

Testing for vocal individual discrimination in adult banded mongooses

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Abstract

The ability to individually recognize conspecifics is acknowledged as one of the prerequisites for the development of sophisticated social relationships in group-living species. It has been hypothesized that the discrimination of individual identities is crucial for the maintenance of social relationships and cooperation based on repeated interactions, and for the evolution of many social behaviours. Previous studies have shown that the close calls of the cooperatively breeding banded mongoose *Mungos mungo* are individually distinct. For instance, banded mongoose pups are able to distinguish between close calls of their escort and of a non-escort. In this study, we used playbacks based on the recently proposed violation-of-expectation paradigm and a dominance/age class recognition setup to investigate whether adult banded mongooses use the individual signature of close calls to distinguish among adult group members. We found no evidence that the individual signature in close calls is used to discriminate identity in banded mongooses. Based on the previous work, we suggest that this is not because banded mongooses are incapable of using signatures as a means of individual discrimination, but because the benefits of such discrimination are low. The study highlights the importance of understanding the function of a signal (e.g. the expected response), timing and the biology of the species when designing and performing playback experiments.

Introduction

The ability to recognize characteristics such as sex, reproductive status, social rank, kinship, identity, group membership and/or familiarity of conspecifics is acknowledged as one of the prerequisites for the development of sophisticated social relationships (Sherman, 1997; Bradbury & Vehrencamp, 1998). Individual recognition of conspecifics is thought to play a major role for the maintenance of social relationships and cooperation based on repeated interactions among group members (Tibbetts & Dale, 2007). It has been hypothesized to be also of vital importance for the evolution of many social behaviours (Hamilton, 1971; Hauser, 1996). Although individual discrimination is believed to be widespread in non-human animals (Tibbetts & Dale, 2007; Seyfarth & Cheney, 2009), it is often hard to demonstrate empirically as it requires a demonstration that discrimination occurs at the level of the individual (Tibbetts & Dale, 2007; Seyfarth & Cheney, 2009; Townsend, Allen & Manser, 2012). Even more challenging is to demonstrate 'true' individual recognition, as this requires showing that receivers match current sensory cues (e.g. sounds) with stored information (i.e. mental representations or templates) of the properties of a conspecific as well as of the identity of a specific individual (Zayan, 1994; Tibbetts & Dale,

2007). Recognition of individuals as belonging to a broader level of categories containing more than one individual is termed 'class level' or 'social' recognition (hereafter class recognition; Mateo, 2004; Tibbetts & Dale, 2007).

While evidence of true individual vocal recognition is limited, several studies do provide evidence that non-primate animals, such as domestic horses *Equus caballus* (Proops, McComb & Reby, 2009), spotted hyaenas *Crocuta crocuta* (Benson-Amram *et al.*, 2011), Greylag Geese *Anser anser* (Scheiber *et al.*, 2011), Jungle crows *Corvus macrorhynchos* (Kondo, Izawa & Watanabe, 2012) and meerkats *Suricata suricatta* (Townsend *et al.*, 2012), recognize the identity of a specific individual through unique vocal properties of the conspecific. The scarcity of evidence for individual recognition in non-primate species may be due to the simple inability of animals to discriminate identity cues, but could also be caused by the lack of suitable test situations. With the possible exception of mother-offspring recognition (Insley, 2001) and other third-party relationship recognition systems (Engh *et al.*, 2005; Cheney & Seyfarth, 2007), recognition of an individual's class (e.g. their dominance status or sex) is sufficient for many interactions and there are only limited situations where individual recognition has a clear advantage over class recognition (Cheney & Seyfarth, 2007; Tibbetts & Dale, 2007).

Additionally, animals may have limited motivation to show a detectable response (Fischer *et al.*, 2001) or they may need to exhibit individual discrimination only in certain periods, for instance, in a period of need or conflict (Reber, Townsend & Manser, 2013; Steiger & Müller, 2010).

