

Temporal segregation of individual and behavioral signatures in banded mongoose close calls

David A.W.A.M. Jansen^{*1} , Michael A. Cant² and Marta B. Manser¹

¹ Animal Behaviour, Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, CH-8057, Switzerland, Zurich

² Daphne du Maurier, Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Cornwall Campus, TR10 9EZ, UK

Email: David A.W.A.M. Jansen^{*} - david.awam.jansen@gmail.com; Michael A. Cant - M.A.Cant@exeter.ac.uk; Marta B. Manser - marta.manser@ieu.uzh.ch;

^{*} Corresponding author

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' to increase the information encoded in their vocalizations. However, encoding multiple vocal signatures 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*) encode multiple vocal signatures 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, 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. 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 temporal segregation of information in a mammalian 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 of vocal signatures is a new and wholly unexplored dimension of information coding in animal vocal communication. We argue that temporal segregation of vocal signatures evolves in species where communication of multiple unambiguous signals is crucial, but is limited by the number of call types produced.

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

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 [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], male quality [12–14], sex [15,16], and reproductive state [17].

Animals can encode signature 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 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]. Vocal signatures potentially provide useful information to the receiver whenever the within-category variation is smaller than the between-category variation [8]. Furthermore, previous research has shown that calls can contain combinations of different signatures [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 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 [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 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 [13,18]. In the 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 [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.

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 [5,7,8,22] and group membership signatures [7,9,11,23]. Contact calls can also contain multiple signatures (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 ($\leq 2\text{kg}$) 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 4 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 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 banded mongooses close calls contain multiple vocal signatures in their close calls, and how these are encoded in the temporal and spectral related aspects of a 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 considerable lower at 11 to 25% and were not significantly different than expected by chance (Table 1). A group-specific signature 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 was found in neither 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 context 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 2.

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 in the same call. 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 of these close calls are meaningful to receivers. Additionally, we provide evidence for group specific signatures. 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. In contrast, temporal features (e.g. duration) of the tonal harmonic second element of the call seem to encode the behavioral signature.

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. 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 frog (*Physalaemus pustulosus*) provides another example of segregation of information, where whines encode the species identity and the chucks refer to male quality [33,34]. Such a system is highly advantageous in providing detailed reliable information in an otherwise ambiguous graded system regarding ongoing contexts.

Human speech [35–38], and elements of some other species' vocal repertoires such as Barbary macaque (*Macaca sylvanus*) [39,40], chimpanzee (*Pan troglodytes*) [41,42] and Japanese macaque (*Macaca fuscata*) [37] are, from the production side, classified as a graded system, yet perceived by the receivers as discrete [38–41,43]. Graded signals have the potential to convey subtle and complex information, but potentially suffer from heightened ambiguity [37,44]. This ambiguity can partly be resolved by meaningful within-category classification of a graded signal into perceptually discrete signals [44,45]. 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 [43,44]. 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.

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. Such a system of encoding individuality mimics to some extent, from a functional perspective, pronouns in human language, where discrete words are used to signal the actor ('I, John'), and this remains consistent irrespective of the change in behavior ('I John eat', 'I John search', 'I John move'). 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 [46,47]. Similar, 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) [48]. Signals in these ‘conversations’ are intentionally selected for their unambiguity to the receivers [37,49]. 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.

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 [3,3,4,50–55]. 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 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 and therefore benefit from temporal segregation of information. Vocal signatures 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. 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 [3,55]. 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. 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 [3,4,56] 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 provide 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.

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, 57]. 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 individuals were habituated to a level that allowed us to follow them with a microphone and to do detailed focal watches. As part of the Banded Mongoose Research Project long term data collection protocol, all animals were tagged with subcutaneous transponders (TAG-P-122GL, Wyre Micro Design Ltd., UK), whereas for field identification individuals were given small hair cuts or, for less habituated fully grown adults, color-coded plastic collar (weight ≤ 1.5 g, regularly checked to ensure a loose fit) [57].

Recording methods

All close calls used in the acoustic analysis were recorded from well habituated adult (less than 1 year) banded mongooses at a distance of approximately 1-2 m, using a Sennheiser directional microphone (ME66/K6 and a MZW66 pro windscreen, frequency response 40-20000 Hz \pm 2.5 dB, Old Lyme, Connecticut, U.S.A.) connected to a Marantz PMD-660 solid state (Marantz Japan Inc.), or a M-Audio Microtrack II (Avid Technology USA Inc). Calls were recorded as part of detailed behavioral focal watches or during Ad Libitum sampling recording sessions. In 2009, audio recordings were made at the same time as video focal watches to record behavior (Canon HF100); in 2010/11, commentaries on behavior were added to the audio recording. It was noted whether the individual was a.) digging, b.) searching, or c.) moving within the foraging patch of the group (Table 4 and for details of behavior see [58]). For the acoustic analysis, calls with high signal-to-noise ratio were selected, using Avisoft SASLab Pro 5.18 (R. Specht, Berlin, Germany). Only individuals for which we had at least five calls for at least two of the behavioral contexts were included in the analysis. For individuals for which more than five calls were available, we randomly selected five calls (Mundry and Sommer, 2007).

