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Audience effect on the alarm calling behaviour of juvenile vervet monkeys

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Abstract

Alarm calls are used by group-living animals as part of antipredator strategies, which facilitate escaping from predators. For example, the three distinct alarm calls that vervet monkeys (*Chlorocebus pygerythrus*) produce while encountering various types of predators, allow listeners to decrease their predation risk by responding to threats appropriately. Even if young vervet monkeys already produce adult-like alarm calls at three months old, they have to learn the associations between the different types of alarm calls and the relevant predators. In our study, we observed the reactions of juvenile vervet monkeys during fake raptor experiments that we conducted under three different audience conditions: "Mothers", "Siblings", "Unrelated audience". Although adults never vocalised while discovering our raptor models, juveniles alarm called to these models, and their vocal behaviour was influenced by the audience's composition. In particular, juveniles alarm called significantly more in the presence of siblings than in the presence of their mothers or unrelated conspecifics. Further analyses showed that the presence of experienced individuals, i.e. older individuals who naturally encountered predators at a higher rate, as well as kin's behaviour, i.e. whether they reacted by being vigilant and alarm called or ignored, also had an important role in their vocal responses. Juveniles produced less calls when experienced individuals were nearby and when siblings reacted. We concluded that observing specific experienced group members during predator exposures, such as mothers, siblings or older individuals, plays a crucial role in the development of juveniles' alarm calling behaviour.

Introduction

Species living in dense habitats, such as forests or jungles, have a complex communication system based primarily on vocal signals (Zuberbühler, Noë et al. 1997). Vocalisations are highly efficient cues due to the poor visibility in such environments. In some cases, vocal signals are crucial as they help individuals to find mates (Mitani 1985), or protect listeners from dangerous situations such as during unexpected encounters with predators. (e.g.yellow bellied marmots, Marmota flaviventris, Blumstein 1997).

Alarm calls are efficient antipredator strategies for two main reasons. First, some alarm calls are directed at the predators themselves (Driver 1969) which discourages them from hunting as their success rate is lower when detected. For example, leopards in Taï forest stopped hunting after hearing alarm calls emitted by Diana monkey species (Cercopithecus diana diana, Zuberbühler, Jenny et al. 1999). Secondly, alarm calls allow nearby listeners to escape from predators (Manser, Seyfarth et al. 2002). By warning nearby conspecifics, such as offspring, kin and potential mates about the presence of dangerous animals, signallers might increase their indirect fitness by aiding the survival of close relatives or important social partners. Consequently, alarm calls might have been favoured both through natural selection and kin selection (Hamilton 1964). In addition to alarm calls encoding information about the type of predator, like the two distinct vocalisations produced by Belding's ground squirrels (*Spermophilus beldingi*) while facing aerial or terrestrial predators (Mateo 1996), alarm calls can also convey information on the distance to predators and the perceived risk of predation. For example, meerkats and white-browed scrub wrens, *Sericornis frontali*, produce different kinds of alarm calls according to the urgency of the situation (Manser 2001, Platzen and Magrath 2005). By receiving information on the type of predators and the level of urgency, receivers can react appropriately, which increases their chance of survival.

By paying attention to the acoustic structure of an alarm call, receivers can respond in adaptive ways even without seeing the actual predator, thanks to the information transmitted by callers on the nature of the event. Upon hearing alarm calls emitted when encountering aerial predators, meerkats respond by running to the nearest refuge. Whereas they approach callers and mob dangerous snakes while hearing alarm calls produced towards terrestrial predators (Manser, Seyfarth et al. 2002). Zuberbühler et al (2001) found that Campbell monkeys (Cercopithecus campbelli) produce different alarm calls according to the type of predator. Using playback experiments they found that Campbell monkeys have two differently structured calls to leopards, *Panthera pardus pardus* and to crowned eagles, *Stephanoaetus coronatus*.

Due to their small sizes, infants are the most vulnerable individuals within a group. For this reason some animals, such as dwarf mongooses (*Helogale parvula*), develop specific alarm calls depending on the level of urgency (Collier 2017). During their first weeks of life, juveniles face high rates of mortality as they are preferred targets for predators (Hollén, Clutton-Brock et al. 2008). However, parental care, feeding offspring and increasing vigilance and alarm call production, increases juveniles' rate of survival (migrating birds: Lind 2004). While infants have an innate skill to produce adult-like vocalisations and respond appropriately, they need to learn quickly how and when to call (Hollén and Manser 2006). Beyond the maturation of their vocal tracts, call production of infants evolves with time by observing the behaviour of older individuals, as they learn to produce appropriate vocalisations in specific contexts (Seyfarth and Cheney 1986). For example, infant marmoset monkeys, *Callithrix jacchus*, separated from their parents still demonstrated infant-like vocal behaviour when they grew older, as they did not have the opportunity to learn from their more experienced kin (Gultekin and Hage 2017). Social feedbacks, especially from important social partners such as older, more experienced individuals, such as siblings and mothers, can be crucial in shaping alarm call production in juveniles (Seyfarth and Cheney 1986).

In their natural environment, vervet monkeys encounter several types of predators: aerial, such as martial eagles, *Polemaetus bellicosus*, and crowned eagles, and terrestrial mammals such as leopards, and snakes such as pythons, *Python sebae* (Seyfarth and Cheney 1980). Their escape responses differ according to the predator type; by looking up for aerial predators, running up into the tips of branches when encountering mammals, or standing vigilant bipedal whilst scanning the ground for snakes (Seyfarth, Cheney et al. 1980). Three main alarm call types have evolved. Despite adults being selective in their call production (i.e. producing vocal signals corresponding to the type of predators encountered), juveniles produce alarm calls to a much wider variety of species, including some harmless animals (Seyfarth, Cheney et al. 1980). Although infant vervet monkeys start to give their first alarm calls at the age of three months old (Seyfarth and Cheney 1986), they make many mistakes at the beginning of their lives, with the accuracy of context production increasing with age and experience. One way of avoiding those mistakes is to learn from conspecifics. One study demonstrated that social learning plays a major role in this species in a feeding context, with infants adopting the same foraging techniques as their mothers (Van de Waal, Bshary et al. 2014). However, little is known about the social influences on the development of alarm calls in juvenile vervet monkeys.

Our project aimed to get a better understanding of the influences of the social environment on the alarm calling behaviour of juvenile vervet monkeys, and more specifically on the role of mothers, siblings and unrelated group members on the development of these vocalisations. For that, we used juveniles from one to two years old as focal individuals, and we exposed them to raptor model experiments to study their reaction when encountering a potentially dangerous animal. We then examined their alarm call production according to the presence and reaction of specific audiences. As it would be adaptive to learn by observing the behaviour of mothers or older, more experienced individuals, we thought that our focal animals would adapt their response according to the audience composition. We expected our focal animals to alarm call more in the presence of younger, less experienced individuals. When in the presence of more experienced individuals, such as mothers or siblings, we expected individuals to alarm call less and only towards predators and not models.

Methods

Study site and species

We conducted our study over six months (29 September 2016-19 March 2017) on three groups of wild vervet monkeys (BD, KB & NH). The study took place within the Inkawu Vervet Project (IVP) based at Mawana game reserve (28° 00.327S; 31° 12.348E), in South Africa. The studied groups contained an average of 84 individuals over the entire study period, and were composed of multiple males (described as adults after their first migration), multiple females (described as adults after they had given birth for the first time), and many juveniles ranging from one to four years old (see Table 1S for detailed composition of each studied group).

Since 2010, researchers from IVP have encountered several types of predators that are potentially dangerous to vervet monkeys, which included a variety of snakes, raptors and mammals (Seyfarth, Cheney et al. 1980). Dangerous snakes included African rock pythons *(Python sebae*), puff adders *(Bitis arietans*), Mozambique spitting cobras (*Naja mossambica*), black mambas *(Dendroaspis polylepis*) and boomslangs *(Dispholidus typus*). Two potentially dangerous raptors were observed: martial eagles (*Polemaetus bellicosus*) and crowned eagles

(*Stephanoaetus coronatus*). Although less frequently encountered, the presence of black-backed jackals (*Canis mesomelas*) can also be dangerous for vervet monkeys. Furthermore, there are several other species of carnivores that could potentially be observed in the field, such as caracals (*Caracal caracal*), leopards (*Panthera pardus pardus*), servals (*Leptailurus serval*) and hyenas (*Crocuta crocuta*).

Data collection

Focal data

We used focal animal sampling (Altmann 1974) to collect data on the main activity and social behaviour of 15 subjects over 20 minutes (collecting scan data every two minutes; N = 9 juvenile males and N = 6 juvenile females; see Table 2S for a detailed description of data collected during those natural observations). We first collected those data as soon as juveniles started foraging at their sleeping site at dawn, when predators are known to be active, in order to increase the chance of collecting data during natural predator encounters. In addition to those baseline data, we again collected 20 minutes of focal data on each subject just after he/she participated in our model experiments. By comparing their behaviour before and after the experiments, this allowed us to underline how the experiment affected their behaviour, for example, when spending more time in close proximity to their mothers.

Ad libitum data

In addition to collecting focal data, we recorded *ad libitum* data (Altmann 1974, see Table 3S and Table 4S for detailed description of ad libitum data collected) as soon as individuals encountered predators to describe the general patterns of their alarm calling behaviour (Mohr 2017, unpublished report). We also collected ad libitum data on their social interactions to define the relationships amongst group members, using all agonistic encounters to calculate their hierarchy and affiliative encounters with proximity data to calculate the strength of their social bonds.

