Vervet monkeys' alarm calls:

context specific or not?

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What’s in a name? That which we call a rose

By any other word would smell as sweet.

— William Shakespeare, *Romeo and Juliet*, 1597

ABSTRACT

Vervet monkeys (*Chlorocebus pygerythrus*) are known to produce three distinctive alarm calls in response to their three main types of predators: leopards, pythons and eagles. Each call elicits a specific and appropriate antipredator behaviour. As these calls are acoustically distinct and produced in a narrow range of contexts, they have been termed “functionally referential”. Nonetheless, some calls that are acoustically very similar to the alarms given towards leopards and other terrestrial predators are also given during encounters with other groups of vervet monkeys, thus transgressing a key criterion of functional reference: context-specificity. To investigate whether calls produced during between-group encounters and to terrestrial predators were different, I ran an acoustic analysis on a large set of calls recorded from five adult vervet monkey males in both contexts. I also compared geographical locations of alarm events during which those similar calls are produced. I found no acoustic differences between the two calls but also found that calls in both contexts occurred mostly in overlapping parts of the home ranges. These results suggest that monkeys must use additional contextual cues in order to properly infer if a caller responded to a terrestrial predator or a neighbouring group. The biased geographical distribution of calls further implies that the predators might be more present or that monkeys are more likely to give false alarms in regions frequented by several monkey groups. I discuss the implications of these findings for an influential theory in animal communication, functionally referential signalling, for how vervet monkeys gather information from others’ vocal behaviour and for how monkeys mentally represent predators.

Keywords: vervet monkey; vocal communication; alarm; ground predator; between-group encounter; functionally referential signal

Introduction

Communication can broadly be defined as a transfer of information between two individuals (Tomasello, 2008). It is found everywhere in both the plant and animal kingdoms. The signals used to convey information can be chemical, such as volatile excretions in plants, visual, like the bees' dance language, olfactory, such as urine markings, or auditory, such as bird songs. The mechanisms, development, evolutionary history, and function of communication signals can be studied through various research fields, including neurobiology (Jürgens, 2009), physiology (Fletcher, 2014), comparative psychology and cognition (Gleitman *et al.*, 2011), philosophy (Cheney and Seyfarth, 1990) or even linguistics (Rendall *et al.*, 2009). Vocal communication studies, especially in non-human primates, have come to play a particularly privileged role, as a way to unravel *when*, *how* and *why* human speech and language have evolved.

Alarm calls are an important part of many species' vocal repertoire. As they are usually given to identifiable external events, there has been an ongoing debate about the underlying mental processes linked with their production. One line of argument has been that alarm calls are not solely expressions of internal emotions of the signaller, but allow callers to convey some level of information about the external event experienced (Evans and Evans, 1999), such as the predator type encountered. As they are usually produced in response to predators (Magrath *et al.*, 2015) they have been under strong selective forces to be part of effective antipredator responses. Alarm calls can be observed in many species. In primates, they have been studied for example in wild bonnet macaques (*Macaca radiata*) (Coss *et al.*, 2007), West African green monkeys (*Chlorocebus sabaeus*) (Price and Fischer, 2014), tufted capuchin monkeys (*Cebus apella nigritus*) (Wheeler, 2010) or diana monkeys (*Cercopithecus diana*) (Riede and Zuberbühler, 2003). In non-primates, alarm calls have been studied in meerkats (*Suricata suricatta*) (Hollén, 2006; Manser, 2001), elephants (*Loxodonta africana*) (King *et al.*, 2010) and Gunnison's prairie dogs (*Cynomys gunnisoni*) but also in avian species, such as parrots (e.g. Lilac-crowned Amazons; *Amazona finschi*) (Montes-Medina *et al.*, 2016), blackbirds (*Turdus merula*) (Curio *et al.*, 1978) or chickens (*Gallus domesticus*) (Gyger *et al.*, 1987; Wilson and Evans, 2012).