Acoustic analysis

To increase the quality of measurements and reduce low pitched background noise (e.g. wind disturbance) a high-pass FIR filter was used. This removed noise below 200 Hz. A 1024-point fast Fourier transformation (Hamming window; time step: 0.07 ms; overlap: 96.87%; frequency range: 44.1 kHz; frequency resolution: 43 Hz) was conducted for all calls, using Avisoft. We manually assigned labels to the whole call, the noisy base of the call and, if present, the harmonic part of the call (Figure 1). We then used a batch processing option to obtain automatic measurements for 16 parameters (Table 3). We also calculated the transition onset (frequency of fundamental frequency (F0) at the onset of call minus frequency of F0 at the middle of the call) and offset (frequency of F0 at the middle of the call minus frequency of F0 at the end of the call) [7]. The automatic measurements were checked by visual inspection of the graphic results of the measurements in the spectrograms. Besides spectrographic measurements, we performed a pulse-train analysis to obtain temporal measurements of the waveform. We used a Rectification + Exponential decay method to calculate the amplitude envelope (time constant 1 ms, threshold 0.15 V and hysteresis 8 dB). Thereafter, a Peak Search with Hysteresis method was used to detect the pulses in the envelope (hysteresis 8 dB and start/end threshold -3 dB). By using the group analysis option, we could use the same labeled sections as used in the pulse-train analysis.

Statistical analysis

We conducted all analyzes in R, version 2.14 (R Development Core Team 2010), using the software packages ‘car’ [59], ‘kla’ [60], ‘lme4’ [61] and ‘MASS’ [62]. The analyses described below were done on the whole call, on the ‘noisy’ base of the call and, and if present, on the ‘harmonic part’ of the call (Figure 1). To determine whether close calls differed in their acoustic structure between the behavioral contexts, we performed linear mixed effect models on the acoustic variables. We controlled for repeated sampling of groups and individuals by fitting ‘individual’ nested in ‘group’ as a random factor [63]. We used an adapted form of the variance inflation factors (VIF) analysis that worked directly on predictors in lmer models (Austin Frank, pers. comm.) to detect multicollinearity in the acoustic parameters. Only parameters with a $VIF \leq 2.5$ were included in the analyses. The remaining parameters were entered into a Discriminant Function Analysis (DFA) to determine the correct classification probabilities of close calls to a) behavior while 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 [60,62]. This method of analyzes 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. 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. This method determined the probability that a cross-validated correct assignment value was achieved by chance [32]. It has been argued that conventional DFA provides grossly inflated levels of overall significance of discriminability when using multiple samples of the same individual [64]. Our data for behavioral, group and sex signatures 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. 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 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, which are part of the long term research program, followed the guidelines of the Association for the Study of Animal behavior [29,57].

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.

Acknowledgements

We are grateful to Uganda Wildlife Authority (UWA) and the Uganda National Council of Science and Technology for permission to work in Queen Elizabeth National Park. We especially thank Aggrey Rwetsiba at UWA HQ, Conservation Area Managers, Tom Okello and Nelson Guma, and Research and Monitoring Warden, Margaret Dricuru, for support in the park. We thank Kenneth Mwesige, Francis Mwanguhya, Solomon Kyabulima and Robert Businge for their invaluable support during the field work. We also want to thank Jenni Sanderson, Emma Vitikainen and Corsin Müller, who were great co-workers in the field. We are grateful to Roger Mundry for providing pDFA scripts, Austin Frank for providing the script to work on collinearity diagnostics of mixed effect models and Raimund Specht of Avisoft for technical support. We finally thank Tim Clutton-Brock for discussions, and Simon Townsend, Christophe Bousquet, and Jennifer Krauser for comments on the manuscript. Financial support was provided by the Institute of Evolutionary Biology and Environmental Studies, University of Zurich.

