Effect of group size and experience on the ontogeny of sentinel calling behaviour in meerkats

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Highlights

- Meerkats started acting as sentinels as subadults around 200 days of age.
- They produced all six sentinel call types when they first acted as sentinel.
- Call rate of the different sentinel call types changed with experience.
- The acoustics of the common double note calls differed between individuals.
- Meerkats showed individual distinctiveness when they first acted as sentinel.

Abstract

Increased vulnerability to predation results in young individuals of many species experiencing higher predation pressure than adults. Consequently, the production of antipredator-related calls by young can differ from that of the same vocalizations given by adults. Sentinel behaviour is a coordinated vigilance behaviour, where one individual climbs on an elevated position and scans the surroundings for predators, while the rest of the group is mainly foraging. Meerkat, *Suricata suricatta*, sentinels produce six distinct sentinel call types, which inform other group members about the perceived predation risk, resulting in the adjustment of personal vigilance behaviour in foraging group members. Here, we investigated the onset of sentinel behaviour and the ontogeny of the different sentinel call types as well as the development of individual vocal signatures in meerkats. We found that meerkats started acting as a sentinel around 200 days of age, but this was highly dependent on group size, with individuals from smaller groups exhibiting sentinel behaviour earlier than individuals from larger groups. All six sentinel call types were already present in the repertoire upon first emergence of the behaviour; however, call rates of 'all-clear' calls increased while 'warning' calls decreased with increasing experience as sentinel. Analysis of one of the most frequent sentinel calls, the double note calls, indicated that fundamental frequency, mean amplitude, duration and entropy differed consistently between individuals, but we found no effect of age. Rather, our results provide evidence that individual signatures in this call type were already developed when young meerkats first started to act as sentinel and changed little with age. To conclude, we showed little ontogenetic change in overall sentinel behaviour as well as in its vocal coordination, indicating potentially high selection pressures on antipredator behaviours, such as the sentinel system, resulting in consistent behavioural responses upon first emergence.

Keywords: acoustic communication, individual vocal signature, ontogeny, sentinel behaviour

As a consequence of living in groups, some animals have evolved specific coordinated antipredator defence mechanisms (Krause & Ruxton, 2002; Kruuk, 1964; Zoratto, Santucci, & Alleva, 2009), such as sentinel behaviour (Horrocks & Hunte, 1986; Manser, 1999; McGowan & Woolfenden, 1989). Sentinel behaviour is a coordinated vigilance behaviour mostly seen in cooperative breeders, where one individual climbs onto an elevated position and scans the surroundings for predators while the rest of the group is foraging (Wright et al., 2001a, Wright et al., 2001b; Wright et al., 2001a, Wright et al., 2001b Wright et al., 2001a, Wright et al., 2001b; Wright et al., 2001a, Wright et al., 2001b; Ridley & Raihani, 2006; Wright, Berg, De Kort, Khazin, & Maklakov, 2001a; Zahavi, 1990). Sentinels have been demonstrated to detect predators more frequently and from greater distances than foraging group members (Manser, 1999; Wright et al., 2001a, Wright et al., 2001b) and foraging group members have a higher foraging efficiency when a sentinel is on guard (Hollén, Bell, & Radford, 2008; Manser, 1999).

When sentinels spot a predator, they produce alarm calls, allowing group members to initiate the proper antipredator behaviour (Bednekoff, 2001; Manser, 2001; Manser, Bell, & Fletcher, 2001; McGowan & Woolfenden, 1989; Rasa, 1989). Alarm calls represent a common antipredator strategy (Caro, 2005; Sherman, 1977), and are thought to be under strong selection. However, selection pressures can vary between different group members, and are generally higher for younger individuals than adults. Thus, offspring environment, including the ability of young to move away from the nesting site or the presence of siblings (Berg, Beissinger, & Bradbury, 2013), and differences in predation risk, owing to higher vulnerability to predation in general or a different set of predators than adults, result in selection pressures that can be very different from those of adults. Consequently, alarm calls produced by young individuals have been shown to differ from calls produced by adults on three levels: (1) vocal production: the development of species-specific calls with a specific set of acoustic properties; (2) vocal usage: the correct choice of call types given the context; and (3) response: the development of the appropriate response to conspecific calls (Hollén & Radford, 2009; Seyfarth & Cheney, 1986). In meerkats, *Suricata suricatta*, for example, young produce higher pitched and longer calls (Hollén & Manser, 2007), they call more often in response to nonthreatening stimuli (Hollén, Clutton-Brock, & Manser, 2008) and newly emerged young respond more strongly to alarm calls which, over the course of ontogeny, become more and more adult like (Hollén & Manser, 2006).

Animals with individually distinct calls including some birds (Jouventin & Aubin, 2002; Lefevre, Gaston, & Montgomerie, 2001; Radford & Ridley, 2008), primates (Cleveland & Snowdon, 1982; Miller & Thomas, 2012; Salmi, Hammerschmidt, & Doran-Sheehy, 2014; Snowdon & Cleveland, 1980), hyaenas (Theis, Greene, Benson-Amram, & Holekamp, 2007) and social mongooses (Jansen, Cant, & Manser, 2012; Manser, 1999; Sharpe, Hill, & Cherry, 2013) provide another aspect of vocal ontogeny: the ontogenetic development of acoustic individuality. Individually distinct vocalizations allow receivers to adjust their behavioural response to the caller's identity (Salmi et al., 2014). In the context of mother–offspring behaviour, discrimination among individuals based on vocal signals provides the potential for reliable recognition of dependent offspring and therefore offspring survival while avoiding misdirected maternal care (Briefer & McElligott, 2011; Volodin, Lapshina, Volodina, Frey, & Soldatova, 2011). In the context of antipredator behaviours, group members of various species have been demonstrated to adjust the response to alarm calls depending on the identity of the caller (or some characteristics of the caller) and the associated quality and relevance of the provided information (Blumstein & Daniel, 2004; Blumstein, Verneyre, & Daniel, 2004; Hare & Atkins, 2001; Ramakrishnan & Coss, 2000). However, whether individuals already possess individually distinctive calls when they first start producing the relevant call types, such as alarm calls, or whether this is something that develops during vocal ontogeny often remains unknown (but see Schneiderova et al., 2015).

