the group and head was predominately faced forward.

Table 2 - Individual ~~signature~~ vocal cue classification

The percentage of correct classification after cross-validation (CV) to individuals within each of the four study groups compared to that expected by chance.

Group	$\#^a$	Random $(\%)^b$	Whole call CV-values (%)	Noisy part CV-values (%)	Harmonic part CV-values (%)
1B	8	12.5	48.1***	45.0***	25.0
1H	14	7	26.1*	40.0***	11.4
11	7	14	42.0***	48.0***	22.0
15	7	14	61.5***	61.1***	22.5

[a] Number of individuals tested
[b] Expected by ~~change~~chance
Results for both the whole call and the noisy part are given; Results for the whole call, noisy part and harmonic part are given; p–values are derived from bootstrapping method [32];
$^\bullet p \leq 0.1$, $^* p \leq 0.05$, $^{**} p \leq 0.01$, $^{***} p \leq 0.001$

Table 3 - Behavioral ~~signature~~ vocal cue classification

The pDFA classification results for pairwise comparisons between behaviors.

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Part analyzed	Behavior	Individuals	ncce
Whole call	digging–searching	30	3.340[•]
	digging–moving	25	40.640[***]
	searching–moving	20	30.610[***]
Noisy part	digging–searching	30	1.500
	digging–moving	25	34.850
	searching–moving	20	23.100
Harmonic part	digging–searching	18	78.040[***]
	digging–moving	30	77.440[***]
	searching–moving	30	67.600[**]

Results for both the whole call and the noisy part are given; Results for the whole call, noisy part and harmonic part are given; The results of the pDFA is the number of correctly cross-classified elements (ncce); $•p \leq 0.1$, $*p \leq 0.05$, $**p \leq 0.01$, $***p \leq 0.001$

Table 4 Overview of parameters used and their values

Overview of parameters used and their values per call part (mean $\pm$ (sd).

Acoustic parameters		Whole call		
		Digging	Moving	Searching
Duration	(s)	$0.05 \pm (0.02)$	$0.12 \pm (0.04)$	$0.09 \pm (0.04)$
Bandwidth	(mean Hz)	$1472 \pm (428)$	$1526 \pm (378)$	$1439 \pm (382)$
F0	(mean Hz)	$263 \pm (100)$	$467 \pm (89)$	$380 \pm (110)$
Onset		$20 \pm (150)$	$-456 \pm (1752)$	$-205 \pm (1020)$
Offset		$-133 \pm (814)$	$204 \pm (1694)$	$-184 \pm (1781)$
Max freq.	(mean Hz)	$1587 \pm (427)$	$1675 \pm (373)$	$1575 \pm (375)$
Min. freq.	(mean Hz)	$114 \pm (31)$	$149 \pm (55)$	$135 \pm (43)$
Peak frequency	(mean Hz)	$370 \pm (167)$	$490 \pm (123)$	$404 \pm (106)$
Quartile 25%	(mean Hz)	$430 \pm (74)$	$525 \pm (82)$	$469 \pm (73)$
Quartile 50%	(mean Hz)	$753 \pm (96)$	$918 \pm (213)$	$846 \pm (199)$
Quartile 75%	(mean Hz)	$1426 \pm (539)$	$2730 \pm (1748)$	$2217 \pm (1615)$
Quartile 25%	(max Hz)	$454 \pm (77)$	$533 \pm (77)$	$481 \pm (78)$
Quartile 50%	(max Hz)	$802 \pm (123)$	$942 \pm (184)$	$898 \pm (240)$
Quartile 75%	(max Hz)	$1803 \pm (1033)$	$2734 \pm (1745)$	$2507 \pm (1738)$
		Inital noisy part		
		Digging	Moving	Searching
Duration	(s)	$0.04 \pm (0.01)$	$0.03 \pm (0.01)$	$0.03 \pm (0.01)$
Bandwidth	(mean Hz)	$1534 \pm (457)$	$1542 \pm (473)$	$1534 \pm (426)$
F0	(mean Hz)	$225 \pm (94)$	$249 \pm (138)$	$218 \pm (92)$
Onset		$45 \pm (138)$	$127 \pm (963)$	$44 \pm (186)$
Offset		$-46 \pm (129)$	$-146 \pm (951)$	$-79 \pm (713)$
Max freq.	(mean Hz)	$1646 \pm (455)$	$1654 \pm (470)$	$1650 \pm (417)$
Min. freq.	(mean Hz)	$112 \pm (26)$	$112 \pm (28)$	$116 \pm (30)$
Peak frequency	(mean Hz)	$380 \pm (186)$	$378 \pm (195)$	$363 \pm (178)$
Quartile 25%	(mean Hz)	$439 \pm (74)$	$473 \pm (90)$	$450 \pm (79)$
Quartile 50%	(mean Hz)	$754 \pm (92)$	$838 \pm (163)$	$795 \pm (110)$
Quartile 75%	(mean Hz)	$1329 \pm (387)$	$2300 \pm (1744$	$1787 \pm (1250$
Quartile 25%	(max Hz)	$465 \pm (77)$	$497 \pm (96)$	$473 \pm (83)$
Quartile 50%	(max Hz)	$797.3 \pm (100)$	$914 \pm (270)$	$849 \pm (157)$
Quartile 75%	(max Hz)	$1654 \pm (865)$	$2847 \pm (1997)$	$2234 \pm (1612)$
		Harmonic extension		
		Digging	Moving	Searching
Duration	(s)	$0.03 \pm (0.02)$	$0.08 \pm (0.04)$	$0.06 \pm (0.03)$
Bandwidth	(mean Hz)	$1185 \pm (405)$	$1307\pm (394)$	$1283 \pm (474)$
F0	(mean Hz)	$350 \pm (70)$	$18 \ 472 \pm (83)$	$410 \pm (82)$
Onset		$-10 \pm (59)$	$-83.0 \pm (1444)$	$-6 \pm (789)$
Offset		$-177\pm (1294)$	$-19 \pm (1134)$	$-176.4 \pm (1284)$
Max freq.	(mean Hz)	$1343 \pm (408)$	$1572 \pm (390)$	$1513 \pm (463)$
Min. freq.	(mean Hz)	$158 \pm (83)$	$264 \pm (93)$	$230 \pm (97)$

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