Experimental data

We collected detailed data on the reactions of our focal individuals during the fake raptor experiments using three clear responses: vigilance state, alarm call production and ignorance state. We classified an individual as “vigilant” when he/she was in a straight posture, potentially bipedal, and looking carefully in a targeted direction (towards specific individuals or objects, such as raptor models). An individual was “alarm calling” as soon as he/she produced any kind of alarm calls, which were characterised as short barks produced once or repeatedly in sequences (Strushaker 1967). Finally, we described an individual as not reacting and carrying on with its previous behaviour (such as resting, feeding, moving or socialising) as an “ignoring” response since he/she did not react to our experiments. In addition to recording the behaviour of the subject, we also documented the reaction of mothers and siblings using the same behavioural responses, considering an individual “reacting” as behaving either vigilant and/or producing at least one alarm call, and “not reacting” as ignoring.

Experimental design

While one observer collected focal data on a juvenile at least 20 minutes before an experiment took place (hoping that it would be the subject of the experiment), the second one prepared the experiment by hiding a raptor model under a piece of material in front of the group, out of sight of the monkeys (Figure 1). We used 15 juveniles as subjects to run 45 predator model experiments under three conditions. In the first condition, we waited until the mother was within 10 meters from the subject to run the experiment (hereafter “Mother” condition), making sure that no other related individuals were present in the audience. In the second condition, we waited until the subject had at least one of his/her siblings within 10m (hereafter “Siblings” condition), whilst making sure that the mother was absent. Finally, in the third condition, we waited until the subject was away from his/her mother and all of his/her siblings but had at least one unrelated monkey within 10m of them (hereafter “Unrelated audience” condition). Therefore, each subject participated three times in our experiments. For each experiment, we collected the date, the audience condition (“Mother”, “Siblings”, or “Unrelated audience”), the type of models used (balancing and randomising the use of the two raptors, Figure 1), the identity of the juvenile who discovered the model (thus becoming our subject), his/her response (vigilant or/and alarm called, ignored), his/her height position (tree or ground), the GPS location of the experiments’ place, the time of arrival when he/she approached within 15m from the model, whether vocalisations were produced by other individuals (and whenever possible the identities of all signallers) and the audience composition (i.e. the identities of all neighbours present within 2 m, 5 m and 10 m of the subject, Table S4).

Figure 1: Picture showing the experimental setup, with the fake raptor still hidden under the textile while some monkeys were slowly approaching from behind. The side pictures represent the two raptor models used during our experiments.

Despite vervet monkeys usually moving as a cohesive group, we tried to run the experiments at the periphery of the group or when it was spread out to expose the model to only a few isolated individuals. While all individuals were habituated to the experimental set-up and did not react until we uncovered the model by lifting up the material (as shown by the monkeys foraging nearby the hidden model in Figure 1), we wanted to avoid individuals getting too used to the models by using isolated subjects. This decreased both model exposure and the number of individuals present in the audience, which also helped to analyse the influences of the social environment more easily. Moreover, we limited the number of experiments to a maximum of three per week to keep our experiments at a realistic rate of natural encounters. We made sure to have a break of at least two days between consecutive experiments in the same group, and a one week break between experiments with the same subject. When the requirements of specific conditions were met, we uncovered the model and lifted it up to around one meter high using a fishing line hung up in the trees (Figure 1) in order to fake the movement of the eagle taking off, which appears potentially dangerous for vervet monkeys. As soon as the subject looked in the direction of the model and/or reacted in any other way, by being vigilant or alarm calling, we dropped and covered the model to avoid other individuals approaching and being exposed to the fake raptor. Whenever the subject stopped reacting and resumed his/her previous activity, we again collected 20 minutes of focal data to investigate how its social and vocal behaviour was modified following his/her reaction during our experiments.

Inter-observer reliability

For our study, five experienced researchers helped collect data (AC, CMP, HSJ, SH, TM). In addition to two months of training before the experiments started, they all passed an identification test showing that they were able to recognise all the monkeys within the study groups three times in a row within 30s. Despite inter-observer reliability being assured by the calculation of Cohen's Kappa scores (Cohen 1960) using data collected simultaneously by two observers on the main behaviour of vervet monkeys, we did not perform such a specific test for the fake raptors experiments. However, we ensured that the data were collected in an appropriate way by using clear definitions (mainly whether individuals ignored, were vigilant, or produced alarm calls) and discussing cases that were ambiguous with a minimum of two observers who participated at each experiment (one following the subject individual and a second one setting up the eagle model and collecting data on participating individuals). Two researchers observed the monkeys' reaction, and all experiments were recorded (using both camera and audio recorder). Consequently, we are confident that our data were collected in a reliable way.

Ethical note

Our project was approved by the University of Cape Town, South Africa. The vervet monkeys responded well to our model experiments, and none of them were injured. Following experiments, they resumed their previous behaviour quickly, and without showing any signs of disturbance. Furthermore, we respected a strict timeline for our experiments, which tried to emulate the natural rate of predator encounters. All animals were well habituated and could be individually identified thanks to individual features such as the colour of the fur, naturally broken fingers, scars or holes in the ears.

Statistical Analyses

1. Alarm calls produced by different age classes

Before performing the analysis we obtained the general proportion of alarm calling by all individuals (number of calls produced divided by the number of individuals who, were within ten meters from the subject). Assuming they call all at the same rate, we calculated the expected proportion of alarm calls by all individuals in each age class (total number of calls produced divided by the total number of individuals that participated in each category). We used a Fisher exact test to check whether the proportion of alarm calls observed in all age classes corresponded to what we expected.

2. Presence of specific audiences

In addition to the first analysis we observed the number of alarm calls that were produced in the presence of three specific audiences: Mothers, Siblings and Unrelated audience. First, we assumed that there were no differences between the number of experiments that generated alarm calling behaviour. From 15 experiments that have been done in each condition, subjects gave

12 alarm calls. Thanks to a Fisher's exact test we checked whether the number of alarm calls observed corresponded to the number of alarm calls expected.

3. Audience conditions

We used a generalized linear mixed model (GLMM; Baayen, Davidson et al. 2008) fitted with a binomial structure and logit-link function to investigate whether juveniles adapted their vocal behaviour according to the audience composition, i.e. the identities of individuals present within 10m (N = 15 subjects tested in three audience conditions). We checked that all assumptions for linear mixed models were met (Zuur, Ieno et al. 2009) by looking at the distribution of residuals (reaching approximately symmetrical distributions and using qq plots, binnedplots and half-normal plots). We used whether subjects produced alarm calls as the response variable (Yes=1/No=0), and we added three predictors describing the audience condition : "Mothers" meaning that the mother of the subject was present (Yes=1) or absent (No=0) from the audience , "Siblings" meaning that at least one sibling of the subject was present (Yes=1) or absent (No=0), and "Unrelated audiences" meaning that neither the mother or siblings of the subject were present but that at least one unrelated individual was present (Yes=1) or absent (No=0). We included the identity of the focal animals as random intercepts to control for repeated measurements.

4. Experienced individuals

We defined "experienced individuals" as individuals older than subjects as we assumed that they had been exposed to predators more frequently, and had thus more opportunities to learn how to react to specific situations compared to younger naïve ones. Consequently, all adults were considered more competent than our subjects, including both older siblings and older unrelated juveniles present in the audience. In contrast, individuals younger than our subjects were considered less experienced. We removed the audience was composed of both younger and older individuals than our subjects. Due to our small sample size of older vs younger individuals presented in the audience (as the individuals were wild, it was impossible to control which individuals approached within 10m), we could not use a GLMM to examine the influence of competent individuals on the vocal behaviour of juvenile vervet monkeys. We thus ran Bayesian binomial tests to investigate the probability that the difference in the proportion of alarm callings produced by our subjects would be higher than chance level, corresponding to 0.5 (as only two options possible: calling or not calling), in presence of younger than older audience. We used a uniform prior distribution of the probability of alarm calling according to the presence of experienced individuals (0 if no alarm calls were produced and 1 if at least one alarm call was emitted by our subjects). We then computed the corresponding posterior distribution, and compared them in order to obtain the probabilities that the difference of these two proportions of alarm callings is higher than 0.5, in presence of younger naïve audience than an older experienced one. Results of such Bayesian tests indicate the probability at which a particular category is significantly different from a second one in eliciting different behavioural responses, in our case, producing alarm calls or remaining silent according to the experience of siblings and unrelated audiences.

5. *Audience reactions*

In addition, to examine the influence of competent individuals (using age as a proxy) on juveniles' alarm calling behaviour, we also used Bayesian binomial tests to investigate how the reactions of mothers and siblings modified the alarm call production of our subjects. We considered an individual as reacting if he/she became vigilant and/or produced at least one alarm call, while individuals carrying on with their natural behaviour during the experiments were defined as not reacting, i.e ignoring. By comparing the uniform prior distribution of the probability of alarm calling according to the reactions of specific audiences with the corresponding computed posterior distribution, we obtained the probability at which a particular category is significantly different from a second one in eliciting different behavioural responses, here, producing alarm calls or remaining silent according to the reactions of mothers and siblings. Although we analysed the reaction of siblings in all the experiments of this audience condition (N=15), we had to remove 3 data points from the mother condition due to a lack of visibility stopping us from clearly observing their reactions (conducting to N=12).