Several hypotheses have been proposed to explain the function and evolution of alarm calls (Stephan and Zuberbühler, 2016). First, alarm calls can warn conspecifics about the presence of a threat (Crockford *et al.*, 2012; Seyfarth and Cheney, 2012), a behaviour that can be explained by kin selection, as demonstrated for example in meerkats that show a greater tendency of alarm calling when close relatives are nearby compared to other audiences (Townsend *et al.*, 2012). Here, alarm calling can be viewed as an altruistic act that helps kin to escape while it might draw the predator's attention to the caller, putting him at higher risk.

Alarm calls can also serve to recruit other group members to mob the predator (Cäsar *et al.*, 2012b, 2012a), which seems to have a deterring effect and induce some predators to leave the area (Coss *et al.*, 2007; Murphy *et al.*, 2013; Schel *et al.*, 2010; Zuberbühler *et al.*, 1999) or abandon a hunt (Zuberbühler and Jenny, 2002). In the same manner, alarm calls can be directed at the predator itself to signal that it has been spotted (Schel *et al.*, 2010; Zuberbühler *et al.*, 1999) and that its hunting success rate will now be reduced due to prey individuals being alert and less vulnerable (Digweed and Rendall, 2009; Zuberbühler, 2006). Importantly, the conspecific warning and predator deterrence hypotheses are not mutually exclusive and the explanation as to why animals alarm call is most probably a complex combination of both of them.

One of the most famous animal alarm systems has been described in vervet monkeys (*Chlorocebus pygerythrus*, previously *Cercopithecus aethiops*) (Seyfarth *et al.*, 1980a, 1980b; Struhsaker, 1967). In the 1960s, Struhsaker (1967) documented over 20 vocalisations produced by vervet monkeys, ranging from soft “rrr” produced by lost babies and playful “purrs” generated by juveniles to distress screams by victims of aggression and loud alarm calls. In addition, monkeys produce at least three distinct alarm calls in response to different types of threat they are facing, each resulting in a corresponding appropriate response. In subsequent playback experiments, vervet monkeys reacted to recordings of the different alarm calls as if the putative predator was nearby (Seyfarth *et al.*, 1980a), suggesting that the acoustic features of the calls alone were sufficient to elicit the appropriate behavioural response, even in the absence of the external referent.

Alarm calls produced by vervet monkeys are specifically prompted by three main classes of predators; raptors, terrestrial mammals and snakes. Each predator type triggers appropriate mutually exclusive responses from listeners depending on the kind of threat (Seyfarth *et al.*, 1980a, 1980b; Struhsaker, 1967). When encountering an aerial predator, such as a martial eagle (*Polemaetus bellicosus*), for example, vervet monkeys emit “rraup” calls while seeking shelter in dense bushes or near the core of a tree if they are already in it. The presence of ground predators, such as leopards (*Panthera pardus*), causes individuals to climb up to the tip of tree branches where large mammals are not able to reach them. While escaping from those ground predators, vervet monkeys often produce acoustically distinct bark-like “leopard alarm calls”, consisting of rapid inhalations and exhalations. Finally, if vervet monkeys spot a dangerous snake, such as a python (*Python sebae*), they engage in mobbing behaviour during which the group gathers around the snake, standing up bipedally, inspecting the ground, while emitting “chutters” and mobbing the predator. For brevity, the three different calls will hereafter be called “eagle”, “leopard” and “snake” alarm calls.

Because the vervet monkeys' alarm system consists of a limited number of calls thought to be produced in a narrow range of contexts, *i.e.* specific to the predator type, each eliciting a specific behavioural response, they were classified as functionally referential signals (Macedonia and Evans, 1993; Townsend and Manser, 2013) and became the corner stone of studies on semantic vocalisations in non-human primates (Manser, 2013). According to the definition proposed by Macedonia and Evans (1993), a functionally referential signal must abide to two criteria: context- and response-specificity. The first one, also known as the "production criterion", requires the call to be produced exclusively when the corresponding stimulus is present. In this case for example, the ground predator alarm call should be elicited only by the presence of a ground predator. The second one, the "perception criterion", means the signal must be consistently perceived in the same manner by listeners, thus the response to the aforementioned call must always be the same.