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 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, **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, Zoetl 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 MB: **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 repertoire 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. Ryan M: **Frequency modulated calls and species recognition in a Neotropical frog.** *Journal of Comparative Physiology* 1983, **150**:217–221.
34. Ryan M: **Sexual selection and communication in a Neotropical frog, *Physalaemus pustulosus*.** *Evolution* 1983, **39**:261–272.
35. Nelson D, Marler: **Categorical perception of natural stimulus continuum; birdsong.** *Science* 1990, **244**:976–979.
36. Dooling R: **Hearing in Birds.** In *The Evolutionary Biology of Hearing*. Edited by Webster D, Fay R, Popper A 1992:545–560.
37. 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.
38. Hauser M: *The evolution of communication*. Cambridge: MIT Press 1996.
39. Fischer J, Hammerschmidt K, Todt D: **Factors affecting acoustic variation in Barbary-macaque (*Macaca sylvanus*) disturbance calls.** *Ethology* 1995, **101**:51–66.
40. Fischer J, Hammerschmidt K: **Functional referents and acoustic similarity revisited: the case of Barbary macaque alarm calls.** *Animal Cognition* 2001, **4**:29–35.
41. 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.
42. Marler P, Mundinger P: **Vocalizations, social-organization and breeding biology of twite *Acanthus flavirostris*.** *Ibis* 1975, **117**:1 – 6.
43. 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.
44. 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.
45. Harnad S: *Categorical perception : the groundwork of cognition*. Cambridge University Press 1987.

46. Stern T: **Drum and Whistle "Languages": An Analysis of Speech Surrogates.** *American Anthropologist* 1957, **59**(3):487–506.
47. 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.
48. Todd S: *The pilot's handbook*. Pilot Handbook Publishing, LLC 2009.
49. Ong W: **African Talking Drums and Oral Noetics.** *New Literary History* 1977, **8**(3):411–429.
50. Crockford C, Boesch C: **Call combinations in wild chimpanzees.** *Behaviour* 2005, **142**:397–421.
51. Clarke E, Reichard UH, Zuberbühler K: **The Syntax and Meaning of Wild Gibbon Songs.** *PLoS ONE* 2006, **1**:e73.
52. 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.
53. 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.
54. Ouattara K, Lemasson A, Zuberbühler K: **Anti-predator strategies of free-ranging Campbell's monkeys.** *Behaviour* 2009, **146**:1687–1708.
55. 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.
56. 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.
57. 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.
58. Bousquet C, Sumpter D, MB M: **Moving calls: a vocal mechanism underlying quorum decisions in cohesive groups.** *Proceedings of the Royal Society B-Biological Sciences* 2011, **287**:1482–1488.
59. Fox S John Weisberg: *An R Companion to Applied Regression*. Sage Publications, 2nd edition 2011.
60. 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.
61. Bates D: *lme4: Mixed-effects modeling with R*. Springer 2011.
62. Venables B W N Ripley: *Modern Applied Statistics with S*. Springer Berlin Heidelberg, 4th edition 2002.
63. Crawley M: *The R book*. John Wiley 2007.
64. Mundry R, Sommer C: **Discriminant function analysis with nonindependent data: consequences and an alternative.** *Animal Behaviour* 2007, **74**:965–976.

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 - Individual signature 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 chance

Results for both the whole call and the noisy part are given; p -values are derived from bootstrapping method [32]; • $p \leq 0.1$, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

Table 2 - Behavioral signature classification

The pDFA classification results for pairwise comparisons between behaviors.