All data were analysed in R studio 3.2.1 (Team 2015). We used the following packages to run all the statistical tests: arm (Gelman 2016), car (Weisberg 2011), effects (John Fox 2009), faraway (Faraway 2016), lme4 (Walker 2015)..

Results

From the 144 trials that have been done, 45 fake raptor presentations using three audience conditions (Mothers, Siblings and Unrelated audience) could be used for our analysis. As vervet monkeys are free-ranging animals, we could not control their behaviour and the number of predators they naturally encountered during and after we showed our fake raptors (6/144). We conducted focal animal samples of 20 minutes each (one before and one after the raptor model presentations) twice for each of our 15 subjects (Table S5 description of 15 subjects). We collected a total of 600 minutes of natural observations.

1. *Proportion of individual who gave alarm call*

From 85 individuals presented, 47 adults, 15 four year olds and 23 juveniles, 18 calls have been produced (18/85). With a call controlling for the number of individuals in each age class we found that adults should call with a frequency of 55.3%, four year olds 17.7% and juveniles 27%. Despite, adults often being present around experiments, they never emitted alarm calls. Out of the 15 four-year old juveniles who were present around experiments, just four of them alarm called and from 23 younger juveniles, 14 alarm called during experiments (Figure 2, Table S6).

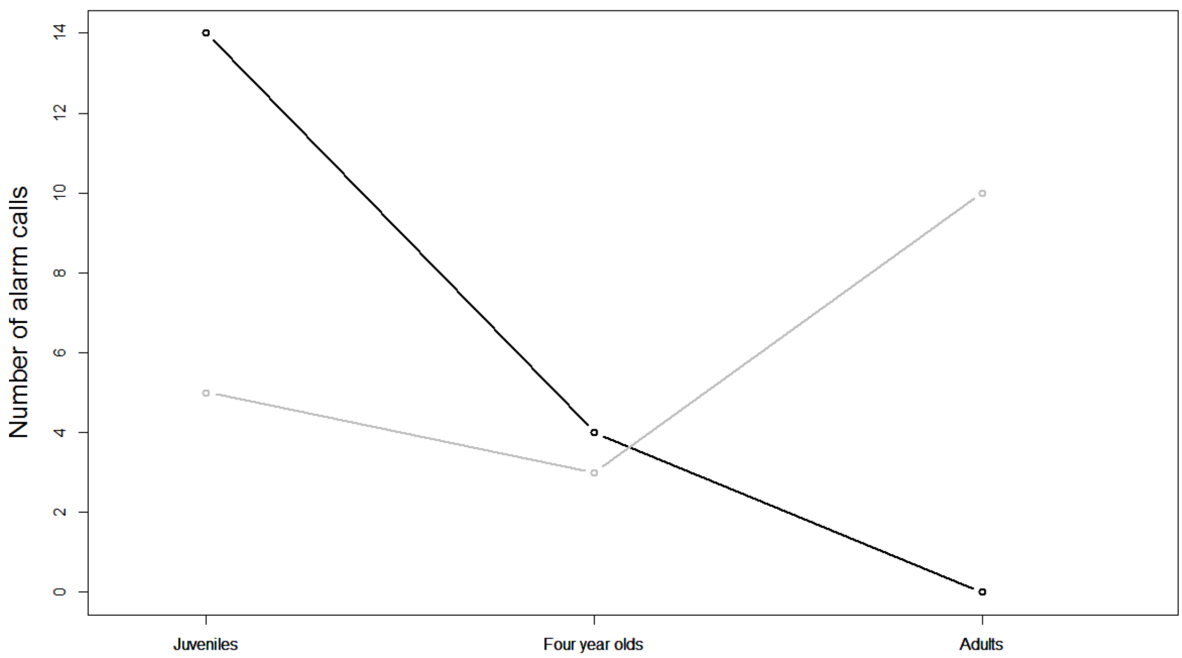


Figure 2: Comparison of the total number of alarm calls during the raptor experiment that were observed (black) and expected (grey) in three different age classes: juveniles, four year olds and adults.

Results from a Fisher test showed that the number of alarm calls produced during experiments differ significantly between different age classes. The graph shows that while juveniles and f our year olds alarm called more than expected, the opposite was found for adults, who alarm c alled at a lower rate than expected (Fisher exact test for count data, df=2, p = 0.0002437)

2. *Presence of a specific audience*

We used Fisher's exact tests to examine whether subjects' alarm call production was distributed randomly or significantly differed according to the presence of an audience. From 15 experiments, subjects gave two calls when in the presence of their mother, seven calls when in the presence of their siblings and three calls when in the presence of an unrelated audience, for a total of 12 alarm calls. Results showed that there are statistically no differences between their alarm call production in the mothers, siblings and unrelated audience conditions (Fisher exact test for count data, $p = 0.581$). Despite differences not being statistically significant, it seems that focal individuals produced more alarm calls than expected when mothers and an audience were absent but produced less alarm calls than expected when siblings were absent (Figure 3).

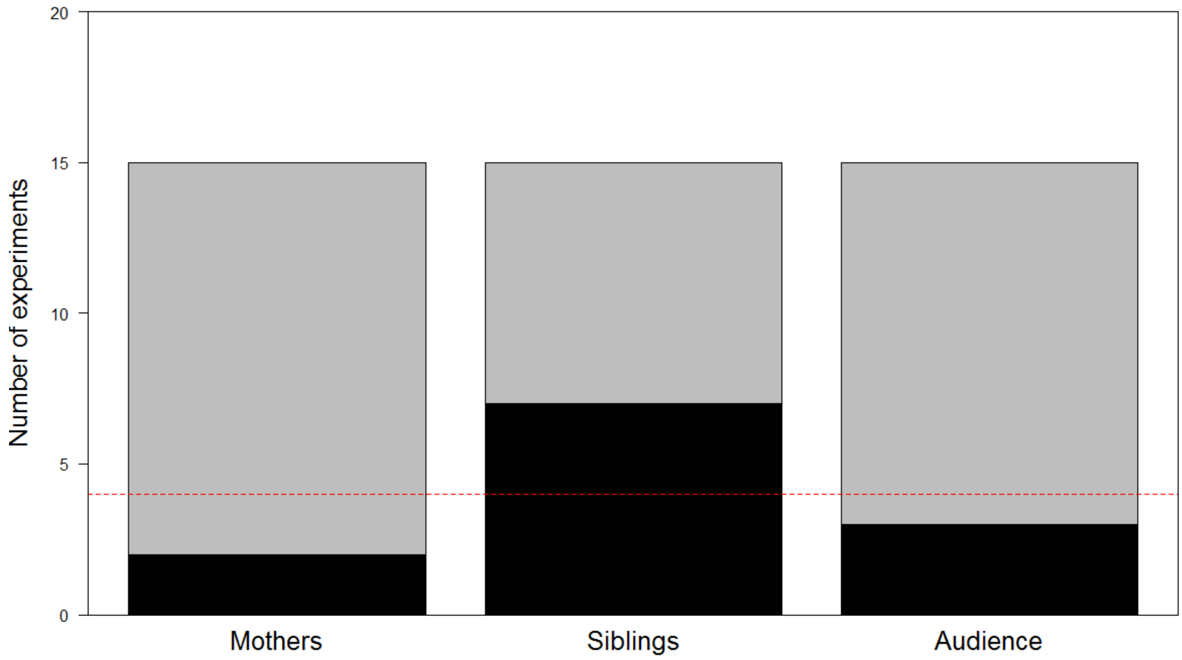
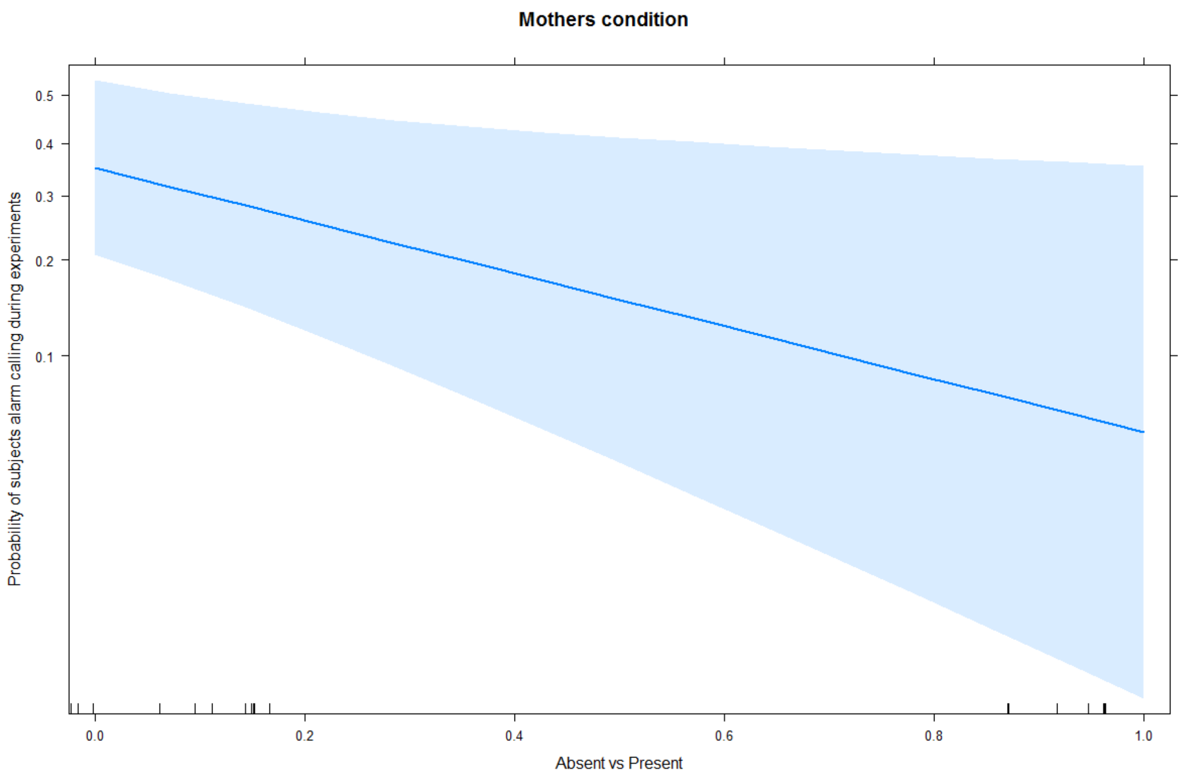