The task of detecting individual recognition of vocalizations may be particularly difficult when studying low-arousal vocalizations such as growls or contact calls (Fischer *et al.*, 2001; Townsend *et al.*, 2012). Townsend *et al.* (2012) proposed a novel violation-of-expectation paradigm to test for individual recognition and to overcome some of these issues. Using a combination of congruent and incongruent playbacks, they showed that meerkats individually discriminate group members. Together with an additional study on social monitoring of the behaviour of dominants by subordinates in meerkats (Reber *et al.*, 2013), Townsend *et al.* (2012) provide convincing evidence that vocalizations are used for individual recognition. They propose that the violation-of-expectation paradigm can be used in a range of species to test for individual discrimination.

In our study, we used this violation-of-expectation paradigm to test for individual discrimination of calls in cooperatively breeding banded mongooses *Mungos mungo*. Banded mongooses are small (≤ 2 kg) social carnivores that show high group cohesion. They live in mixed sex groups which average around 20 individuals, but groups occasionally increase to more than 70 individuals (Cant, 1998). They cooperate in pup care, predator avoidance and territory defence (Rood, 1975; Cant, 1998). Aggression within groups is usually low and restricted to competition over food (Rood, 1975). However, intense competition among males is observed during the limited period (2–7 days) when females are in oestrus. During this period, males exhibit a clear dominance hierarchy that determines success in gaining access to breeding females (Nichols *et al.*, 2010). Older females are classed as socially dominant because they aggressively evict younger females; younger females, by contrast, do not evict older females (Cant *et al.*, 2010). Older females mainly initiate aggression towards younger females, followed by targeted aggression of other group members (Cant *et al.*, 2010). During some periods of female evictions, males are also evicted (Cant, Vitikainen & Nichols, in press).

As in other cooperatively breeding species, banded mongooses could potentially gain from individual recognition to coordinate behaviours and to avoid conflict. Similar to other social group-living species, keeping track of conspecifics could be advantageous to coordinate behaviours and to avoid conflict. Banded mongooses use a range of vocalizations to coordinate behaviours and to maintain group cohesion (Messeri *et al.*, 1987). Foraging banded mongooses move in and out of dense vegetation and they dig for food items in the soil with their heads down. Besides digging, they also search for food on the surface, which is mainly done in the thickets. They are therefore generally visually constrained during foraging and vocalizations likely play a critical role in keeping individuals informed of the social and ecological environment. While foraging they frequently emit close calls (Fig. 1), which most likely function in the main-

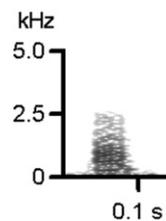


Figure 1 Typical example of a banded mongoose *Mungos mungo* digging close call (Gauss, FTT = 1024, overlap = 97.87%, frequency resolution = 43 Hz).

tenance of group cohesion as described in other species (Kondo & Watanabe, 2009). The close calls of banded mongooses have been shown to be individually distinct (Müller & Manser, 2008a; Jansen, Cant & Manser, 2012). Specifically banded mongoose pups are able to distinguish between playbacks of close calls of their escort and of a non-escort, suggesting that they are able to discriminate adult group members based on the individual signature in the close call (Müller & Manser, 2008a). However, it is unclear whether this vocal recognition also exists among adults. In this study, we used the violation-of-expectation paradigm playback experiments based on Townsend *et al.*'s (2012) method to test whether adult banded mongooses use the individual signature of close calls to distinguish among group members. Additionally, we performed a class recognition playback experiment based on differences in dominance status and age class (hereafter dominance/age class).

Materials and methods

Study population

The study was performed at the Banded Mongoose Research Project in the Queen Elizabeth National Park, Uganda (0°12'S; 29°54'E). Cant (1998) has described the study site and the habituated population in detail. During the three periods of data collection between February 2009 and August 2011, the study population consisted of four to six habituated groups and three semi-habituated groups, with group sizes ranging from 6 to over 50 (average 20 individuals). In four groups, most individuals were habituated to a level that allowed us to follow them with a microphone and to conduct behavioural focal watches within 5 m.

Recording methods

All close calls used in the playback experiments were recorded from habituated adult (≥ 1 year) banded mongooses at a distance of *c.* 1–2 m using a Sennheiser directional microphone (ME66/K6 and a MZW66 pro windscreen, frequency response 40–20 000 Hz \pm 2.5 dB, sampling rate 16 bit, Old Lyme, CT, USA) connected to a Marantz PMD-660 solid state recorder (Marantz Japan Inc., Kanagawa, Japan) or an M-Audio Microtrack II (Avid Technology, Burlington, MA, USA).