In addition to alarm calls, sentinels in some species continuously produce specific sentinel calls, in social mongooses also referred to as the ‘Watchman's song’, which allow foraging group members to obtain acoustic information about the presence of a sentinel individual (Hollén, Bell, & Radford, 2008; Manser, 1999; Rasa, 1986). The structure and information content of sentinel vocalizations varies greatly, with some species producing one type of sentinel call to announce their presence (pied babbler, *Turdoides bicolor*: Hollén et al., 2011). In contrast, others produce graded information contained in the call rate of one (dwarf mongoose, *Helogale parvula*: Kern & Radford, 2013) to several sentinel call types (meerkats,: Rauber, Kranstauber, & Manser, 2020; Rauber & Manser, 2017), which informs the rest of the group about temporary changes in the perceived predation risk. However, little is known about the ontogeny of sentinel behaviour (Bednekoff, 2015), and nothing about the ontogeny of sentinel vocalizations. Thus, it remains unknown at what age the different sentinel calls are produced and whether and how sentinel calls of young differ from those of adults.

In this study we investigated the onset and vocal ontogeny of sentinel behaviour in meerkats. Meerkats are small, highly sociable mongooses occurring in the Kalahari Desert in southern Africa (Clutton-Brock, Gaynor, et al., 1999a; Clutton-Brock & Manser, 2016). They are cooperative breeders living in groups of three to 50 individuals (average 17), containing one dominant breeding pair and multiple subordinate helpers, which help to rear the dominant's offspring by providing them with food and protection (Clutton-Brock et al., 1998; Clutton-Brock, Gaynor, et al., 1999a; Clutton-Brock & Manser, 2016). Although all members of a group contribute to sentinel behaviour, individual contributions vary within and between groups (Clutton-Brock, O'Riain, et al., 1999b; Rauber & Manser, 2018), whereby individuals from smaller groups have a higher daily likelihood of acting as sentinels (30%) than individuals from larger groups (10%; Rauber, Clutton-Brock, & Manser, 2019). Meerkats on sentinel duty produce six different sentinel call types (Manser, 1999; Rauber & Manser, 2017) and if a predator is detected they give functionally referential alarm calls (Manser, 1999, Manser, 2001; Manser et al., 2001). The six described, discrete sentinel call types all differ in their acoustic structure and include single note, double note, triple note, multiple note, di-drrr and wheek calls (Fig. 1, Appendix Fig. A1; Manser, 1999). Previous work on the function of sentinel calls in meerkats has demonstrated that sentinel calming calls, including single and double note calls, are produced when no predator is in sight and function as an ‘all-clear’ signal, leading to an increase in foraging behaviour and a decrease in vigilance behaviour by the foraging group members (Rauber & Manser, 2017). In contrast, sentinel warning calls, which contain di-drrr and wheek calls, are produced when the sentinel individual experiences an increase in perceived risk and function as an early stage of alarm calls, leading to an increase in vigilance behaviour and a decrease in foraging by receivers (Rauber & Manser, 2017). Moreover, meerkat sentinel calls are individually distinct (Manser, 1999) and foraging group members adjust their behavioural response to sentinel calming calls based on the experience levels of the caller (Rauber & Manser, 2018). Alarm calls, on the other hand, contain information about different urgency levels of a flight response as well as information about the predator type, i.e. terrestrial or aerial (Manser, 2001; Manser et al., 2001; Manser, Seyfarth, & Cheney, 2002). Having these varying levels of urgency, i.e. sentinel calming calls, sentinel warning calls and alarm calls, all produced by the individual on sentinel guard, allows us to compare vocal ontogeny of sentinel calls with that of alarm calls regarding potential differences between subadults and adults in terms of vocal usage and development of individual signatures.

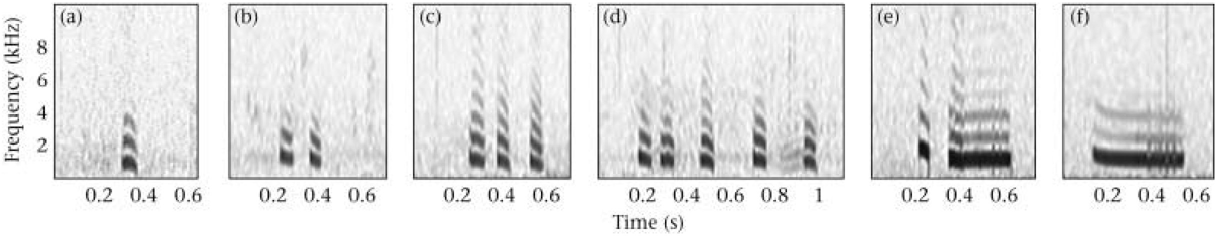

Figure 1. Spectrograms of the six distinct sentinel call types produced by adult meerkats acting as sentinel: (a) single note call, (b) double note call, (c) triple note call, (d) multiple note call, (e) di-drrr call, (f) wheek call. (a, b) Sentinel calming calls, (c, d) middle calls and (e, f) sentinel warning calls. Reproduced after Manser, 1999, Fig. 1, permission granted by M.M.