In the case of the vervet monkeys' alarm system, those criteria are met by both the aerial and the snake alarm calls, but it appears that the situation concerning the ground predator alarm call is not that clear cut. Although leopard alarm calls have long been considered the paradigmatic case for a functionally referential signal (Gleitman *et al.*, 2011, chap. 10), various researchers (Cheney and Seyfarth, 1990; Struhsaker, 1967) have observed that vervet monkeys sometimes produce leopard-like alarm calls in contexts other than ground predator encounters, which does not comply with the production criterion (Macedonia and Evans, 1993). Leopard alarm calls are particularly given during aggressive interactions with other groups of vervet monkeys (Price *et al.*, 2015).

Vervet monkeys roam in geographically defined territories (Chapman and Fedigan, 1984; Pasternak *et al.*, 2013) but the home ranges of different groups often overlap to the effect that neighbouring groups run into each other from time to time. Such cases are called intergroup- or between-group encounters (Cheney, 1981). Intergroup encounters vary in length and level of aggressiveness (Arseneau-Robar *et al.*, 2016; Cheney, 1981; Hauser *et al.*, 1986; Isbell *et al.*, 1991), which also has consequences on the vocal behaviour of the vervet monkeys. They can last for merely a second, just until one group becomes aware of the presence of the other and scatters away almost instantly. But they can resemble a trench warfare with the two groups holding their positions for hours (Arseneau-Robar *et al.*, 2016). Some encounters are peaceful and allow the monkeys to sniff and groom each other, or copulate. Others are highly violent, involving chasing, injuries, or even death (Hauser *et al.*, 1986). During some of those agonistic encounters between neighbouring groups (Price *et al.*, 2015; Struhsaker, 1967, p. 303), male vervet monkeys produce bark-like vocalisations that strongly resemble leopard alarm calls (Figure 4) (Seyfarth et al., 1980b, p. 1073; Struhsaker, 1967, p. 286).

Although both calls sound similar, between group calls and leopard calls are produced in two different contexts, when encountering a neighbouring group (Price *et al.*, 2014) or a mammalian ground predator. If the two calls were in fact identical, this would be in disagreement with the context-specificity criterion used to define such functionally referential calls (Macedonia and Evans, 1993). The aim of this study was thus to compare the acoustic features of those vocalisations that were produced in two distinctive contexts to verify whether those signals are identical or not. Secondly, we examined the geographical locations of those type of calls to see whether they occur at random places within the home ranges of the monkeys, or if vervet monkeys could use other contextual cues, to respond appropriately.

HYPOTHESES & PREDICTIONS

If between group calls and leopard alarm calls encoded specific information on the context in which they were produced, their acoustic properties should differ, thus allowing to discriminate the two call types through acoustic analysis. However, if they were identical in their acoustic properties, this would suggest that vervet monkeys used other cues than vocal ones to respond appropriately. Furthermore, as between-group encounters were more likely to arise in overlapping areas of neighbouring groups, while predator encounters were unpredictable but more likely near rivers (Mercier *et al.*, 2017, *in press*), I predicted that the geographical distribution of leopard and between group calls should reflect the chances of encountering one or the other threat. Consequently, I expected leopard calls to occur equally in both exclusive (*i.e.* in which only one group is living) and overlapping areas (*i.e.* used by multiple groups), as chances of meeting a ground predator should be overall the same throughout the territory. In contrast, I expected between-group encounter calls to occur more often in overlapping regions of home ranges, as that was where groups were more likely to encounter each other.