Playback protocol

Calls used in playback experiments were randomly selected close calls of adult group members. For playbacks, calls with high signal-to-noise ratio were selected using Cool Edit Pro 2000 (Syntrillium Software Corporation, Phoenix, AZ, USA). Playback experiments were conducted on adult banded mongooses belonging to four different groups. During the experiments, we kept track of the spatial position of the adults whose calls were played back to ensure they were over 10 m away from the test subject. Calls were then played back from a Marantz PMD-660 solid state or an M-Audio Microtrack through a loudspeaker (JBL on tour, JBL, Northridge, CA, USA). The loudspeakers were attached to the lower leg of the observers at the height similar to that of the head of a foraging banded mongoose (5–10 cm above ground; Reber *et al.*, 2013; Townsend *et al.*, 2012). Because close calls are generally soft and, as the amplitude is often less than that of background noise (e.g. bird song), it was not possible to use a sound level meter. Calls were therefore played back at natural occurring amplitudes estimated by hearing. A subject was followed until it was foraging at a clearly defined foraging spot (e.g. a pile of elephant dung), preferably in the open. Before the call was played back, we filmed using a digital camera (Canon HF100, Cannon Inc, Tokyo, Japan or Toshiba Camileo S20, Toshiba, Tokyo, Japan) the behaviour of the subject for a minimum of 30 s. Thereafter, we performed one of two different playback experiments. The playback was paused if the subject went out of sight, the group started moving or an alarm call was given. Only one playback experiment per subject was done per day and a minimum of 3 days of separation was used between experiments to avoid habituation.

Playback 1 – Violation of expectation

We randomly selected digging close calls of two adult group members to create two playback conditions: (1) control (congruent); (2) test (incongruent). Both conditions consisted of two playbacks containing three close calls each, which were separated by *c.* 3 s (within natural calling rate of the banded mongoose; median = 12 min⁻¹; range = 0–60; Jansen, 2013). In the test condition, both playback files consisted of close calls recorded from the same individual. In the control condition, one playback file consisted of close calls (Fig. 1) from the same group member as used in the test condition and the second playback file consisted of close calls from a different group member. The test condition simulated a situation where an individual is foraging on one side of the subject and then a few seconds later appears on the opposite side, which is physically unlikely (Fig. 2). By presenting subjects with different calls from the same individual, we ensured that any violation-of-expectation response in the incongruent condition would be based on the listener's recognition that the calls came from the same individual, not that they constituted the exact same stimulus (Townsend *et al.*, 2012). During playbacks, the first experimenter (D. J.) was positioned *c.* 2 m from the subject and filmed the behaviour from close distance. The second experimenter (K. M.) stood at *c.* 5 m from the subject and 7 m

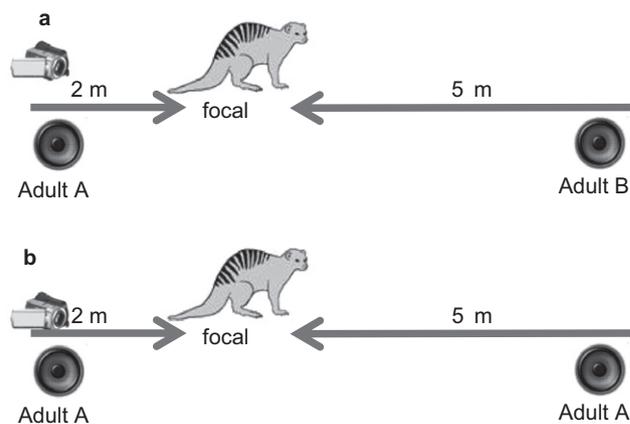


Figure 2 Playback protocol for experiment 1. Protocol was used in both the (a) congruent (control) and (b) incongruent (test) conditions. Camera indicated position of observer (D. J.) recording the behaviour of the focal.

from the first experimenter to ensure a sufficient shift to induce the violation of expectation. These distances ensured that observer (D. J.) had a clear view of the subject and could record all behaviours. The order of the distance, 2 m versus 5 m, from where the first call was played back, randomized. The setup of test and control conditions was kept the same and the order in which subjects heard the test or control conditions was randomized. In case the playback had to be paused, the experiment was restarted after a break of at least 30 min. Calls used for playbacks originated from 20 different individuals of these four groups (3–6 individuals per group).