In this study we investigated at what age meerkats begin to act as sentinels and whether and how group size may influence the onset of this behaviour. Individual contribution to sentinel behaviour decreases with increasing group size (Clutton-Brock, O'Riain, et al., 1999b). Accordingly, individuals in smaller groups might have to contribute to this coordinated vigilance behaviour at a younger age than individuals from larger groups. Alternatively, it is possible that in larger groups, which on average more often have an individual on raised guard (Clutton-Brock, O'Riain, et al., 1999b), individuals learn more quickly from other group members, and perform the behaviour at a younger age. Second, we determined the age when different sentinel call types were first produced by young meerkats and how call rates changed with increasing experience as a sentinel. Based on the different urgency levels of sentinel calming and warning calls and due to the higher vulnerability of young individuals to predation, we expected young individuals to produce more warning calls and fewer calming calls. Lastly, focusing on double note calls, one of the two most frequent sentinel call types, we examined how individual distinctiveness in this call type changed with increasing age of the signaller.

Methods

Study Site and Population

This study was carried out between February and July 2017 at the Kalahari Meerkat Project (KMP) located at the Kuruman River Reserve in South Africa. Additionally, the analyses relied on long-term data collected for the KMP between 1996 and 2017 (see Behavioural data from long-term database below). The study site has a semiarid climate with perennial grasses, shrubs and trees as the main vegetation (see Clutton-Brock, Gaynor, et al., 1999a; Doolan & Macdonald, 1996 for more information about the habitat and climate at the study site). All animals recorded during this study were habituated to close human observations and sound-recording equipment, allowing for recording distances of less than 1 m from the calling meerkat. Information about individual identity, age and frequency of sentinel behaviour was collected as part of the KMP's long-term data collection. In total, we recorded sentinel calls of young meerkats from eight groups with group size varying between nine and 24 individuals (mean±SD=14.1±6.25). Age classes were characterized as the following: individuals younger than 3 months, i.e. pups, are for the most part dependent on food provisioning and protection from adult group members; juveniles, 3–6 months, start to forage on their own, but still get complementary feeds from adults; subadults, 6–12 months, forage independently and show more adult like behaviours, including offspring care or burrow maintenance; individuals over 12 months of age are sexually mature and considered adults.

Behavioural Data from the Long-Term Database

As part of the daily data collection at the KMP, researchers observe groups of foraging meerkats for 3 h in the morning and 1–2 h in the evening, conducting ad libitum observations whenever they see a specific behaviour. Each group is observed for 4–5 days a week, so, over a whole month, observation durations are equalized across all groups. We extracted the age at the first sentinel bout that was equal to or longer than 1 min for all meerkats born between 1996 and 2017, resulting in a total of 1411 individuals from 39 different groups ($N = 755$ males, $N = 656$ females). One minute was chosen to exclude individuals that were just climbing up an object and were mistakenly noted down as a sentinel individual. When individuals stay in the raised position (at least 0.1 m higher than the surrounding area) for 1 min or longer, we can assume that this individual is acting as a sentinel and not just exploring its surroundings. To compare the onset of sentinel behaviour with the onset of the other cooperative behaviours, we also extracted the age when they first participated in pup feeding and babysitting (Clutton-Brock & Manser, 2016) from the same set of individuals and time period used to analyse the onset of sentinel behaviour.

Acoustic Recordings

We recorded a total of 189 sentinel events in eight groups (5–69 recordings per group; mean = 21) containing 7119 calls from 48 different individuals between 112 and 380 days old. Recordings were conducted during naturally occurring sentinel bouts using a Sennheiser directional microphone (ME66/K6) connected to a Marantz PMD-670 solid-state recorder (Marantz Japan Inc.; sampling frequency 44.2 kHz, 16 bits accuracy). A windshield (Rainhardt, W200) was attached to the microphone to ensure high-quality recordings under variable wind conditions. To avoid disturbing the meerkats, the microphone was attached to a 1.5 m telescopic pole enabling the person recording the meerkat to keep 1 m away, while the recording distance was <0.5 m allowing for a high signal-to-background ratio.

Extraction of Acoustic Parameters

Each vocalization in the recordings was manually assigned to one of the six described sentinel call types (Fig. 1) or alarm calls using a combination of visual inspection of the spectrogram and acoustic classification of calls in Adobe Audition 2015.0 Release (Manser, 1999; Rauber & Manser, 2017). Previous work on meerkat call combinations demonstrated that silence intervals between calls are significantly shorter than within call combinations, such as the double or triple note calls (Collier, Townsend, & Manser, 2017), allowing us to categorize each call by visual and audio inspection as one of the six described sentinel call types. To extract acoustic parameters of one of the two most frequent sentinel call types, the double note call, we used Avisoft SASLab Pro version 5.2.12 (Avisoft Bioacoustics, Berlin, Germany). Upon loading the sound file into the program, we first removed noise levels below 250 Hz, applying a high-pass domain finite impulse response (FIR) filter. Afterwards we created spectrograms (FFT length=512, overlap=87%) and visually checked the tracking of the fundamental frequency, which for sentinel double note calls is the same as the peak frequency, and the duration of the first note of the call. Calls that were not of high enough signal to noise quality and thus were not tracked correctly by the program were removed from the analysis. The minimum number of high-quality calls we collected from the same individual was 16 (range 16–106, mean = 58.6), recorded from at least three independent sentinel events (minimum=3, maximum=7, mean=4.6), resulting in a sample size of 72 recordings containing 937 double note calls from 18 individuals. Fundamental frequency (which was equal to peak frequency in the measured calls), peak amplitude and entropy were measured at 10 regular segments throughout the first note of each double note call. Similar to work on transmission characteristics in primate vocalizations (Maciej, Fischer, & Hammerschmidt, 2011), only measurements 2–9 were used to calculate the means, as the very beginning and end of calls were often the most imprecise and affected by background noise. Duration was measured for the complete first note of each double note call.