MATERIAL & METHOD

STUDY SITE

The study was conducted over eight months in South Africa at the Inkawu Vervet Project (IVP). It is a research station devoted to the study vervet monkeys run conjointly by the Universities of Neuchatel and Zurich, Switzerland. This project is situated in the Mawana game reserve (S 28° 00.327; E 031° 12.348), a 12,000 h private farm in the KwaZulu Natal province (Figure 1). Since its creation in 2010, various studies have been conducted there, mainly on vervet monkey social behaviour, such as social transmission of behaviour (van de Waal *et al.*, 2015), food preferences (van de Waal *et al.*, 2013), social hierarchy (Borgeaud *et al.*, 2015, 2013) and social relationships (Arseneau *et al.*, 2015; Borgeaud *et al.*, 2016). The centre is used by students, researchers and volunteers from all around the world who are trained on site through a Master-Apprentice model, where more experienced researchers teach the newcomers about the behaviour of vervet monkeys, the terrain, the local fauna and flora and the way the project deals with data collection.

*Figure 1: Map of South Africa showing the location of the Inkawu Vervet Project study site. Source: E. **Google Earth**, version 7.1.8.3036, 2017, available at https://www.google.com/earth/*

STUDY SPECIES

Vervet monkeys (*Chlorocebus pygerythrus*) are an Old World monkey species commonly found in the Eastern part of the African continent except for the North of Somalia (Kingdon *et al.*, 2008). They show a sexual dimorphism: males are bigger than females (about 6.0kg versus 3.5kg, respectively (Bolter and Zihlman, 2006; Pasternak *et al.*, 2013); Figure 2) and have a distinctive blue scrotum and red penis (Figure 3). They live in multi-male, multi-female groups (Isbell *et al.*, 2004; Pasternak *et al.*, 2013) of variable size that can range from four to over a hundred individuals (Galat and Galat-Luong, 1976). Although males are dominant over females in one-to-one interactions, vervet monkey groups are governed by a matrilineal hierarchy (Horrocks and Hunte, 1983): females form coalitions to assert their power over males and social ranks of each individual is directly inherited through the female lineage. The offspring of a high-ranking female will automatically be high-ranked, too. Females have one offspring per year and are philopatric (Hauser *et al.*, 1986): they will stay in the same group their entire life. Males, on the other hand, will migrate to other groups once they reach sexual maturity around the age of four (Cheney and Seyfarth, 1990, 1983). I categorised social makeup as follows: infants (from birth until the next brood, ca. 1 year old), juvenile males (from 1 year old until their first migration, ca. 4 years old), juvenile females (from 1 year old until their first infant, ca. 3 years old), adult males (males that migrated at least once), and adult females (once they had at least one offspring). The population of monkeys at the IVP site during this study consisted of eight monitored groups ranging from six to over fifty individuals (Table 1). In addition to those groups, an unclear number of undocumented groups are ranging at the borders of the reserve and in the surroundings of the studied groups. All the monkeys were habituated, though at different stages, to the presence of researchers, recognisable by their blue cap. Furthermore, we were able to identify individually all animals using various physical features, such as brow shapes, ear notches or naturally broken fingers but mainly by their unique facial features.

Figure 2: Adult male on the left resting next to an adult female, with a few weeks old baby climbing on him

Figure 3: The same male's blue scrotum and red penis

Table 1: Average headcounts of the eight monitored groups over the 12-months period covered by this study.

Group	Number of individuals
Ankhase (AK)	28
Baie Dankie (BD)	53
Crossing (CR)	42
I Family (IFam)	9
Intaka (IN)	6
Kubu (KB)	17
Lemon Tree (LT)	39
Noha (NH)	53
Total	*247*

DATA COLLECTION

I used data from the IVP covering a 12 months period, from 1st May 2015 to 30th April 2016, collected by 26 researchers and volunteers, including myself (see Appendix A1). We collected data six days out of seven from sunrise to sunset over a. We used handheld computer devices loaded with preformatted forms using Pendragon (version 5.1) and then transferred the data onto a desktop computer at the end of each working day. Once a week in each group over a period ranging from sunrise to sunset (see Appendix A2), we collected scan data (Altmann, 1974) on the monkeys' whereabouts and activities every 30 minutes during 10 minutes. We also collected predator encounter data whenever we heard an alarm call or observed signs of disturbance (see Appendix A3). Finally, we started collecting between-group encounter data whenever two neighbouring groups were within a 100 meters of each other (Arseneau *et al.*, 2015; see Appendix A4).