Playback 2 – Dominance / age recognition

Playbacks were performed using digging close calls of group members that belonged to one of the following dominance/age classes: (1) likely to be higher in social hierarchy (i.e. more dominant and older); (2) littermate (same age); (3) likely to be lower in the social hierarchy (younger). Categorization selection was based on behavioural observation in the few weeks prior to the playback. Behavioural observations included aggression, submission, mating, attempts of eviction and outcomes of foraging competitions. In most cases, older individuals were classed as dominants and younger individuals as subordinates. Sets of three close calls of a group member of the same sex as the subject were selected per class. Close calls were separated by *c.* 3 s. With sets of three calls, we created blocks with calls of individuals of the three different dominance/age classes. The order of the classes within the blocks was randomized. All three possible orders were played back consecutively (e.g. *A – B – C*, *B – C – A*, *C – B – A*). Therefore, the complete playback consisted of 27 calls. During playbacks, the experimenter (D. J.) was positioned *c.* 2 m from the subject and filmed behaviours from a close distance. Nineteen playback trials were performed with 16 different individuals from four different groups (2–5 subject individuals per

group). Calls used for playbacks originated from 28 different individuals of these four groups.

Behavioural responses

We analysed videos using Media Player Classic (Sourceforge.net 2011, VA Software, Fairfax County, VA, USA). Close calls are a regularly emitted low-arousal state vocalization and we therefore did not expect a strong response. We focused on vigilance behaviour and noted: (1) each time the subject scanned the surrounding area; (2) the duration of each vigilance bout (i.e. looking time). Behavioural responses were noted from the onset of the first call of the playback up to 5 s after the last call.

Statistical analysis

All statistical analyses were done in R 2.15.2 using the R packages ‘lme4’ (Bates, 2011), ‘coin’ (Hothorn *et al.*, 2006) and ‘AICcmodavg’ (Mazerolle, 2012). As the experimental setup of the first experiment (violation of expectation) followed a within-subject design and sample sizes were small, we used exact Wilcoxon signed-rank tests to analyse the effect of playback type (congruent or incongruent) on vigilance duration and number of looks. We computed 95% confidence interval (CI) for effect sizes using a bootstrapping method with 10 000 repetitions to establish the significance of our sample.

To investigate whether vigilance behaviour was affected by dominance category in the second experiment (dominance/age class recognition), we performed a series of generalized linear mixed models with a binomial (0 = no vigilance response, 1 = vigilance response) and Gaussian distribution (vigilance duration). The dominance/age class and the identity of the caller were included as fixed factors and the identity of the focal individual as a random factor. Because of the small sample size, we used Akaike’s second-order information criteria (AICc) to select the most plausible model (Mazerolle, 2012). Lower AICc values correspond with better relative support for each model and terms were only kept in the model if their removal inflated AICc by more than two (Mazerolle, 2012). The minimal model consisted of an intercept and the random factor. To validate that there was no improvement to the minimal model, all original terms were returned to the model one by one, creating a model together with the basic model, containing only the intercept and the random term.

Results

Violation of expectation

The response of the subjects to the congruent (control) and incongruent (test) conditions of the playbacks did not differ. There was no difference in vigilance behaviour between the control and the test conditions (number of looks: exact Wilcoxon test: $Z = -0.95$, $P = 0.40$, $n = 15$, $r = -0.16$; vigilance duration (s): $Z = -0.84$, $P = 0.43$, $n = 15$, $r = -0.14$). Eight out

Table 1 Overview of responses in the violation-of-expectation playback

Part	Congruent		Incongruent	
	Looks	Duration (s)	Looks	Duration (s)
Before	1 (0–1)	0 (0–1)	1 (0–1)	0 (0–1)
After	0 (0–1)	0 (0–2)	0 (0–4)	0 (0–2)

Given are the median (range).

of the 15 tested subjects showed a vigilance response during the control condition, whereas in the test condition this happened four times. Baseline vigilance behaviour measured during the 30 s before the calls were played also did not differ between conditions (number of looks: $Z = 1.45$, $P = 0.33$, $n = 14$, $r = 0.16$; vigilance duration (s): $Z = 1.31$, $P = 0.33$, $n = 14$, $r = 0.16$; Table 1). Bootstrapping of the effect sizes and calculation of 95% CIs verified that the reported effect sizes did not significantly differ from 0 and that our sample size was sufficiently large enough (Fig. 3).