Statistical Analysis

All statistical analyses were done using R Version 3.3.0 (R Core Team, 2018). To analyse the effect of group size on the age at the first sentinel bout, we applied a linear mixed model (LMM) with age (days) as a response and sex and group size as fixed effects. Group identity was included as a random factor. As the proportion of time that individuals spend on sentinel guard is higher in smaller than larger groups (Clutton-Brock, O'Riain, et al., 1999b), the acquisition of experience gained by acting as a sentinel may differ with group size rather than absolute age: individuals from smaller groups are expected to gain experience faster than individuals in larger groups. Hence, for further analysis of the ontogeny of sentinel vocalizations, we used ‘GuardSum’ as a proxy for experience, which we calculated as the total duration of all sentinel events of a given individual until the day of the recording. To test whether the presence of a given call type in the recordings was affected by experience, we used a generalized linear mixed model (GLMM) with the presence of a call type as a binomial response variable and group size and GuardSum as fixed effects. Sentinel ID nested in group ID and date were used as random factors. To determine whether the fixed effects had any significant effect on the response variable, we used likelihood ratio tests (LRT) to compare whether the model with the fixed effect included differed significantly from the same model with the fixed effect excluded (Crawley, 2012). To analyse the development of call rates (total number of calls for each call type divided by the duration of the sentinel bout) with increasing experience, while at the same time reducing the number of multiple tests, we grouped the six sentinel calls into categories, which have been shown to represent functionally distinct call categories: single and double note calls together as sentinel calming calls and di-drrr and wheek calls as warning calls (Rauber & Manser, 2017). The last two call types, the triple and multiple note calls, were grouped together as ‘middle calls’. This was done to reduce the number of multiple tests. We then used all recordings where the call rate of each of these categories was above zero and log transformed them to use as a response variable in a GLMM. Again, we used GuardSum (our proxy for experience), group size and the potential interaction between them as fixed effects as well as sentinel ID nested in group ID and date as random factors. To investigate how the acoustic parameters produced in the first note of double note calls changed with age, we conducted an LMM with the mean fundamental frequency, mean peak amplitude, duration and mean entropy as response variables, age as a fixed effect and sentinel ID and a unique recording ID as random factors. Following the methods used in Salmi et al. (2014) we also compared the variation between the first note of the double note calls of different individuals to the variation measured within individuals to assess whether calls show the potential for individual coding (PIC). To do this we measured the acoustic variability of each acoustic parameter (derived for each first note of a double note call) by calculating the interindividual variation means ($\text{Mean}_{\text{inter}}$ = average mean of the measured parameter over the calls of all individuals) and the standard deviation (SD_{inter} = SD of the measured parameter over the calls of all individuals). Then we calculated the coefficients of variation between individuals ($CV_{inter} = 100\times(SD_{inter}/Mean_{inter})$) and within individuals (CV_{intra} = mean of individual CV values; with $CV=100\times(SD/Mean)$ for each individual). PIC was calculated as CV_{inter}/CV_{intra}: values above 1 indicate higher variation between than within individuals and thus the potential for this variable to encode individual information (Salmi et al., 2014). To test for any changes in individual distinctiveness across ontogeny, we used discriminant function analysis (DFA; Klecka & Iversen, 1980) on the measured acoustic variables of 10 individuals, when they were younger than 250 days, and 10 individuals at 250–380 days of age to get the percentage of correct assignment of calls to individuals, using the leave-one-out cross-validation method (Hair, Anderson, Tatham, & Black, 1995; McGarigal, Cushman, & Stafford, 2013; Mundry & Sommer, 2007). Since we had 13 individuals between 250 and 380 days with enough high-quality calls, of which five were the same as in the younger than 250 days category and eight were different individuals, we randomly selected 10 of these 13 using the sample function in R. For both age categories we used 16 calls per individual resulting in 160 calls each. Whenever we had more than 16 calls from an individual, we randomly selected 16 calls using the sample function in R. To calculate the chance level correct assignment, we used a randomization approach whereby correct assignment by chance correct assignment by chance was averaged from DFAs conducted on 1000 randomized permutations of the data set (separately for younger and older individuals; McGarigal et al., 2013; Solow, 1990).

Ethical Note

All the recordings and observations used in this study were conducted with the permission of the ethical committee of Pretoria University and the Northern Cape Conservation Service, South Africa (Permit Number: ECO31-13).

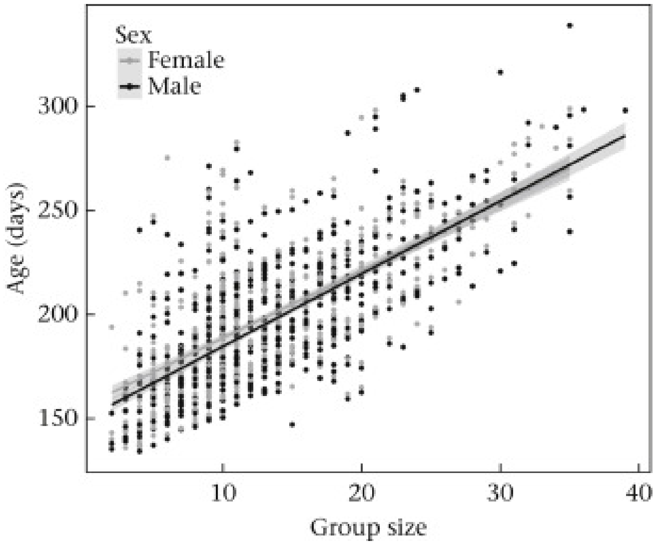

Figure 2. Influence of group size on age when females and males were first recorded to act as sentinels for at least 1 min. The lines are predicted values from the LMM and the shaded areas represent 95% confidence intervals.

Results

Starting Age to Act as Sentinel

Meerkats first began to act as sentinel for 1 min or longer at 202.12 ± 65.4 days (mean ±SD). Young meerkats in larger groups conducted their first sentinel bout at a later age than meerkats in smaller groups (LRT: $\chi^2{}_1 = 161.53$, $P < 0.001$; LMM: $\beta = 0.12$, SE = 0.009, $P < 0.001$; Fig. 2); males did not differ significantly from females (LRT: $\chi^2{}_1 = 0.511$, $P = 0.475$; LMM: $\beta = -0.07$, SE = 0.10, $P = 0.475$). Comparing the starting age to act as sentinel with that of other cooperative behaviours for the same set of individuals showed that pup feeding started at 191.43±73.84 days and babysitting at 211.77±76.44 days.