Figure 3: Graph showing number of experiments generating alarm calls in subjects in the presence (black) and absence (grey) of each audience category: Mothers, Siblings and Audience. The red line describes the expected alarm call if subjects call at the same rate (N=4).

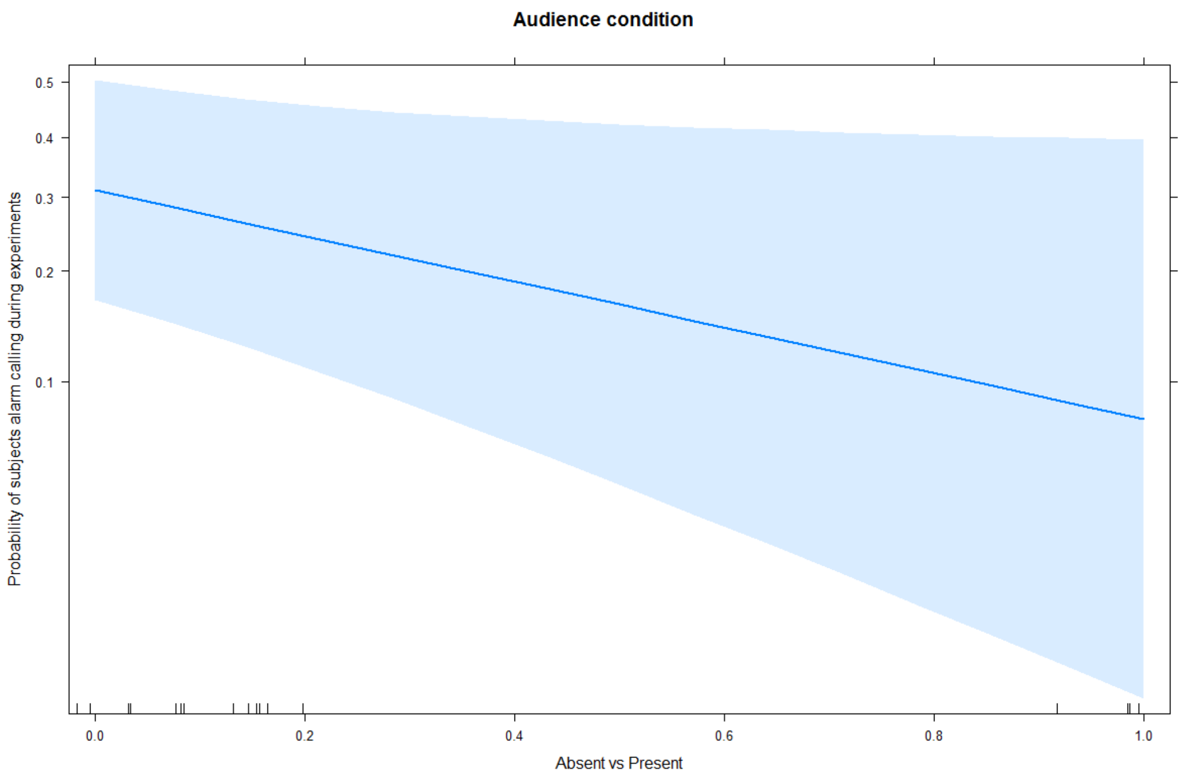
3. Audience condition

We analysed 45 experiments to examine the general alarm calling behaviour of one and two year old vervet monkeys (Table S7). A likelihood test ratio test showed a significant difference between our full and null models *(*ANOVA, X^2_3= 13.082, p<0.005). Vocally, subjects behaved differently according to the audience composition. Juveniles significantly decreased their production of alarm calls when in the presence of their mother (GLMM, p = 0.022) and when in proximity to an audience (GLMM, p = 0.045). Instead, subjects did not significantly alter their calls in the presence of siblings (GLMM, p = 0.803, Figure 4,5,6).

4)



5)


Audience condition
Probability of subjects alarm calling during experiments
0.5
0.4
0.3
0.2
0.1
0.0
0.2
0.4
0.6
0.8
1.0
Absent vs Present

6)

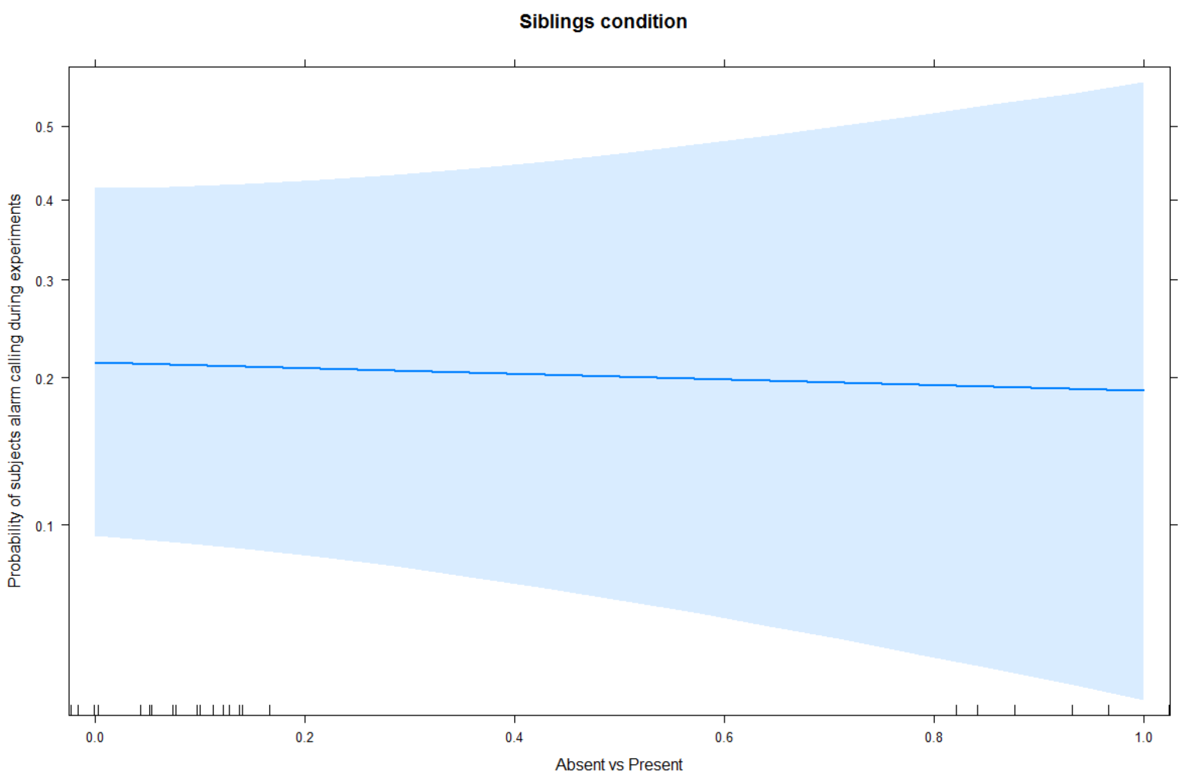

Siblings condition
Probability of subjects alarm calling during experiments
0.5
0.4
0.3
0.2
0.1
0.0
0.2
0.4
0.6
0.8
1.0
Absent vs Present

Figure 4, 5, 6: Proportion of alarm call production during the raptor experiments according to the different audience condition: “Mothers”, “Siblings” and “Audience”. The blue line represents means, and the pale blue area represents the confidence intervals.

4. Experienced individuals

We used Bayesian tests to examine the influence of the presence of competent individuals on the alarm call production of our subjects. We found that juveniles had a 91% chance of adapting their alarm calling behaviour (i.e. more than chance level at 0.50 using Bayesian binomial tests) according to the age of their siblings. Subjects alarm called less when they were in the presence of younger and presumably less experienced siblings (3/7), while they alarm called more in the presence of older, more experienced ones (4/7). However, juveniles called less than expected in the presence of older siblings, while calling more than expected in the presence of younger siblings (Figure 7). In addition, juveniles had a 31% chance of modifying their vocal behaviour (i.e. a smaller probability than 0.50 chance level using Bayesian binomial tests), according to the age of an unrelated audience. Although subjects seem to alarm call at a higher rate when they were in the presence of a competent unrelated audience than when they were with less experienced, younger unrelated individuals, this difference was not statistically significant, meaning that the age of an unrelated audience did not affect their vocal behaviour (Figure 7, Table S8). To summarise, siblings were more likely to influence the alarm call production of our subjects around fake raptor experiments than unrelated audiences.