Dominance/age class recognition

Mongooses overall showed low vigilance behaviour during the playbacks testing a discrimination between members of different dominance/age classes [median number of looks: 3 (range: 0–7), $n = 19$; median duration (s): 7 (0–32.5), $n = 19$; see Table 2 for responses per block]. Thirteen individuals responded at least once during the playbacks [median number of looks: 4 (1–7), $n = 19$; median duration (s): 8 (1–32.5), $n = 19$]. The likelihood of responding or vigilance duration was not affected by dominance or identity of caller (Table 3). For all test conditions, the basic model that only contained the identity of the receiver as a random factor was the best model.

Discussion

We found no evidence that banded mongooses respond differently to close calls of different individuals or dominance/age class categories. This suggests that adult banded mongooses do not discriminate between individuals based on the individual signature that is present in the close calls. One explanation for this result is that banded mongooses simply do not possess the ability to recognize individuals. However, previous work has demonstrated that pups can discriminate between close calls of their escorts versus other escorting individuals in the group. Escorts showed increased responsiveness towards distress signals of their escorted pup versus a different pup (Müller & Manser, 2008a). While this ability could simply be based on familiarity, it nevertheless shows that banded mongooses do possess the cognitive ability to discriminate between individuals in the context of alloparental care. Consequently, the lack of recognition among adults is rather surprising, and suggests that individuals discriminate close calls of other group members only in social contexts where such discrimination is particularly useful or profitable.

A lack of response by the receivers may reflect a lack of motivation rather than an inability to discriminate between

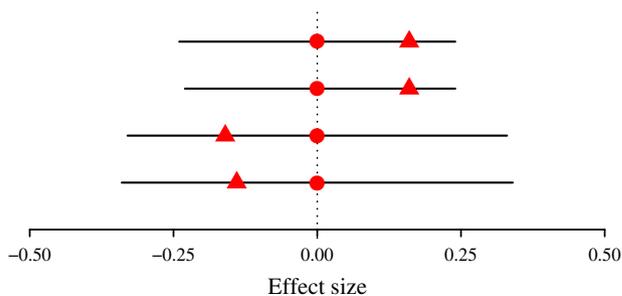


Figure 3 Summary of repeatability of effect estimations: (i) duration of vigilance in test versus control condition; (ii) number of looks in incongruent (test) versus congruent (control) condition; (iii) duration of vigilance in first playback versus second playback; (iv) number of looks in first playback versus second playback. The X-axis represents the effect size. Triangles are the computed estimates of effect based on our data. The solid circles represent the calculated mean effect based on bootstrapping. The horizontal lines represent the 95% confidence intervals of the bootstrapped effect sizes.

Table 2 Overview of responses per block in the dominance/age class recognition playback experiment

Block	Class ^a	Looks	Duration
1	D	0 (0–1)	0 (0–4)
1	L	0 (0–1)	0 (0–5)
1	S	0 (0–1)	0 (0–23)
2	D	0 (0–1)	0 (0–4)
2	L	0 (0–1)	0 (0–6.5)
2	S	0 (0–1)	0 (0–9)
3	D	0 (0–1)	0 (0–9)
3	L	0 (0–1)	0 (0–0)
3	S	0 (0–1)	0 (0–4)

Given are the median (range).

^aDominance/age class; D = dominant (older); L = littermate (same); S = subordinate (younger).

Table 3 GLMMs investigating the factors that predict the likelihood of vigilance duration and number of looks in a class/age recognition playback experiment

Model	Description	Duration		Looks	
		AICc	Δ^a	AICc	Δ^a
	Basic ^b	1789	0	288	0
1	Full	1817	28	1744	1456
2	Dominance/age class only	1795	7	298	10
3	Caller ID only	1823	34	391	103

^a $\Delta_i = AICc_i - AICc_{min}$.