Likelihood of Producing Different Sentinel Call Types and Call Rates

All six described sentinel call types were present in recordings of the youngest individuals (112–127 days old; see Fig. A1 for spectrograms of subadult sentinel call types). Accordingly, the likelihood of finding any of the six sentinel call types in a given recording was not affected by the sentinel's experience, i.e. GuardSum (min), the total amount of time an individual had been recorded as sentinel (Table 1, Fig. 3). However, the call rates of sentinel calming calls (single and double note calls) and sentinel warning calls (di-drrr and wheek calls) produced during sentinel behaviour changed with experience of the calling individuals (Table 2). Calming calls significantly increased with increasing experience as sentinel, i.e. GuardSum, whereby individuals in larger groups had shallower slopes than individuals in smaller groups (Table 2). In contrast, the call rate of warning calls decreased with increasing experience of the caller. Again, this effect was smaller in larger groups, i.e. individuals in smaller groups decreased the call rate of sentinel warning calls faster than individuals in larger groups.

Table 1. Effect of sentinel experience on the probability of producing each of the six sentinel call types

Call type	Call category	Estimate	SE	*P*
Single note	Calming calls	0.32	0.34	0.336
Double note	Calming calls	0.38	0.38	0.320
Triple note	Middle calls	-0.11	0.27	0.701
Multiple note	Middle calls	0.84	0.44	0.078
Di-drrr call	Warning calls	-0.49	0.32	0.123
Wheek	Warning calls	-0.03	0.24	0.908

Estimates, SEs and *P* values are from the GLMM.

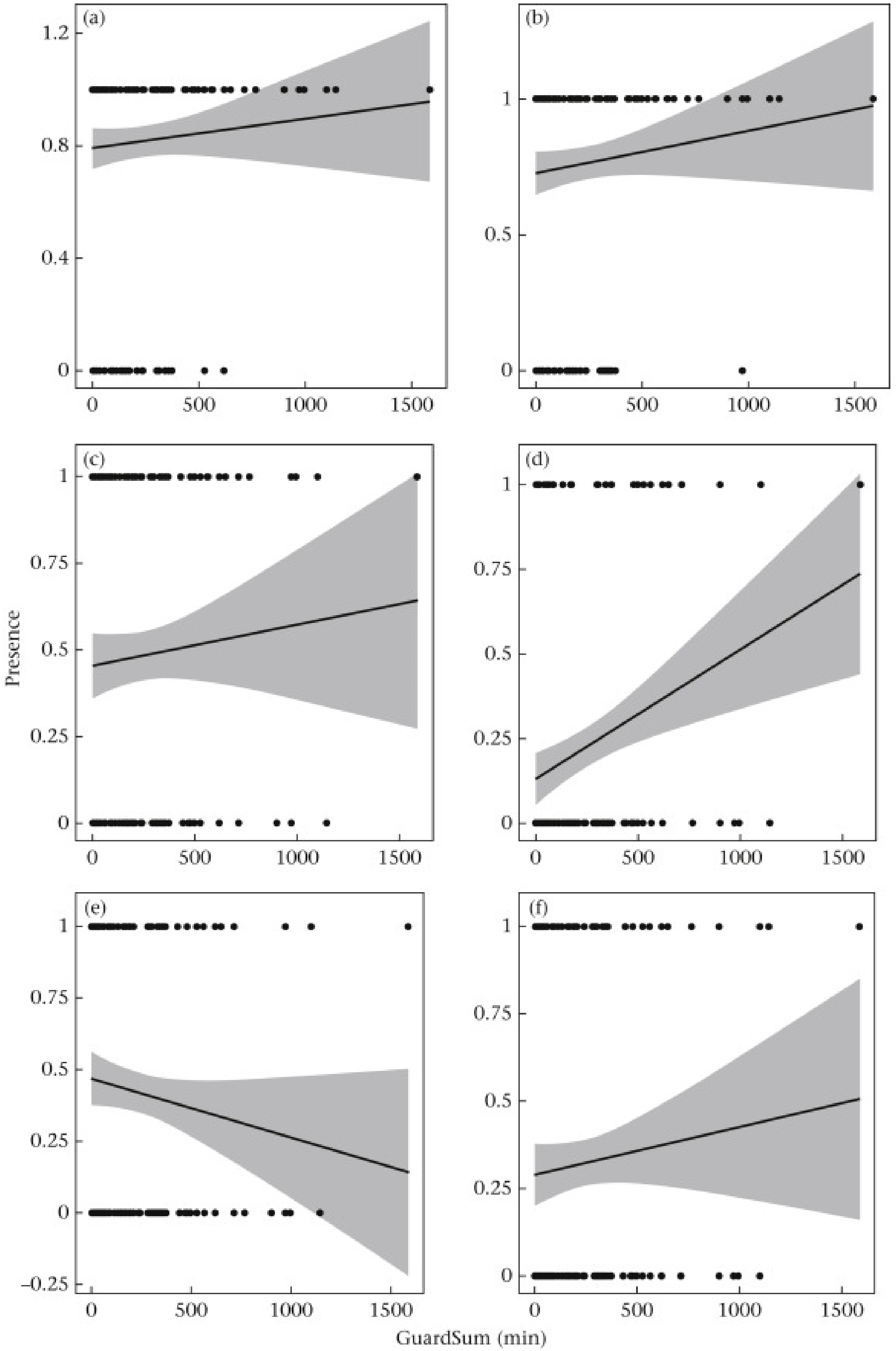

Figure 3. Appearance of each of the six sentinel call types in sentinel recordings of meerkats between the ages of 6 and 15 months in relation to sentinel experience, i.e. the total amount of time (GuardSum, min) an individual has been recorded as sentinel. (a) Single note call, (b) double note call, (c) triple note call, (d) multiple note call, (e) di-drrr call, (f) wheek call. The lines are predicted values from the GLMM and shaded areas represent 95% confidence intervals.