Furthermore, we recorded all occurrence vocalisations of the monkeys whenever possible, using a Marantz PMD 660 recorder and Sennheiser directional microphone (K6/ME 66). Additional ground predator alarm calls were recorded using a stuffed leopard that we presented to the monkeys, as implemented in other studies (Arnold *et al.*, 2008; Coss *et al.*, 2007). Audio tracks were subsequently transferred onto a computer and cut with Praat (version 5.4.22, http://www.fon.hum.uva.nl/praat/, (Boersma and Van Heuven, 2001).

Acoustic Data

I used alarm calls produced by five individually identified adult males in two contexts: between group and ground predator encounters. Audio tracks originated from recordings collected personally and by Stéphanie Mercier during the length of this study. Only calls from events that were clearly documented as either between-group or ground predator encounters were selected, *i.e.* during which both the caller and the stimulus were identified. Ground predator encounter audio recordings resulted of the presentation of a stuffed fake leopard model to the monkeys and of one encounter with dogs. Within those recordings we extracted single exhalation-inhalation units (Figure 4; Struhsaker, 1967, p. 284) of bark-like between group calls and leopard alarm calls that were considered of good audio quality with minimal background noise or distortion and no overlap with other sounds, especially with other monkeys calling or human speaking. I extracted acoustic properties of those call units using an automated script in Praat (E. Briefer, personal communication). I excluded six calls of poor quality based on visual verification of the spectrograms and an additional one due to missing values in the extracted parameters. The resulting data pool comprised a total of 248 calls (112 between-group encounter calls and 136 leopard calls; Figure 5). I used 12 acoustic parameters (Table 2 and Appendix A5) to investigate whether the alarm calls produced during between-group encounter and predator encounters could be discriminated (see Appendix A6 for excluded parameters).

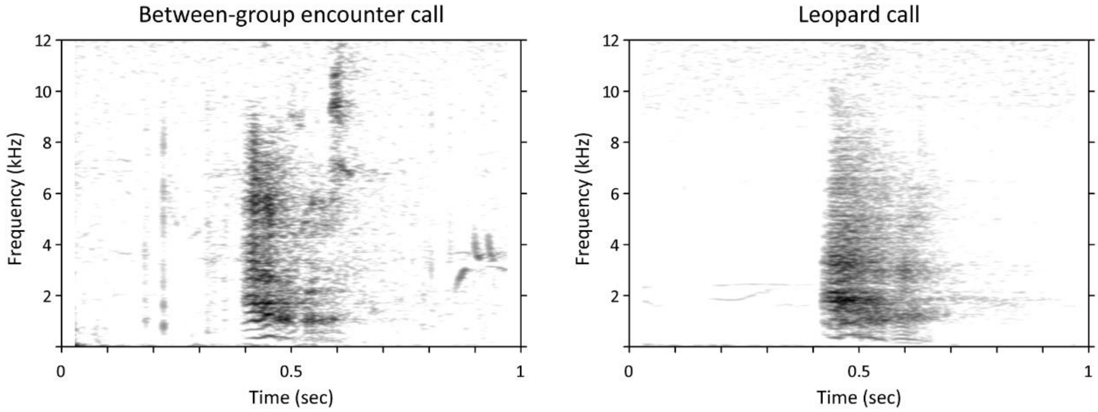

Figure 4: Example spectrograms of bark-like between-group encounter call on the left and leopard call on the right produced by the same vervet monkey male. Call units consist of an exhalation subunit followed by an inhalation subunit. On the left spectrogram (between-group encounter call) at 0.9 sec is a bird call.