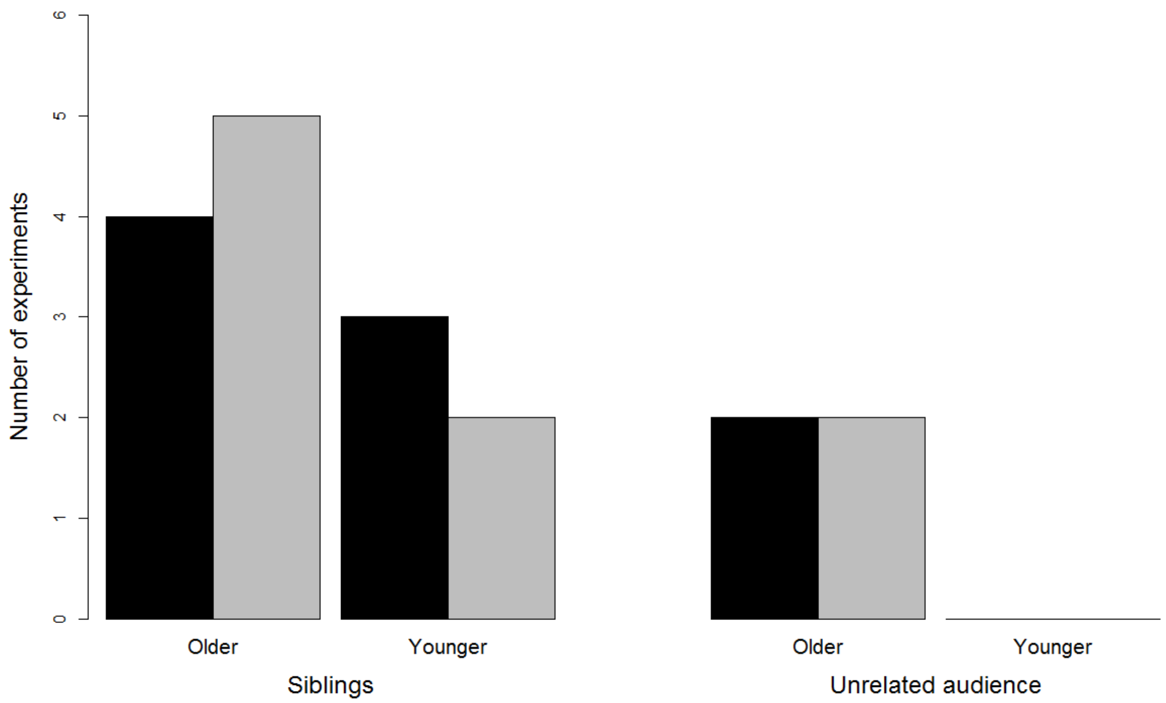


Figure 7: Comparison of the total number of experiments in which alarm calls have been observed (black) and expected (grey) according to the experience of audiences

5. *Audience reactions*

We used Bayesian binomial tests to investigate how reactions of mothers and siblings (reacting, not reacting) affected the alarm call production of our subjects. We found that juveniles had a 96% chance of adapting their alarm calling behaviour (i.e. more than chance level at 0.5 using Bayesian binomial tests) according to the reactions of their mothers. Although subjects never vocalised when their mothers reacted, by either being vigilant or alarm calling, they elicited alarm calls in two experiments which the mothers ignored. However, subjects had a 7% chance of modifying their vocal behaviour according to the reactions of siblings (which is less than chance level of 0.5 using Bayesian binomial tests). While subjects never vocalised when siblings ignored, they alarm called as expected when siblings reacted by either being vigilant or alarm called (Figure 8, Table S9).

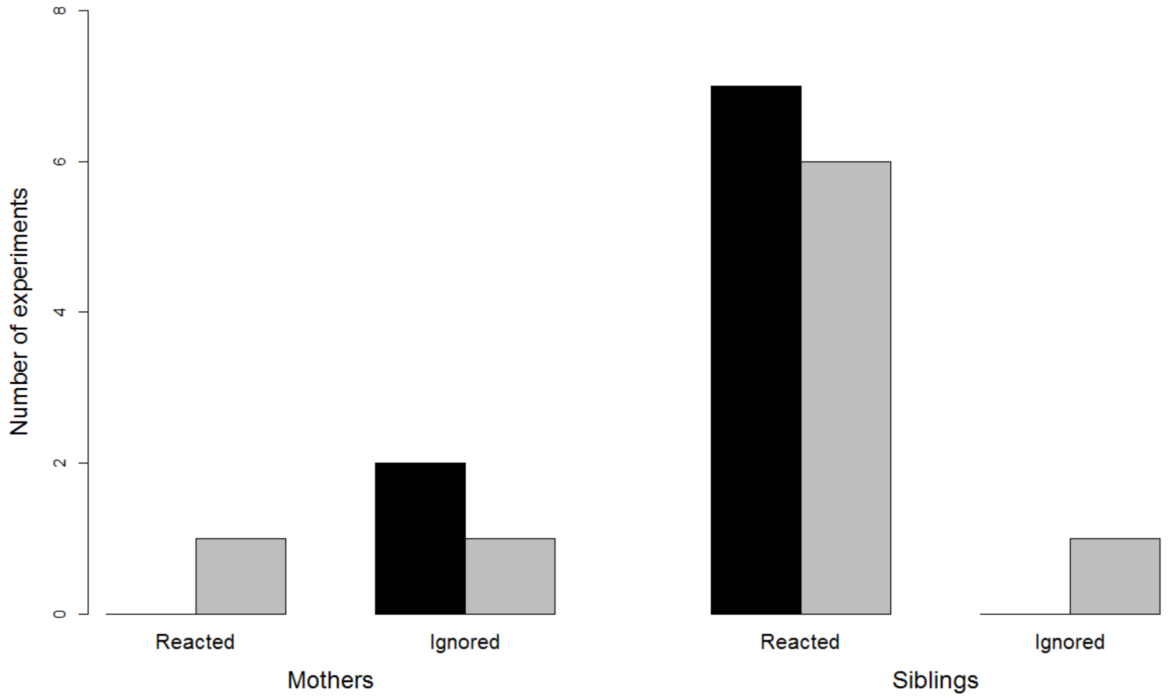


Figure 8: Comparison of the total number of experiments in which alarm calls have been observed (black) and expected (grey) according to the reactions of mothers and siblings.

Discussion

Despite individuals from all age-sex classes reacting by being vigilant, only juveniles alarm called during our predator model experiments, and adults never vocalised. However, the vocal behaviour of our subjects was influenced by the presence of specific audiences, the experience of siblings and unrelated audiences, as well as by the reactions of mothers and siblings. This means that our subjects adapted their alarm calling behaviour according to their social environment.

1 Alarm calls produced by different age classes

Although vervet monkeys in all groups alarm call when encountering various predator types (Seyfarth et al. 1980, Mohr unpublished work 2016), the probability of alarm calling during our fake raptor experiments differed between individuals from different age classes. We found that the production of alarm calls decreased with age. Juveniles (including one, two and three year olds) were indeed the most vocally active individuals emitting alarm calls in 31.11% of our experiments (14/45), followed by four year olds who alarm called in 8.89% of our experiments (4/45), whereas adults remained silent. As adults have had the opportunity to encounter many predators throughout their lives, they have developed an appropriate alarm calling behaviour, vocalising only to dangerous predators and not to models. In contrast, juveniles that have faced fewer natural predators were less experienced and thus more likely to make mistakes, emitting alarm calls to a wider range of animals, including harmless ones (Seyfarth, Cheney et al. 1980). This might explain why only inexperienced juveniles alarm called at our models, whilst older experienced individuals, such as adults, did not.

2 Presence of specific audiences

The mere presence of specific audiences such as mothers, siblings or an unrelated audience within 10m of our subjects did not influence their vocal behaviour during our fake raptor experiments. Although our focal individuals alarm called less in the presence of their mothers (2/15 = 13.33%) and when unrelated individuals were in the audience (3/15 = 20%) than when they were surrounded by siblings (7/15 = 46.67%), the difference was not statistically significant. The fact that juveniles seem to alarm call more in the presence of their siblings might be explained by kin selection theory (Hamilton 1964). While individuals should remain silent when alone or surrounded by an unrelated audience, kin selection would predict that individuals should alarm call more in the presence of siblings as warning related group members about the presence of a danger will decrease their predation risk. For example, this is the case in domestic chickens, *Gallus gallus*, where it has been shown that females called more in the presence of their own chicks than they did when in the presence of an unrelated one (Karakashian, Gyger et al. 1988). Consequently, it might be beneficial for juveniles to alarm call in the presence of vulnerable siblings. However, decreasing alarm call production in the presence of their experienced mothers, or when unrelated audiences are nearby, might decrease some potential costs such as attracting the predators' attention towards signallers.