Table 2. Effect of sentinel experience and group size on changes in call rate of the sentinel calming calls (single and double note calls), middle calls (triple and multiple note calls) and sentinel warning calls (di-drrr and wheek calls)

Call type	Variable	Estimate	SE	*P*
Calming calls	GuardSum	1.01	0.43	**0.023**
	GroupSize	0.74	0.54	0.193
	GuardSum∗GroupSize	-1.01	0.44	**0.027**
Middle calls	GuardSum	0.23	0.16	0.167
	GroupSize	0.39	0.54	0.472
Warning calls	GuardSum	-1.19	0.44	**0.008**
	GroupSize	-0.61	0.56	0.263
	GuardSum∗GroupSize	1.05	0.43	**0.018**

Estimates, SEs and *P* values are from the LMM. Significant *P* values are in bold.

Acoustic Parameters and Individuality

Visual inspection of the plotted mean fundamental frequency, mean peak amplitude, duration and mean entropy of the first note of the double note calls showed high variation in the amount (total difference between first and last recording) and degree of change (slopes) for different individuals over age (Fig. 4). Accordingly, we found consistent individual differences in the mean of all measured parameters (different intercepts; LRT: fundamental frequency: $\chi^2_1 = 46.47$, $P < 0.001$; amplitude: $\chi^2_1 = 14.71$, $P < 0.001$; duration: $\chi^2_1 = 63.09$, $P < 0.001$; entropy: $\chi^2_1 = 8.90$, $P = 0.003$), but no general effect of age (Table 3, Fig. 4). Owing to the data structure we were unable to test whether individuals also differed from each other across age (different slopes). The PIC of all measured variables was above 1 (duration: PIC=1.65; mean fundamental frequency: PIC=1.46; mean peak amplitude: PIC=1.46; mean entropy: PIC=1.22); thus, all variables had the potential to be individually distinct. DFA analysis resulted in 65% correct assignment of 10 individuals younger than 250 days, which was significantly higher than expected by chance (confidence interval, CI=0.57–0.72, mean ± SD chance of correct assignment = 10 ± 5%, $P < 0.001$). Call analysis of 10 individuals between 250 and 400 days showed a correct assignment of 57.7% (CI = 0.57–0.77, mean ± SD chance of correct assignment = 10 ± 5%, $P < 0.001$), which suggests consistent individual distinctiveness when individuals first act as sentinels up to 6 months later.

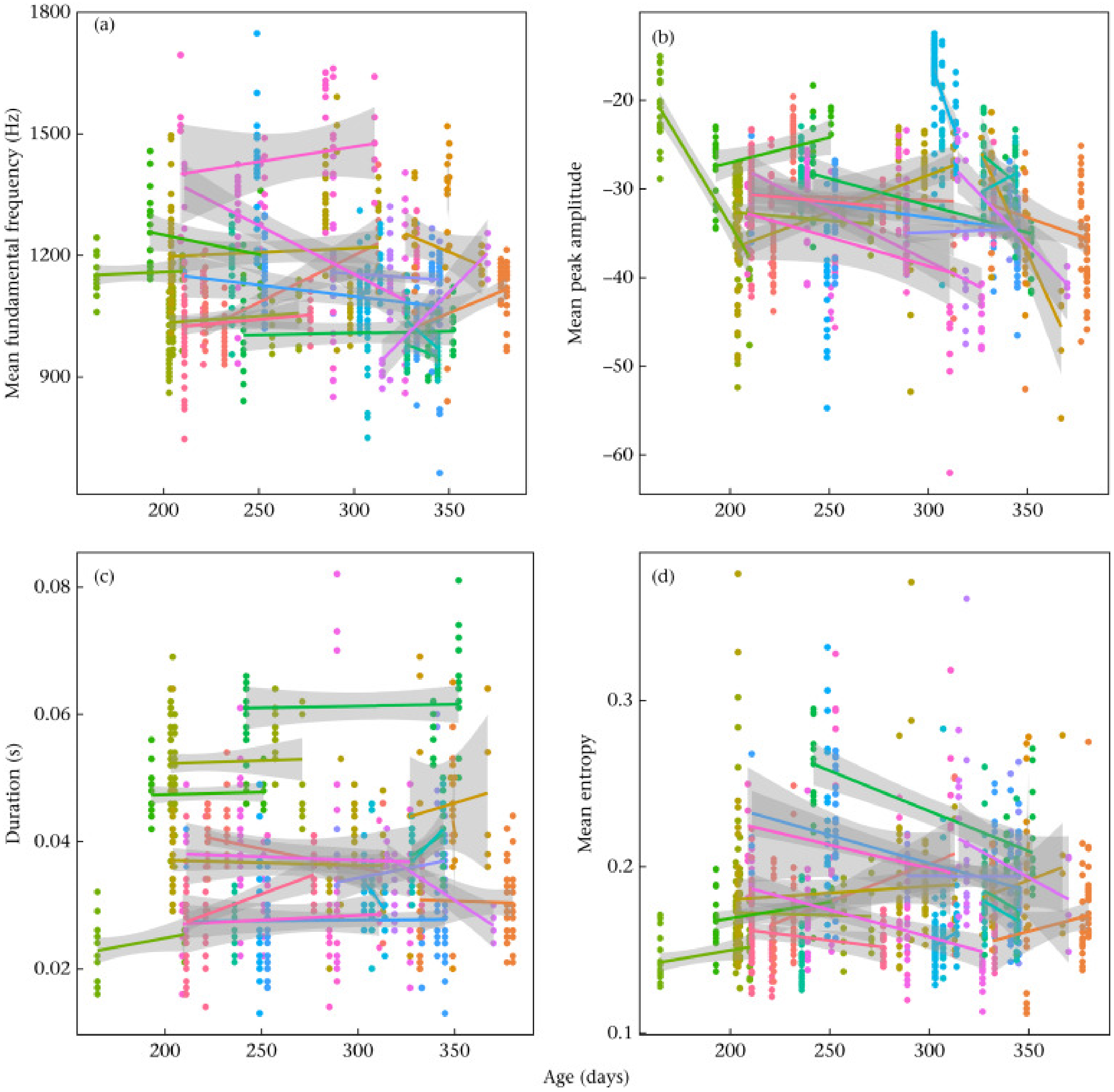

Figure 4. Ontogenetic development of (a) mean fundamental frequency, (b) mean peak amplitude, (c) duration and (d) mean entropy of the first note produced in double note calls with increasing age of the caller. Colours and connecting lines indicate identity of the 18 individuals with three or more high-quality recordings.