Table 2: Description of the 12 acoustic parameters used for the statistical analysis

Parameter	Unit	Description
Sound duration	Sec	Duration of the call unit
Start F0	Hz	Frequency of F0 at the beginning of the call unit
F0 abs. slope	Hz/s	Absolute slope of the mean of F0 of the entire call unit
Q50	Hz	Frequency quartile that divides the call unit into two intervals of equal energy calculated over the entire call unit
Q75	Hz	Frequency quartile that divides the call unit into two intervals containing 75% and 25% of the energy calculated over the entire call unit
Energy of peak frequency	dB	Energy of Fpeak
Percentage time max Intensity	%	Time point of the maximum intensity of F0 expressed as a percentage of the total duration of the call unit
Amplitude modulation	dB/sec	Mean variation of amplitude per second
Amplitude modulation rate	Cps	Number of complete cycles of amplitude modulation per second
Amplitude modulation extent	dB	Mean peak-to-peak variation of each amplitude modulation of the intensity contour of the call unit
Jitter	%	Cycle-to-cycle frequency variation of F0 across all time segments
Shimmer	%	Cycle-to-cycle amplitude variation of F0 across all time segments

Home range data

Home ranges were mapped from global positioning system (GPS) points from one full day of scan per month whenever possible from 1st May 2015 to 30th April 2016 (N = 1281 GPS coordinates). I extracted and cleaned geographical data in a conservative manner: discarding events whenever there was a missing part, missing GPS or ambiguous information. GPS points were then converted into keyhole mark-up language files (KML) using an online tool (http://www.mapsdata.co.uk/online-file-converter/) and imported into Google Earth and Google Earth Pro (available at https://www.google.com/earth/). Polygons were hand drawn from the most external points. Despite scan data being unbalanced (see Appendix A7), I decided to use even small datasets in order to not disregard the presence of some groups. For instance, the "I family" was a small group of four individuals that were very shy and for which we had not been able to gather as much data points as for the other groups.

Encounter data

I used GPS coordinates of the location of naturally occurring alarm events during which leopard calls were produced only when researchers could classify vocalisations as leopard alarm calls and the stimulus (Table 3) was sighted. Similarly, I used the GPS points for the between-group encounters only from events during which bark-like alarm calls were produced and the presence of another group within a 100 meters was confirmed. I overlaid those two types of GPS coordinates over the previously drawn home ranges map (n leopard alarm calls = 20, and n between-group encounter alarm calls = 23, Figure 6; see Appendixes A8 and A9 respectively), then scored whether each encounter occurred in exclusive areas (*i.e.* in places where only one group was living) or in overlapping areas (*i.e.* that multiple groups could use, see Appendix A10). Whenever the situation was ambiguous, I excluded the data point. Consequently, I removed two ground predator encounters and four between-group encounters (see Appendix A11) because they were located in regions known to be close to unmonitored groups. I used an online tool to calculate the areas of the exclusive and overlapping regions (http://www.earthpoint.us/Shapes.aspx; see Appendix A10) in order to control for disparities in type of regions and adjust number of theoretical expected calls accordingly. Proportion of scan points in each type of area (72.60% in exclusive area and 27.40% in overlapping area) was used to control for time spent observing in each area type to further adjust number of theoretical expected leopard (Figure 7) and between-group calls (Figure 8).

Statistical analysis

Prior to statistical analysis, I checked the symmetry of distribution of the raw data and transformed it accordingly whenever needed in order to reach an approximate normal distribution of residuals. Collinearity between variables was verified and I excluded all parameters that scored a Pearson's correlation coefficient higher than 0.8. Parameters that contained too many missing values or did not meet assumptions of linearity or normality of residuals even after transformations were discarded (Appendix A6). I used R (R Core Team, 2017) to run all tests and significance was set at $\alpha = 0.05$.