^bOnly contains intercept and the random factors. GLMM = generalized linear mixed model; AICc = Akaike’s second-order information criteria.

specific individuals. Close calls are frequently emitted during social foraging and are of low arousal. Therefore, upon hearing a close call the receiver in many cases may just acknowledge the presence of a group member without the need to respond, visually or vocally, to such a low arousal call. A similar pattern of an infant’s ability to discriminate between calls, but lack of response in adults, was observed in

- i.) duration of vigilance (test vs. control)
- ii.) number of looks (test vs. control)
- iii.) duration of vigilance (first vs. second playback)
- iv.) number of looks (first vs. second playback)

chacma baboons *Papio cynocephalus ursinus*. Infant baboons discriminated between the commonly used graded bark variations: the intermediate alarm barks and clear contact barks (Fischer, Cheney & Seyfarth, 2000). Adult chacma baboons, however, failed to show a difference in response between these two call variations (Fischer *et al.*, 2001). As infants were able to discriminate, the authors suggest that the lack of response is due to a lack of motivation rather than an inability to do so (Fischer *et al.*, 2001).

The lack of motivation to respond may differ for the two playback experiments we conducted in the banded mongoose. The setup of the first experiment (violation-of-expectation paradigm) is based on the assumption that the sudden shift of position of the caller violates the expectation of the receiver (Townsend *et al.*, 2012). Banded mongooses, however, often forage in dense vegetation with many position shifts, both in distance to nearest neighbour and in relative position within the group (Rood, 1975). Therefore, sudden shifts in position might not be a violation of expectation for a foraging banded mongoose in the way it appears to be for the closely related meerkat (Townsend *et al.*, 2012). This does not exclude that banded mongoose may not also socially monitor the position of other group members by their vocalizations.

The lack of response to the dominance/age class recognition playback may indicate that response to close calls is only beneficial during specific periods of conflict or other socially relevant times. For example, adult subordinate female meerkats recognize the dominant female vocally based on close calls, but test subjects only show a response to these calls when they are under threat of eviction, and not during non-conflict periods (Reber *et al.*, 2013). It is likely that similar periods of enhanced sensitivity occur in the banded mongoose. In particular, in the daily life of a group, conflict is likely to be limited to competitions over food (Rood, 1975). Mongooses frequently forage on large ungulate dung piles. These piles are meticulously taken apart in search of dung beetles and their larvae. Especially, the presence of fresh elephant *Loxodonta africana* dung can lead to high congregation of mongooses, leading to high levels of foraging competition (Rood, 1975). Occasionally, higher levels of aggression do occur. Males, for

instance, compete for access to females during oestrus, and have been shown to respond stronger to olfactory cues of the specific females in oestrus than females not in oestrus at the same time (Müller & Manser, 2008b). In addition, both sexes occasionally aggressively evict mostly younger group members during periods of oestrus or early pregnancies (Cant *et al.*, 2010; Nichols *et al.*, 2010). In these periods of heightened conflict, the pay-offs of discriminating and responding appropriately to particular individuals may be much greater than at other times.

We performed our playback experiments during normal foraging behaviour in periods with no breeding or overt aggression in the group, and therefore outside of the temporal window (e.g. during oestrus or periods of cooperative offspring care) for which it is beneficial for adult banded mongooses to discriminate between group members. However, during potential sensitivity periods such as oestrus, increased aggression or eviction, individuals spend little time continuously foraging and therefore experiments with the current set-up are extremely difficult. Also, in certain non- or reduced conflict situations, it can be beneficial to distinguish between group members. This is, for instance, the case of the stable close associations between pups and their escorting adults (Müller & Manser, 2008a).

Close calls of the banded mongoose are graded and besides an individual signature contain a temporally separated behavioural cue indicating whether the individual is 'digging', 'searching' or 'moving' (Jansen *et al.*, 2012). In this experiment, we used 'digging' close calls as stimuli during playbacks, as these calls are emitted by individuals that are stationary and digging for food items. The individual signature in the banded mongoose close calls is encoded only in the initial noisy part of the close calls. The harmonic extension indicating the behaviour is not individually distinct (Jansen *et al.*, 2012). The 'digging' close calls consist only of the initial noisy part and no harmonic extension. The 'searching' or 'moving' is not more individually distinct, but includes additional information regarding the current behaviour of the caller (Jansen *et al.*, 2012). We therefore do not expect that a more individualistic response would have been shown to these variations of the close calls.