Table 3. Effect of age on mean fundamental frequency, mean peak amplitude, duration and mean entropy of the first note produced in double note calls

Acoustic parameter	**Estimate±SE**	***t***	***P***
Mean fundamental frequency	0.03±0.25	0.15	0.88
Mean peak amplitude	-0.03±0.02	-1.71	0.09
Duration	-0.01±0.01	-0.79	0.43
Mean entropy	-0.02±0.02	-1.19	0.24

Estimates, SEs and *P* values are from the LMM.

Discussion

This study addressed the ontogeny of sentinel behaviour in meerkats, in particular the age at which they first start to act as sentinels, the likelihood of producing the six distinct sentinel call types and their respective call rates, as well as the acoustic properties and the development of individual signatures in sentinel calls. We have shown that the onset of acting as a sentinel guard was highly dependent on group size. Individuals from smaller groups exhibited sentinel behaviour at an earlier age than individuals from larger groups. This study also provides new evidence that, although all six described sentinel call types were already present in the repertoire upon first emergence of the behaviour, subadult meerkats increased the call rate of calming calls (single and double note calls) and decreased the call rate of warning calls (di-drrr and wheek calls) with increasing experience as sentinel guard. For both categories of sentinel calls individuals from smaller groups demonstrated faster changes in call rates than individuals from larger groups given the same amount (total duration) of sentinel experience. Analysis of double note calls indicated that mean fundamental frequency, mean amplitude, duration and entropy differed consistently between individuals, but we found no general effect of age. Lastly, our results provide evidence that the individual signature of meerkats was already developed in their calls when they first started to go on sentinel guard and changed little with age.

The mean onset of sentinel behaviour of around 202 days of age was similar to that of the other cooperative behaviours including pup feeding (191 days) and babysitting (212 days). This might suggest that young individuals, which may be less efficient foragers and are still investing energy in growth, did not have the necessary condition to contribute to the different cooperative behaviours. Supplementary feeding experiments of adult meerkats demonstrated that sentinel behaviour, as well as pup feeding, is highly condition dependent (Clutton-Brock et al., 2001; Clutton-Brock, O'Riain, et al., 1999b; Wright et al., 2001b). However, it is also possible that acting as a sentinel requires individuals to have the necessary experience to correctly assess the surroundings for potential threats. In line with this, meerkats younger than 6 months produce fewer correct predator-specific alarm calls than adults, suggesting that individuals gradually learn to associate specific external stimuli with the correct calls (Hollén & Manser, 2007). Our result that group size highly affected when young meerkats started to act as sentinels suggests that the development of sentinel behaviour is not related to absolute age or maturity but is highly dependent on the social environment. This is supported by previous work demonstrating that individual contribution to sentinel behaviour decreases with increasing group size (Clutton-Brock, O'Riain, et al., 1999b). The risk of being predated is higher in smaller groups, and potentially even higher for young individuals (Clutton-Brock, Gaynor, et al., 1999a). Therefore, young individuals benefit from acting as sentinels as this is supposed to be the safest position in the group (i.e. sentinels usually reach shelter first; Bednekoff, 2001; Clutton-Brock, O'Riain, et al., 1999b; Wright et al., 2001b). Future research could investigate whether in smaller groups young individuals that start acting as a guard might even be lighter in weight, but because of the higher predation pressure invest more in antipredator behaviours than same-aged and potentially heavier individuals from larger groups. We encourage more work on the onset of sentinel behaviour and other cooperative behaviours in other species to enable cross-species comparisons of ontogenetic development of these behaviours.

The fact that all the six different sentinel call types were already produced when individuals first started to act as sentinels could be due to several reasons. First, sentinel call types might be innate and thus appear in their repertoire as soon as the context (sentinel behaviour) is shown by young meerkats. Second, sentinel call types are not exclusively used in the context of sentinel behaviour, but also in social and other vigilance contexts including allogrooming and sunning behaviour in the morning and babysitting at the burrow (Collier et al., 2017; Manser, 1998). Pups themselves already produce the single note calls within the first few weeks of their life either as single calls or as units within longer call series (Manser, 1998). Consequently, by the time young meerkats start to go on guard, they have already learned how to produce the different call types in other contexts. Third, it is likely that young individuals pick up the different sentinel call types from an early age, as they are exposed to these calls from the first days of foraging with the group when they are about 4 weeks old. Previous work on the ontogeny of the behavioural response to alarm calls showed mixed results: while some behavioural responses seemed to undergo the biggest ontogenetic changes before young become independent foragers (within 3 months), other characteristics, such as reaction time and response duration only developed later (Hollén & Manser, 2006). Further research, such as acoustic recordings of younger individuals, i.e. pups and juveniles, during different contexts, is needed to fully understand when and how young meerkats include in their vocal repertoire acoustically similar or the same call types used in the sentinel context. Moreover, while we have accounted for potential differences between groups by adding group ID as a random effect, additional factors, including social learning from group members or habitat characteristics, may further influence the ontogenetic development of sentinel behaviour, such as the likelihood of producing specific call types or the order of use of call types.