3 Audience conditions

Results from GLMM showed that mothers were the most influential audience regarding the alarm call production of our subjects. Juveniles refrained from calling more in the presence of their mothers than in the presence of unrelated audiences or siblings. As juveniles spend most of their time with their mother, learning from them is crucial in developing appropriate behaviours. However, the weaker effect of the presence of an unrelated audience and siblings on juvenile alarm calling behaviour might suggest that other factors, such as the experience level of each individual, might also affect their vocal behaviour. In the presence of unrelated audiences and siblings, juveniles might advance their reputation by showing the group members their capacity to alarm call when they encounter danger. Subjects might demonstrate to the group that they can help defend them and in turn the group members should warn them whenever there is a predator nearby.

4 Experienced individuals

In addition to the mere presence of specific audiences, the experience of bystanders, reflected by their age, might also play an important role in the alarm calling behaviour of our subjects. Juveniles indeed alarm called in a higher number of experiments when in the presence of younger siblings (3/4 = 75%) than older ones (4/11 = 36%). These results could be explained by the level of vulnerability of individuals nearby. In presence of younger siblings, our subjects might give more alarm calls to protect them, as younger individuals might be less experienced and so more vulnerable to predators. On the other hand, when they are in proximity to older siblings they might decrease their alarm call production as it is costly to alarm call when it could potentially attract predators. However, our focal individuals alarm called in a higher number of experiments in the presence of older unrelated individuals (2/6 = 33%) than younger ones (0/1 = 0%). In their study Baldellou and Henzi (1992) found that vervet monkey ranks can be influenced by the activity of individuals against predators. Juveniles alarm calling might show to other members of the group their capacity to defend the group, thereby increasing their reputation and receiving a social reward, such as grooming. Unfortunately, because of the number of older individuals within the study groups, our probability of having a younger one was low. There was only one experiment where our subject was in the presence of only younger, unrelated individuals. We need more experiments to confirm whether they alarm call less or more than what we observed.

5 Audience reactions

In addition, the reaction of experienced bystanders, i.e whether they ignored or reacted to our raptor models by being vigilant or alarm calling, also influenced the vocal behaviour. We found that juveniles alarm called more when mothers ignored our model presentations and they alarm called more when siblings reacted to the predator model (by either being vigilant or alarm calling). By not reacting and ignoring the model, to the juveniles, mothers seemed to be unaware of the danger. It is thus possible that juveniles alarm called in this situation in order to warn them about the presence of an unknown, potentially dangerous, object. However, if mothers reacted by being vigilant, subjects observed them not alarm calling and returning rapidly to their normal activity. This could have been a potentially important situation during which juveniles learn that this specific situation is not dangerous, and does not require the production of alarm calls.

In contrast, subjects alarm called in a higher number of experiments when siblings reacted. As adult females give birth to one offspring per year (Cheney and Seyfarth 1992), siblings are relatively close to each other in age. Consequently, it is possible that siblings, despite being slightly older than the subjects, also made mistakes and reacted strongly by being vigilant and emitting alarm calls to our fake raptors. Their reactions could have influenced our subjects that adopted a similar behaviour. As demonstrated in a field experiment, not only can mothers be influential, but the whole matriline, as juveniles acquired the same processing technique as their matrilines (van de Waal, Krützen et al. 2012). However, this should decrease with growing siblings, as they should produce less mistakes over time. Another potential explanation is that while encountering predators, vulnerable young individuals preferred to adopt a “better safe than sorry” strategy, by alarm calling more in the presence of siblings, even when in the presence of non-dangerous predators such as our models.

Influence of adult males

Although we unfortunately did not have paternity data and could not control which individual participated in the audience, the presence of adult males, who potentially fathered some of our subjects, might also influence their vocal behaviour. During our experiments, juveniles alarm called less when at least one adult male was present in the audience (0/5 = 0%) than when no adult males were nearby (3/10= 30%). Similarly to mothers, adult males are experienced individuals and they are the most active against predators within a group ((Baldellou 1992). Consequently, by observing the reactions of adult males to our models, juveniles might have had the opportunity to learn how to develop appropriate anti-predator behaviour. Consequently, adult males might also serve as role models to juveniles who are learning how and when to alarm call.

Influence of locations

Another factor that might have influenced the alarm calling behaviour of juveniles is their location during our experiments. Juveniles might call differently when they are in a dangerous position, such as when they are on the ground next to our models, or while they are safe in trees. As we already had many conditions to meet prior to running an experiment (e.g. waiting for an appropriate audience condition with the mother being present, but siblings and other relatives absent), we unfortunately could not wait for subjects to be either on the ground or in the trees, and thus we could not control for this factor. However, a brief look at our data showed that juveniles alarm called more than expected when they were safe in trees (9/23 = 39%), compared to when they were near the raptor models on the ground (3/22 = 14%). When in trees or bushes, juveniles are already in a relatively safe position, therefore they might have a better view where they are able to judge the situation more efficiently, and in turn they will have more time to produce alarm calls. In contrast, while being near our models, juveniles might not take the time to call as they should rather focus on getting to a refuge to decrease their chance of predation (Appendix 9).

Conclusion

Alarm calls are efficient antipredator strategies as they allow receivers to effectively escape from predators. Thanks to the information transmitted in the acoustic structure of vocal signals, listeners can indeed extract crucial cues from an ongoing event, such as the presence of specific dangerous predators. As this increases the survival of bystanders, kin selection predicts that signallers should modify their calling behaviour according to the presence of specific audiences, increasing their call rate when in the presence of related individuals. Although traditional studies focused on the production of alarm calls during such encounters, our study examined the alarm calling behaviour of juveniles to investigate how individuals within a group, such as mothers, siblings or unrelated conspecifics, contribute to their vocal development. In addition, our subjects also modified their vocal behaviour according to the experience (using age as a proxy) and reactions of individuals present in the audience. This shows that the subjects were influenced by the mere presence of specific individuals. To develop an appropriate vocal behaviour, juvenile vervet monkeys need not only to encounter regularly natural predators, but social feedbacks are also crucial to learn when and how to react appropriately to each specific situation. Consequently, our results highlight the importance of the social context on the vocal development of alarm calls in this species.

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All experiments were filmed with two digital cameras (Camera Panasonic HC-V777 and Camera Panasonic HDC-SD90), one being fixed on a tripod filming an overview of the surroundings of the fake model and a second one used by the observer filming the reaction of the subject. We also recorded all vocalisations that were produced around the experiments using a Marantz PMD661 recorder and a directional Sennheiser MKH4KT microphone placed near the model.

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Supplements

Appendix 1.

Table 1: Composition of three wild groups (BD, KB, NH) of vervet monkeys used in the projects.

Group	Adult males	Adult females	Subadults	Four year olds	Three year olds	Two Year olds	One year olds	Babies	Total
Baie Dankie (BD)	5	14	3	5	2	11	4	2	46
Kubu (KB)	1	6	0	0	3	2	0	5	17
Noha (NH)	2	7	0	2	8	6	4	3	32
Total	8	27	3	7	13	19	8	10	95

Table 2: Description of data collected during one experiment.

Data	Description
Date	Date of the day we collected the data
Group	Group to which focal individual belongs
Time	Time at which fake eagle model was showed
GPS	GPS location of the experiments' place
Type_model	Type model used during the experiment
ID Focal	Identity of the juvenile who was follow before the raptor model
Subject	Identity of the juvenile who discovered the model
Alarm call	Whether subject gave an alarm call
Audience composition	The identity of all neighbours present in 2m, 5m and 10m from the subject.

Appendix 2.

Table2: Description of data collected when a natural alarm call has been produced.

Data	Description
Date	Date of the day we collected the data
Group	Group to which focal individual belongs
Time	Time at which fake eagle model was showed
GPS	GPS location of the experiments' place
Type alarm call	Type alarm call produced: Leopard, snake or eagle)
Predator	Identity of the animal who elicited an alarm call
Id Caller	Identity of the juvenile who produced the alarm call
Track Nb	Number of track whether alarm calls have been recorded
Audience composition	The identity of all neighbours present in 2m, 5m and 10m from the subject.
Behaviour	Reaction of first individual observed after alarm calls have been produced. Behaviour has been collected from Seyfarth, Cheney et al. ((Seyfarth, Cheney et al. 1980)

Appendix 3.

Table 4: Detailed description of raptor experiments ran with 15 juveniles belonging to three groups.