Permuted discriminant function analysis (pDFA)

Because I used several recordings from five individuals to determine if their calls (N = 248; Figure 5) were acoustically distinguishable according to the context, I had repeated measurement that were not independent. Therefore, I conducted a permuted discriminant function analysis (pDFA; Fichtel, Perry, & Gros-Louis, 2005; Mundry & Sommer, 2007) for fully crossed design to counterbalance the non-independency of the data. With this method, non-independence of the data was managed by permuting the non-independent points in blocks, defined by a control factor, and allowing further permutations within those blocks or of entire block but not between different blocks. In my particular dataset, for example, this meant that several calls given by a specific individual in one context would be permuted in block with another block of several calls given by that same individual in the other context. However, calls from different individuals would not be permuted between them (for detailed procedure see Mundry and Sommer, 2007). I used a function for R provided by Roger Mundry (Mundry and Sommer, 2007) to run the pDFA on this dataset. I did a thousand permutations and a hundred random selections on the 12 acoustic parameters (Table 2) with the context (leopard or between-group encounter context) as the test factor and identity of caller (N= 5) as the control factor. In order to get a balanced design, I restricted the number of cases per combination to five as per limiting number of calls provided by the male *Gov* in the between-group encounter context (Figure 5).

Exact binomial tests

As predators are mobile and can be encountered everywhere, I expected the proportion of leopard calls to be equal in both overlapping and exclusive areas (50/50). In contrast, as between-group encounters happen mainly at the border of two neighbouring territories, I expected the proportion of between-group encounter calls to be higher in overlapping than exclusive areas. I ran a two-tailed exact binomial test to check if leopard calls occurred randomly throughout the territory. To verify whether the proportion of between-group encounter calls was higher in overlapping regions than in exclusive ones, I conducted an upper-tailed exact binomial test. Note that overlapping area was 6.2 times smaller than exclusive area (representing 13.90% and 86.10% of the home ranges respectively; Appendix A10), and we spent 2.65 more time observing in exclusive area (72.60% of time spent in exclusive area and 27.40% in overlapping area). Consequently, I adjusted the proportions of leopard and between-group encounter calls according to the size of each region and time spent observing in each type of area. Resulting proportions are 5.74% of leopard calls and >5.74% between-group encounter calls theoretically occurring in overlapping regions of the home ranges. These percentages correspond to one leopard calling event (Figure 7) and one between-group encounter call events in overlapping region (Figure 8).

RESULTS

RATE OF LEOPARD ALARMS AND GROUP ENCOUNTERS

During the 12 months covered by this study, 26 researchers and volunteers compiled 7581 hours of observation on eight groups of free-ranging vervet monkeys. We witnessed 120 ground predator alarm events during that period (*i.e.* one encounter every 63 hours of observations). Monkeys produced leopard alarm calls during 16.7% of these encounters (20 out of 120), remaining silent for the rest of them. During those 20 events, the stimulus (Table 3) that prompted a ground predator behaviour and corresponding vocalisations was mostly jackals and dogs (12 out of 20). Three times the monkeys exhibited leopard response to animals that were non-threatening (impalas and an owl), and twice towards eagles who are a threat to vervet monkeys but require a different response; this shows an error rate of 25% (5 out of 20). They called once to human poachers accompanied by their dogs. And in two cases, they displayed a leopard response to a solitary male vervet monkey.

Table 3: List of stimulus eliciting ground predator response and leopard calls in the population of vervet monkeys of the IVP from 1st May 2015 to 30th April 2016. These are the events used to investigate the geographical occurrence of leopard calls during ground predator encounters.