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; 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 3 Overview of parameters used and their valuesOverview 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)	1472 \pm (428)	1526 \pm (378)	1439 \pm (382)
F0 (mean)	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)	1587 \pm (427)	1675 \pm (373)	1575 \pm (375)
Min. freq. (mean)	114 \pm (31)	149 \pm (55)	135 \pm (43)
Peak frequency (mean)	370 \pm (167)	490 \pm (123)	404 \pm (106)
Quartile 25% (mean)	430 \pm (74)	525 \pm (82)	469 \pm (73)
Quartile 50% (mean)	753 \pm (96)	918 \pm (213)	846 \pm (199)
Quartile 75% (mean)	1426 \pm (539)	2730 \pm (1748)	2217 \pm (1615)
Quartile 25% (max)	454 \pm (77)	533 \pm (77)	481 \pm (78)
Quartile 50% (max)	802 \pm (123)	942 \pm (184)	898 \pm (240)
Quartile 75% (max)	1803 \pm (1033)	2734 \pm (1745)	2507 \pm (1738)
Variables	In ital noisy part		
	Digging	Moving	Searching
Duration (s)	0.04 \pm (0.01)	0.03 \pm (0.01)	0.03 \pm (0.01)
Bandwidth (mean)	1534 \pm (457)	1542 \pm (473)	1534 \pm (426)
F0 (mean)	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)	1646 \pm (455)	1654 \pm (470)	1650 \pm (417)
Min. freq. (mean)	112 \pm (26)	112 \pm (28)	116 \pm (30)
Peak frequency (mean)	380 \pm (186)	378 \pm (195)	363 \pm (178)
Quartile 25% (mean)	439 \pm (74)	473 \pm (90)	450 \pm (79)
Quartile 50% (mean)	754 \pm (92)	838 \pm (163)	795 \pm (110)
Quartile 75% (mean)	1329 \pm (387)	2300 \pm (1744)	1787 \pm (1250)
Quartile 25% (max)	465 \pm (77)	497 \pm (96)	473 \pm (83)
Quartile 50% (max)	797.3 \pm (100)	914 \pm (270)	849 \pm (157)
Quartile 75% (max)	1654 \pm (865)	2847 \pm (1997)	2234 \pm (1612)
Variables	Harmonic extension		
	Digging	Moving	Searching
Duration (s)	0.03 \pm (0.02)	0.08 \pm (0.04)	0.06 \pm (0.03)
Bandwidth (mean)	1185 \pm (405)	1307 \pm (394)	1283 \pm (474)
F0 (mean)	350 \pm (70)	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)	1343 \pm (408)	1572 \pm (390)	1513 \pm (463)
Min. freq. (mean)	158 \pm (83)	264 \pm (93)	230 \pm (97)
Peak frequency (mean)	350 \pm (88)	485 \pm (115)	409 \pm (84)
Quartile 25% (mean)	414 \pm (76)	536 \pm (89)	471 \pm (81)
Quartile 50% (mean)	769 \pm (316)	967 \pm (285)	895 \pm (301)
Quartile 75% (mean)	2346 \pm (1514)	2861 \pm (1927)	2784 \pm (2037)
Quartile 25% (max)	419 \pm (76)	546 \pm (91)	491 \pm (98)
Quartile 50% (max)	802 \pm (280)	976 \pm (210)	940 \pm (317)
Quartile 75% (max)	2505 \pm (1598)	2797.6 \pm (1821)	2801 \pm (1956)

Table 4 - 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.

Additional Files

S1

Example of a digging close call. (wav.file)

S2

Example of a searching close call. (wav.file)

S3

Example of a moving close call. (wav.file)

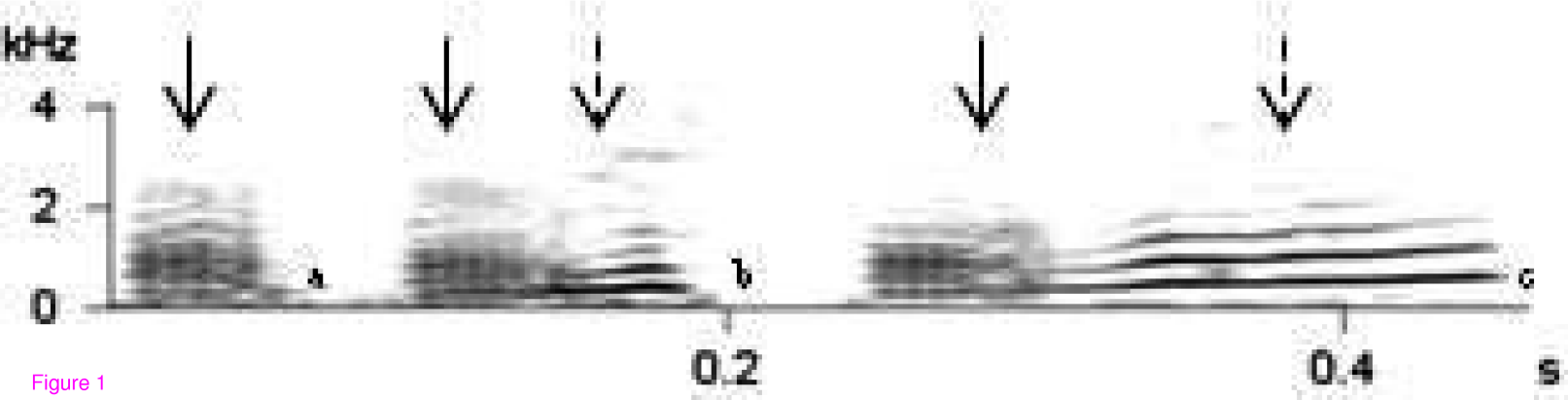


Figure 1

Additional files provided with this submission:

Additional file 1: S1_digging_close_call.wav, 26K

<http://www.biomedcentral.com/imedia/1689172077771161/supp1.wav>

Additional file 2: S2_searching_close_call.wav, 13K

<http://www.biomedcentral.com/imedia/1573138654771161/supp2.wav>

Additional file 3: S3_moving_close_call.wav, 26K

<http://www.biomedcentral.com/imedia/1400894602771161/supp3.wav>