Group	Date	Type of model	Whether Subject Vocalised	Name of the focal individual before the experiment	Subject = targeted individual to which model was presented	Names of all individuals present within 2m of subject	Names of all individuals present within 5m of subject	Names of all individuals present within 10m of subject
BD	2016-10-04	1	Yes	Heilweis	Adder	NA	Siele	NA
BD	2017-03-08	1	No	NA	Adder	Asseblief	Hwahwaza	Obelisk
BD	2017-03-11	2	No	Oortjie	Adder	NA	Hwahwaza	Asis, Engel, Littleblind
BD	2016-10-20	1	No	Obelisk	Asseblief	NA	NA	Bullebak, Vulkan
BD	2016-12-14	2	Yes	Adder	Asseblief	Add	Aapi	NA
BD	2017-01-03	2	Yes	NA	Asseblief	NA	Asis	NA
NH	2017-02-24	1	No	Pruskow	Granada	Babies	NA	Bela, Xian, Umtata
NH	2017-03-13	2	No	Granada	Granada	Pretoria, Pruskow, Tiruan	Bela, Boston, Glastonberry, Propriano	Ulaanbaatar, Umtata, Lima, Gaia
NH	2017-03-18	1	No	Granada	Granada	NA	NA	Geneva, Bela, Xian, Propriano, Boston, Praia, Ulaanbaatar
BD	2016-12-08	2	No	Safari	Heilweis	NA	NA	Mielis, Gesel, Mvula, Bullebak, Nurks, Eina
BD	2017-02-02	1	Yes	Heilweis	Heilweis	Hippie	Obelisk	Pale, Prinsess, Pannakokie, Rakker, Asseblief, Gaaf

BD	2017-03-03	2	No	Adder	Heilweis	Obelisk	Oulik	Oortjie, Heerlik, Siele
KB	2016-10-07	1	No	Arno	Malawi	NA	NA	Mississipi
KB	2016-11-04	1	No	Malawi	Malawi	NA	Nessie, Aare, Arno, Yangtze	NA
KB	2016-11-22	2	Yes	Arno	Malawi	NA	Avon	Mara
BD	2016-11-01	1	No	Adder	Nooiens	Nurks	Rakker	Vulkan, Hippie
BD	2017-01-30	1	No	Redelik	Nooiens	NA	Vakie	Hwahwaza, Numbies
BD	2017-02-25	2	Yes	Nooiens	Nooiens	Add	NA	NA
BD	2017-01-10	2	Yes	Obelisk	Obelisk	NA	Rooikat, Nurks, Pieperig	Vakie, Potjie
BD	2017-01-28	1	No	Redelik	Obelisk	Rattle	Aapi, Polka, Nooiens, Oortjie	Wurm, Redelik, Heilweis
BD	2017-02-27	2	No	Heilweis	Obelisk	NA	NA	Oulik, Heerlik, Rooikat
BD	2017-02-23	1	No	NA	Oortjie	NA	NA	Ububhibhi, Mielis, Aapi, Gaaf
BD	2017-02-25	2	No	Nooiens	Oortjie	Rooikat, Aapi, Obelisk	NA	NA
BD	2017-03-14	2	Yes	Oortjie	Oortjie	NA	Oulik	Potjie
BD	2016-12-01	2	No	Safari	Polka	Ratel, Redelik, Wurm, Gaaf	NA	Adder, Aapi, Rooikat, Potjie
BD	2017-01-17	2	No	Polka	Polka	NA	NA	Rooikat, Hwahwaza, Bullebak
BD	2017-01-25	1	No	Heilweis	Polka	NA	Rooikat	Prinsess, Adder, Nooiens, Oortjie

NH	2017-01-04	2	No	Propriano	Propriano	Boston, Bela	Glastonberry	Reva, Rheban
NH	2017-01-12	2	Yes	Reykovik	Propriano	NA	Glastonberry, Reykovik, Umtata	Propriano
NH	2017-01-25	1	No	Propriano	Propriano	Boston, Ulaanbaatar	Umtata	Bela, Pretoria, Upsala
NH	2017-02-24	1	No	Pruskow	Pruskow	Jixi, Glastonberry	NA	Tiruan, Reva, Pretoria
NH	2017-03-03	2	No	Pruskow	Pruskow	Gaia	Gaia's Baby	Umtata
NH	2017-03-07	1	Yes	Pruskow	Pruskow	Praia	NA	Boston, Umtata
BD	2016-12-19	2	No	Adder	Ratel	Redelik	Bullebak, Pieperig, Eina	Nooiens
BD	2016-12-27	2	No	NA	Ratel	Oortjie	Nurks	Hwahwaza, Siele, Rissiepit, Heerlik
BD	2017-02-18	1	No	Oortjie	Ratel	NA	NA	Hippie
BD	2017-01-21	2	No	Redelik	Redelik	NA	Neuchâtel, Nurks, Potjie	Aapi
BD	2017-02-06	2	Yes	Redelik	Redelik	Hwahwaza	Rattle, Polka, Oortjie, Adder, Asseblief, Potjie	Pieperig, Prinsess, Rooikat
BD	2017-02-13	1	Yes	Redelik	Redelik	Heerlik's Baby, Heerlik, Prinsess	Littleblind	Rissipit
BD	2016-12-17	2	Yes	Polka	Safari	Adder, Engel, Hippie, Eina	Aapi, Nurks, Hwahwaza	NA
BD	2017-01-30	1	No	Heilweis	Safari	Nurks, Adder	NA	Numbies, Neuchâtel, Snorrtjie
BD	2017-02-10	1	No	Heilweis	Safari	Neuchâtel	Asis	Hippie, Heerlik, Vakie, Siele

NH	2017-02-01	1	No	Ulaanbaatar	Ulaanbaatar	Rose, Reykovik, Propriano	Pruskow, Glaston	Tiruan
NH	2017-02-09	2	No	Ulaanbaatar	Ulaanbaatar	Upsala, Granada	Geneva, Rheban	Gaia
NH	2017-02-14	2	No	Ulaanbaatar	Ulaanbaatar	Renne	Ugi	Xian, Boston

Appendix 4

Table5: Description of the 15 subjects we used for our experiments.

Name	Age	Sex	Mother' name	Number of Siblings	Number of experiment	Number of call has been produced
Adder	One year old	Male	Asis	2	3	1
Asseblief	Two year old	Male	Asis	2	3	2
Granada	Two year old	Female	Geneva	2	3	0
Heilweis	Two year old	Male	Heerlik	1	3	0
Malawi	Two year old	Male	Mara	1	3	1
Nooiens	Two year old	Female	Numbies	1	3	1
Obelisk	Two year old	Male	Oulik	1	3	1
Oortjie	One year old	Female	Oulik	1	3	0
Polka	One year old	Male	Prinsess	3	3	1
Propriano	Two year old	Male	Pretoria	2	3	1
Pruskow	One year old	Male	Pretoria	2	3	0
Ratel	One year old	Female	Rissiepit	3	3	3
Redelik	Two year old	Female	Rissiepit	3	3	0
Safari	Two year old	Female	Snorrtjie	1	3	0
Ulaanbaatar	One year old	Male	Upsala	2	3	1

Appendix 5

Table6: Number of alarm calls observed and expected by three different age classes during the raptor model experiments. Individuals were considered adults when they were more than five years old, and juveniles when they were between one and three years old.

Age	Number calls observed	Number of individual in age/class group	Number of individuals in age/class group	Proportion of all calls produced by different age category	Percentage group belonging to age category	Number calls expected
Adults	0	47	0	55.29411765	9.952941176	10
Four year olds	4	15	0.266666667	17.64705882	3.176470588	3
Juveniles	14	23	0.608695652	27.05882353	4.870588235	5
Total	18	85	0.211764706	100	18	18

Appendix 6

*Table 7: Number of experiments generating alarm calls in subjects in the presence and absence of each audience condition: ("Mothers" which include*s *the presence of the mother of the subject within ten meters without any other related individuals, "Siblings" which include*s *the presence of at least one siblings of the subject within ten meters without mother and "Audiences" composed of unrelated individuals of the subject within ten meters without any other related individuals. As we tested 15 juveniles, we ran 15 experiments for each condition, leading to a total of 45 experiments for each category (N = 15 in the presence of the specific audience and N = 30 in its absence). All number where corrected to get N = 15 in each conditions*.

Condition	Mothers	Siblings	Audience
Presence	2	7	3
Absence	13	8	12
Total	15	15	15

Subjects alarm called in 26.67% of the experiments (12 out of 45). However, vervet monkeys adapt their calling behaviour according to audience composition (ANOVA, X^2_3= 13.082, df=3, p = 0.004463).

Table 8: Number of alarm calls produced according to the age of siblings and the audience, corrected for number of experiments

	Siblings		Audience	
	Older	Younger	Older	Younger
Alarm calls observed	4	3	2	0
Alarm calls expected	5	2	2	0

Appendix 7.

Table 9: Number of alarm calls produced by subjects according to the reaction of mothers and siblings, corrected for number of experiments. We considered individuals as reacting (Reacted) when they were vigilant and/or vocalised, while they were classified as not reacting when they ignored the model and did not vocalise(Ignored).

	Mothers		Siblings	
	Reacted	Ignored	Reacted	Ignored
Alarm calls observed	0	2	7	0
Alarm calls expected	1	1	6	1

Appendix 8.

With additional analysis, we assessed the difference between the probabilities of alarm calling in the presence or absence of at least one adult male. Despite subjects never vocalising when one adult male was present, they alarm called three times in the absence of adult males (difference in frequency of alarm calling is more than 0.5 by a probability of 0.92).

Table 10: Number of alarm calls production according the presence of males. We considered male presence when at least one adult male, considered as competent individuals, where within 10 meters from subjects during raptor experiments.