Bates *et al.* (2008) used an expectancy-violation paradigm experiment to demonstrate that African elephants recognize others using olfactory cues and monitor their location. When adult females unexpectedly encountered urine samples from group members that were either absent or located behind the focal individual (and so could not have produced the cue), they showed an increased response to this incongruent and unexpected situation. Future research could attempt to investigate if banded mongooses identify and monitor the location of individual conspecifics using a similar expectancy-violation paradigm experiment. During evictions, group members are either temporally or permanently evicted from their natal group (Cant & Field, 2001; Cant *et al.*, 2010). During these evictions, playbacks of close calls from current group members and evicted group members could be used to investigate if adult mongooses also recognize and have an expectation as to the whereabouts of specific individuals.

In conclusion, our results did not show that the individual signature in the close calls is used on a day-to-day basis in adult banded mongooses. This seems surprising considering the earlier findings that banded mongoose pups are able to distinguish adults based on their close calls. A lack in response to the playback of signals does not necessarily mean that the cognitive capacity is absent, it rather may indicate a lack of motivation or no obvious need to respond. It is possible that adults use the signature in specific situations (i.e. as the pups do in the pup-escort associations; Müller & Manser, 2008a) or during socially sensitive periods, like in periods of targeted aggression during eviction or oestrus. The lack of response in adult banded mongooses to close calls highlights the importance of understanding the function of a signal (e.g. its expected response) and its timing (i.e. aiming for the sensitivity period).

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References

- Bates, D.M. (2011). *Lme4: mixed-effects modeling with R*. New York: Springer.
- Bates, L.A., Sayialel, K.N., Njiraini, N.W., Poole, J.H., Moss, C.J. & Byrne, R.W. (2008). African elephants have expectations about the locations of out-of-sight family members. *Biol. Lett.* **4**, 34–36.
- Benson-Amram, S., Heinen, V.K., Dryer, S.L. & Holekamp, K.E. (2011). Numerical assessment and individual call discrimination by wild spotted hyaenas, *Crocuta crocuta*. *Anim. Behav.* **82**, 743–752.
- Bradbury, J.W. & Vehrencamp, S.L. (1998). *Principles of animal communication*. New York: Sinauer Associates.
- Cant, M.A. (1998). *Communal breeding in banded mongooses and the theory of reproductive skew*. PhD thesis, University of Cambridge, Cambridge, UK.
- Cant, M.A. & Field, J. (2001). Helping effort and future fitness in cooperative animal societies. *Proc. Roy. Soc. B.-Biol. Sci.* **268**, 1959–1964.
- Cant, M.A., Hodge, S.J., Bell, M.B.V., Gilchrist, J.S. & Nichols, H.J. (2010). Reproductive control via eviction (but not the threat of eviction) in banded mongooses. *Proc. Roy. Soc. B.-Biol. Sci.* **277**, 2219–2226.