While previous work on the ontogeny of meerkat alarm calls demonstrates that young meerkats (<12 months) show a high correct classification along the level of urgency (correct assignment of low- and high-urgency contexts; Hollén & Manser, 2007), we found an increase in the call rate of sentinel calming calls (low perceived risk) and a decrease in the call rate of sentinel warning calls (higher perceived risk) with increasing experience of the caller. We did not find any change in call rates of sentinel middle calls, which may indicate that these changes are more subtle than changes in either sentinel calming calls or sentinel warning calls, thus requiring a larger sample size to be able to detect any potential change with experience. In both cases where we see a change in call rates, sentinel calming and warning calls, there was a significant interaction with group size, with smaller groups showing a faster increase or decrease in call rate compared to larger groups. The increase in calming calls is probably due to meerkats becoming more confident in their assessment of urgency levels with more experience. The higher call rate of warning calls when individuals are younger could be an overestimation of the perceived predation risk, similar to infant vervet monkeys, *Cercopothecus aethiops*, which frequently produce alarm calls to nonthreatening stimuli and only restrict their alarm calls to actual predator species over time (Seyfarth & Cheney, 1986). In such situations, when young show a stronger reaction to nonthreatening stimuli, the question is whether this represents an adaptive adjustment to age-dependent differences in predation risk, or whether young are just overreacting and still need to improve discrimination between threatening and nonthreatening situations. As young meerkats did not show an increased fear response to predators that present a greater threat for young compared to adults (Hollén, Clutton-Brock, & Manser, 2008), this may indicate that in the context of sentinel behaviour higher call rates of warning calls may not necessarily be adaptive, but rather increasing experience improves the discrimination abilities between different levels of danger. This is supported by the results that young from smaller groups, which still experience higher relative predation pressures than young from larger groups, but are faster in accumulating experience as sentinels, show a faster decrease in warning calls and a faster increase in calming calls.

In line with the absence of changes in acoustic parameters of the double note calls, one of the two most frequently produced, individually distinct sentinel calls (Manser, 1999), our results indicate that individual distinctiveness was already as high as in adults when individuals started to act as sentinels. This is in contrast to studies showing an increase in individuality with increasing age in domestic goat kids, *Capra hircus* (Briefer & McElligott, 2011), goitred gazelles, *Gazella subgutturosa* (Lapshina et al., 2012) and chicks of nonpasserine birds (Insley, Phillips, & Charrier, 2003; Jones, Falls, & Gaston, 1987; Klenova, Volodin, & Volodina, 2009; Lefevre, Montgomerie, & Gaston, 1998). However, meerkats only started to act as sentinels when they were 200 days old, and it is therefore possible that they do undergo acoustic development and changes in individual distinctiveness at a younger age. This seems likely when considering that the double note calls are also produced in several other contexts which are shown before the onset of sentinel behaviour (Collier et al., 2017). Alternatively, it has been argued that discrimination between signallers may play an important role in particular in systems where callers have variable thresholds to call, such as for example in young or inexperienced individuals (Blumstein & Daniel, 2004) or where calls refer to the perceived risk of the caller (Blumstein & Armitage, 1997), potentially leading to an early development of individual distinctiveness for these calls. This supports recent work demonstrating that sentinel double note calls refer to the caller's perceived risk (Rauber & Manser, 2017), whereby individuals probably differ in their assessment of the level of risk. Moreover, foraging meerkats (adults and subadults) discriminate between the calming calls of different sentinel individuals and adjust the extent to which they rely on social information provided by these individuals (Rauber & Manser, 2018).

To conclude, we have shown that subadult meerkats started acting as sentinels when they were around 200 days old (simultaneous with other cooperative behaviours) and other than slight adjustments in call rates demonstrated little change in vocal call patterns with increasing age and experience. As the majority of sentinel calls are also produced in other contexts, it is possible that vocal ontogeny takes place at a younger age. Alternatively, but not mutually exclusive, our results may suggest strong selection pressures on antipredator behaviours such as the sentinel system, resulting in a fully functional behavioural and vocal response upon first emergence of sentinel behaviour. A third possibility is that the similar calling behaviour of subadults and young adults may indicate that, in contrast to the alarm call system, which are directly related to the presence of a predator and show ontogenetic development (Hollén, Clutton-Brock, & Manser, 2008; Hollén & Manser, 2006, 2007), individuals of different ages experience similar levels of risk when producing sentinel calls, that is, in the absence of a predator, therefore showing the same behavioural and vocal responses. Further research on individual vocalizations of pups (up to 3 months) and juveniles (3–6 months) is needed to understand the extent of ontogenetic development on the different call types and the roles of social environment and age-specific selection pressure.

Declaration of Interest

We declare we have no competing interests.

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Appendix.

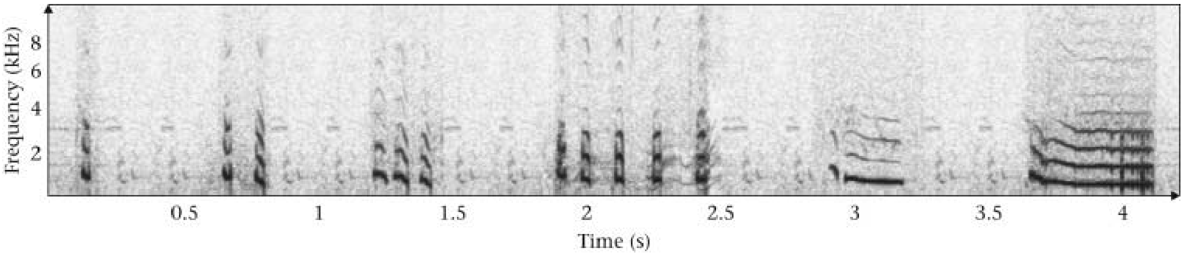

Figure A1. Spectrograms of the six distinct sentinel call types produced by subadult meerkats on sentinel guard. From left to right: single note call, double note call, triple note call, multiple note call, di-drrr call and wheek call.

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