	Male	
	Present	Absent
Alarm calls observed	2	10
Alarm calls expected	3	9

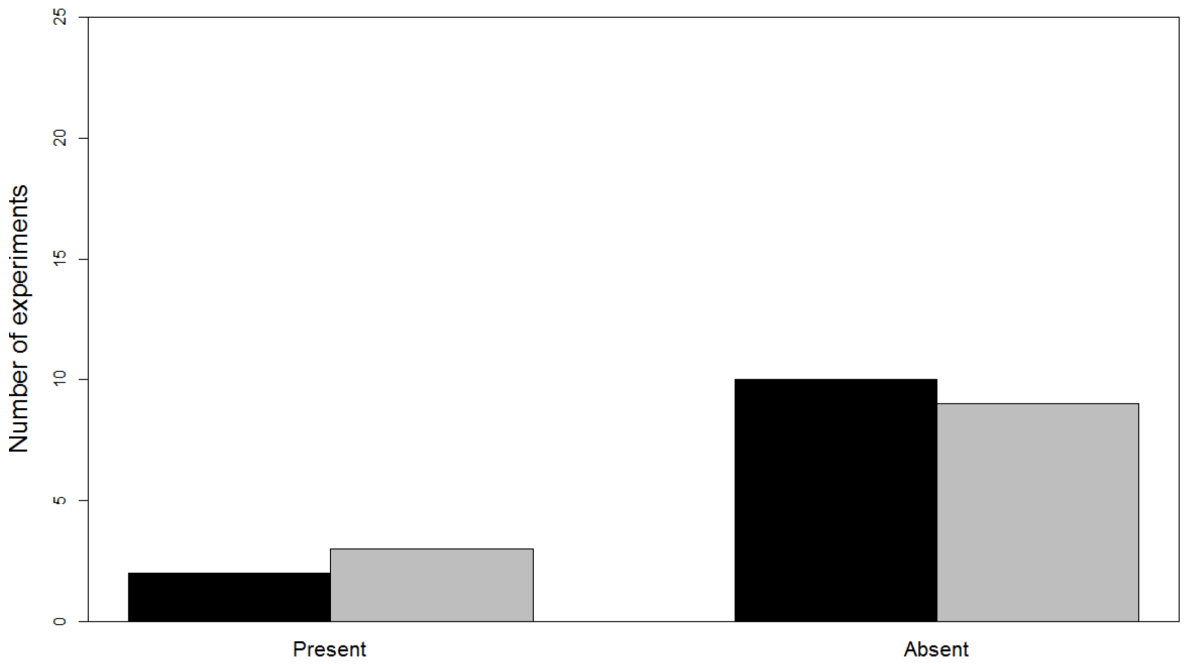

Figure 1: Comparison between the number of experiments in which alarm calls have been observed (black) and expected (grey) according to the presence of at least one adult male.

Appendix 9

Subjects heights

As individuals in a tree were already in a refuge protected from predators, we investigated how the position of the subjects (in trees vs on the ground) at the beginning of the experiment (just before the model was uncovered) influenced their vocal behaviour. We used Fisher's exact tests (Routledge 2005) to examine whether their alarm call production was distributed randomly or significantly differed according to subjects height.

Table 11: number of experiments in which alarm calls were observed and expected according to the height of the subject during the raptor experiments, corrected for number of experiments.

	Tree	Ground
Alarm calls observed	9	3
Alarm calls expected	6	6

The position of the subjects at the beginning of the experiments influenced the production of alarm calls, with individuals increasing their call rate while being up in trees (Fisher Exact test, $Z = 0.253$, $df = 1$, $p = 0.09$). Juveniles produced nine alarm calls when they were in trees (75%) and only three alarm calls (25%) when they were on the ground (Figure 2S).

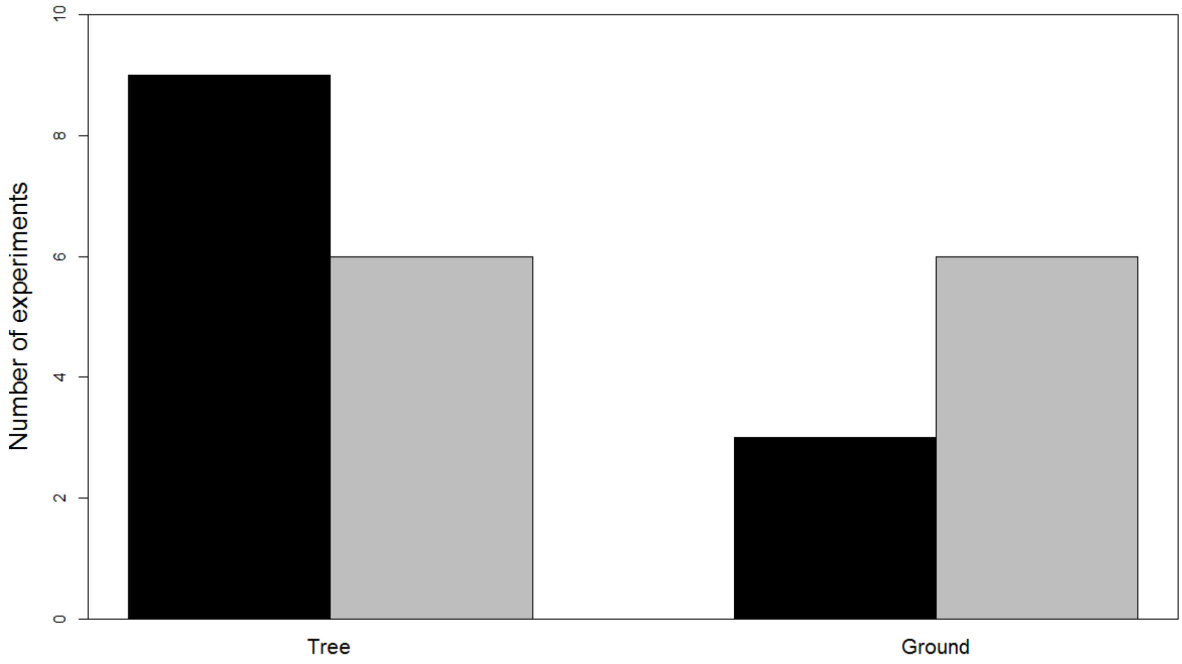

Figure2: Graph showing the comparison of alarm calls observed (black) and expected (grey) according to the position of the subject before raptor models were uncovered: tree or ground.

Appendix 10.

Table 12: conditions required for the success of the experiments. We analysed all subjects in three conditions (Mother, Siblings and Audience). The siblings condition was divided between older and younger individuals; the audience condition was composed of unrelated individuals; and the mother condition was when the mother was within ten meters from the subject.

Group	Date	Subjects	Audience conditions	Individuals needed for success condition
BD	2016-10-04	Adder	Audience	Unrelated
BD	2017-03-08	Adder	Siblings	Asseblief (Older) , Aapi (Older)
BD	2017-03-11	Adder	Mother	Asis
BD	2016-10-20	Asseblief	Audience	Unrelated
BD	2016-12-14	Asseblief	Siblings	Adder (Younger), Aapi (Older)
BD	2017-01-03	Asseblief	Mother	Asis
NH	2017-02-24	Granada	Audience	Unrelated
NH	2017-03-13	Granada	Siblings	Glastonberry (Older), Gaia (Older)
NH	2017-03-18	Granada	Mother	Geneva
BD	2016-12-08	Heilweis	Audience	Unrelated
BD	2017-02-02	Heilweis	Siblings	Hippie (Older)
BD	2017-03-03	Heilweis	Mother	Heerlik
KB	2016-10-07	Malawi	Siblings	Mississipi (Older)
KB	2016-11-04	Malawi	Audience	Unrelated
KB	2016-11-22	Malawi	Mother	Mara
BD	2016-11-01	Nooiens	Siblings	Nurks (Older)
BD	2017-01-30	Nooiens	Mother	Numbies
BD	2017-02-25	Nooiens	Audience	Unrelated
BD	2017-01-10	Obelisk	Audience	Unrelated

BD	2017-01-28	Obelisk	Siblings	Oortjies (Younger)
BD	2017-02-27	Obelisk	Mother	Oulik
BD	2017-02-23	Oortjies	Audience	Unrelated
BD	2017-02-25	Oortjies	Siblings	Obelisk (Older)
BD	2017-03-14	Oortjies	Mother	Oulik
BD	2016-12-01	Polka	Siblings	Potjie (Older), Pieperig (Older), Pannekoekie (Older)
BD	2017-01-17	Polka	Audience	Unrelated
BD	2017-01-25	Polka	Mother	Prinsess
NH	2017-01-04	Propriano	Audience	Unrelated
NH	2017-01-12	Propriano	Siblings	Pruszkow (Younger), Praia (Older)
NH	2017-01-25	Propriano	Mother	Pretoria
NH	2017-02-24	Pruzkow	Mother	Pretoria
NH	2017-03-03	Pruzkow	Audience	Unrelated
NH	2017-03-07	Pruzkow	Siblings	Propriano (Older)
BD	2016-12-19	Ratel	Siblings	Redelik (Older), Rakker (Older), Rooikat (Older)
BD	2016-12-27	Ratel	Mother	Rissiepit
BD	2017-02-18	Ratel	Audience	Unrelated
BD	2017-01-21	Redelik	Audience	Unrelated
BD	2017-02-06	Redelik	Siblings	Ratel (Younger), Rakker (Older), Rooikat (Older)
BD	2017-02-13	Redelik	Mother	Rissiepit
BD	2016-12-17	Safari	Audience	Unrelated
BD	2017-01-30	Safari	Mother	Snorretjie
BD	2017-02-10	Safari	Siblings	Siele (Older)
NH	2017-02-01	Ulaanbaatar	Audience	Unrelated
NH	2017-02-09	Ulaanbaatar	Mother	Uppsala
NH	2017-02-14	Ulaanbaatar	Siblings	Umtata (Older), Uji (Older)