- Cant, M.A., Vitikainen, E. & Nichols, H. (in press). Demography and social evolution in banded mongooses. *Adv. Study Behav.* **45**, 407–445.
- Cheney, D.L. & Seyfarth, R.M. (2007). *Baboon metaphysics: the evolution of a social mind*. Chicago: The University of Chicago Press.
- Engh, A.L., Siebert, E.R., Greenberg, D.A. & Holekamp, K.E. (2005). Patterns of alliance formation and postconflict aggression indicate spotted hyaenas recognize third-party relationships. *Anim. Behav.* **69**, 209–217.
- Fischer, J., Cheney, D.L. & Seyfarth, R.M. (2000). Development of infant baboons responses to graded bark variants. *Proc. Roy. Soc. B.-Biol. Sci.* **267**, 2317–2321.
- Fischer, J., Metz, M., Cheney, D.L. & Seyfarth, R.M. (2001). Baboon responses to graded bark variants. *Anim. Behav.* **61**, 925–931.
- Hamilton, W.D. (1971). Geometry for the selfish herd. *J. Theor. Biol.* **31**, 295–311.
- Hauser, M.D. (1996). *The evolution of communication*. Cambridge, MA: MIT Press.
- Hothorn, T., Hornik, K., van de Wiel, M.A. & Zeileis, A. (2006). A lego system for conditional inference. *Am. Stat.* **60**, 257–263.
- Innsley, S.J. (2001). Mother–offspring vocal recognition in northern fur seals is mutual but asymmetrical. *Anim. Behav.* **61**, 129–137.
- Jansen, D.A.W.A.M. (2013). *Vocal communication in banded mongoose (Mungos mungo)*. PhD thesis, Institute of Evolutionary Biology and Environmental Studies, University of Zurich.
- Jansen, D.A.W.A.M., Cant, M.A. & Manser, M.B. (2012). Segmental concatenation of individual signatures and context cues in banded mongoose (*Mungos mungo*) close calls. *BMC Biol.* **10**, 97.
- Kondo, N. & Watanabe, S. (2009). Contact calls: information and social function. *Jpn. Psychol. Res.* **51**, 197–208.
- Kondo, N., Izawa, E.-I. & Watanabe, S. (2012). Crows cross-modally recognize group members but not non-group members. *Proc. Roy. Soc. B.-Biol. Sci.* **279**, 1937–1942. doi: 10.1098/rspb.2011.2419
- Mateo, J.M. (2004). Recognition systems and biological organization: the perception component of social recognition. *Ital. J. Zool.* **41**, 729–745.
- Mazerolle, M.J. (2012). AICcmodavg: model selection and multimodel inference based on (Q)AIC(c) [Computer software manual].
- Messeri, P., Masi, E., Piayya, R. & Dessifulgheri, F. (1987). A study of the vocal repertoire of the banded mongoose (*Mungos mungo*). *Ital. J. Zool., Suppl.* **22**, 341–373.
- Müller, C.A. & Manser, M.B. (2008a). Mutual recognition of pups and providers in the cooperatively breeding banded mongoose. *Anim. Behav.* **75**, 1683–1692.
- Müller, C.A. & Manser, M.B. (2008b). Scent-marking and intrasexual competition in a cooperative carnivore with low reproductive skew. *Ethology* **114**, 174–185.
- Nichols, H.J., Amos, W., Cant, M.A., Bell, M.B.V. & Hodge, S.J. (2010). Top males gain high reproductive success by guarding more successful females in a cooperatively breeding mongoose. *Anim. Behav.* **80**, 649–657.
- Proops, L., McComb, K. & Reby, D. (2009). Cross-modal individual recognition in domestic horses (*Equus caballus*). *Proc. Natl Acad. Sci. U.S.A.* **106**, 947–951.
- Reber, S., Townsend, S.W. & Manser, M.B. (2013). Social monitoring via close calls in meerkats. *Proc. R. Soc. B* **280**, doi: 10.1098/rspb.2013.1013.
- Rood, J.P. (1975). Population dynamics and food habits of the banded mongoose. *E. Afr. Wildl. J.* **13**, 89–111.
- Scheiber, I., Hohnstein, A., Kotschal, K. & Weiß, B. (2011). Juvenile greylag geese (*Anser anser*) discriminate between individual siblings. *PLoS ONE* **6**, e22853.
- Seyfarth, R.M. & Cheney, D.L. (2009). Seeing who we hear and hearing who we see. *Proc. Natl Acad. Sci. U.S.A.* **106**, 669–670.
- Sherman, P.W. (1997). Recognition systems. In *Behavioural ecology: an evolutionary approach*: 69–96. Krebs, J. & Davies, N. (Eds). Oxford, UK: Blackwell Science.
- Steiger, S. & Müller, J.K. (2010). From class-specific to individual discrimination: acceptance threshold changes with risk in the partner recognition system of the burying beetle *Nicrophorus vespilloides*. *Anim. Behav.* **80**, 607–613.
- Tibbetts, E.A. & Dale, J. (2007). Individual recognition: it is good to be different. *Trends Ecol. Evol.* **22**, 529–537.
- Townsend, S.W., Allen, C. & Manser, M.B. (2012). A simple test of vocal individual recognition in wild meerkats. *Biol. Lett.* **8**, 179–182.
- Zayan, R. (1994). Mental representations in the recognition of conspecific individuals. *Behav. Process.* **33**, 333–246.