Stimulus eliciting ground predator response and leopard calls	Number of events
Black-backed jackal (*Canis mesomelas*)	7
Domestic dog (*Canis familiaris*)	5
Human poachers with domestic dogs	1
Solitary male vervet monkey (*Chlorocebus pygerythrus*)	2
Eagle (*Accipitridae* family, unidentified genus and species)	2
Impala (*Aepyceros melampus*)	2
Owl (*Strigidae* order, unidentified family, genus and species)	1
Total number of events	*20*

We documented a total of 195 between-group encounters resulting in a rate of approximately one every 39 hours of observation. During 72.3% of these between-group encounters (141 out of 195), the monkeys produced vocalisations that were not bark-like, such as grunts, aggression or contact calls, while they produced bark-like calls during 11.8% of them (23 out of 195). During the remaining 15.9% of encounters (31 out of 195) the monkeys did not vocalise. We acknowledge that these occurrences might be underestimated as researchers might not have been present to observe all interactions and the presence itself of researchers could have had a deterring effect on neighbouring monkeys and on predators (Isbell and Young, 1993).

ACOUSTIC ANALYSIS

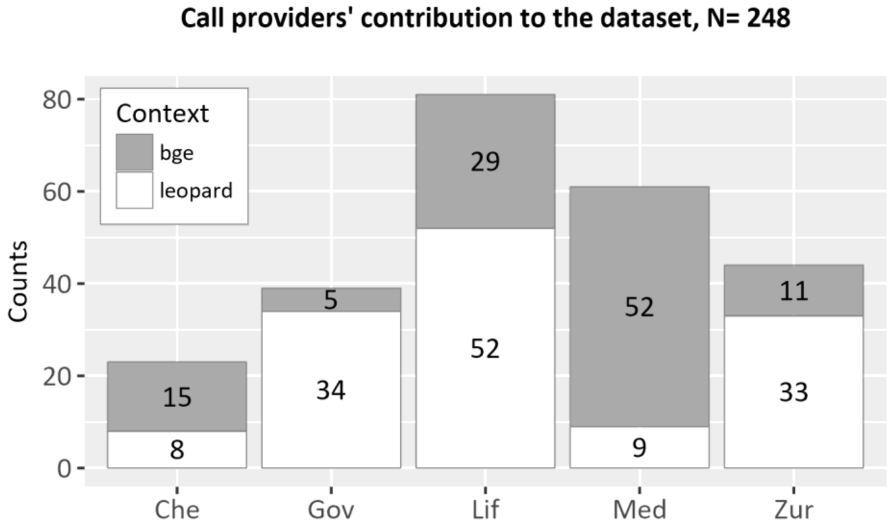

Figure 5: Number of call units analysed for each of the five adult males studied (N = 248).

Results from the pDFA did not allow to discriminate between the two types of calls. I obtained a mean score of 87% of correct assignment of the original dataset, which was not significantly higher than the mean score of 83% of correct assignment obtained for a random dataset (binomial test, *P*= 0.304). The cross-validation test for the original dataset also showed a mean score of 72% correct assignment, which was not significantly different from the 73% correctly classified of the random dataset (binomial test, *P*= 0.625).

GEOGRAPHICAL ANALYSIS

I used 18 ground predator encounters and 19 between-group encounters to investigate localisation of events involving bark-like alarm calls. A third (6 out of 18) of ground predator encounters leopard calls and 42.1% (8 out of 19) of between-group encounter during which similar bark-like calls were produced took place in overlapping regions of the home ranges (Figure 6). After controlling for size difference between overlapping and exclusive regions and time spent in each, I found that the proportion of bark-like between-group encounter calls occurring in overlapping regions was indeed significantly higher in overlapping regions of the home ranges (exact binomial test (upper-tailed), *P*= 0.000005). But, contrary to my predictions, the proportion of events involving leopard calls during ground predator encounters was significantly different from the expected proportion of 50% in both exclusive and overlapping areas (exact binomial test (two-tailed), *P* = 0.0003). Therefore, vervet monkeys did not produce leopard alarm calls in response to ground predators at random throughout their home ranges.

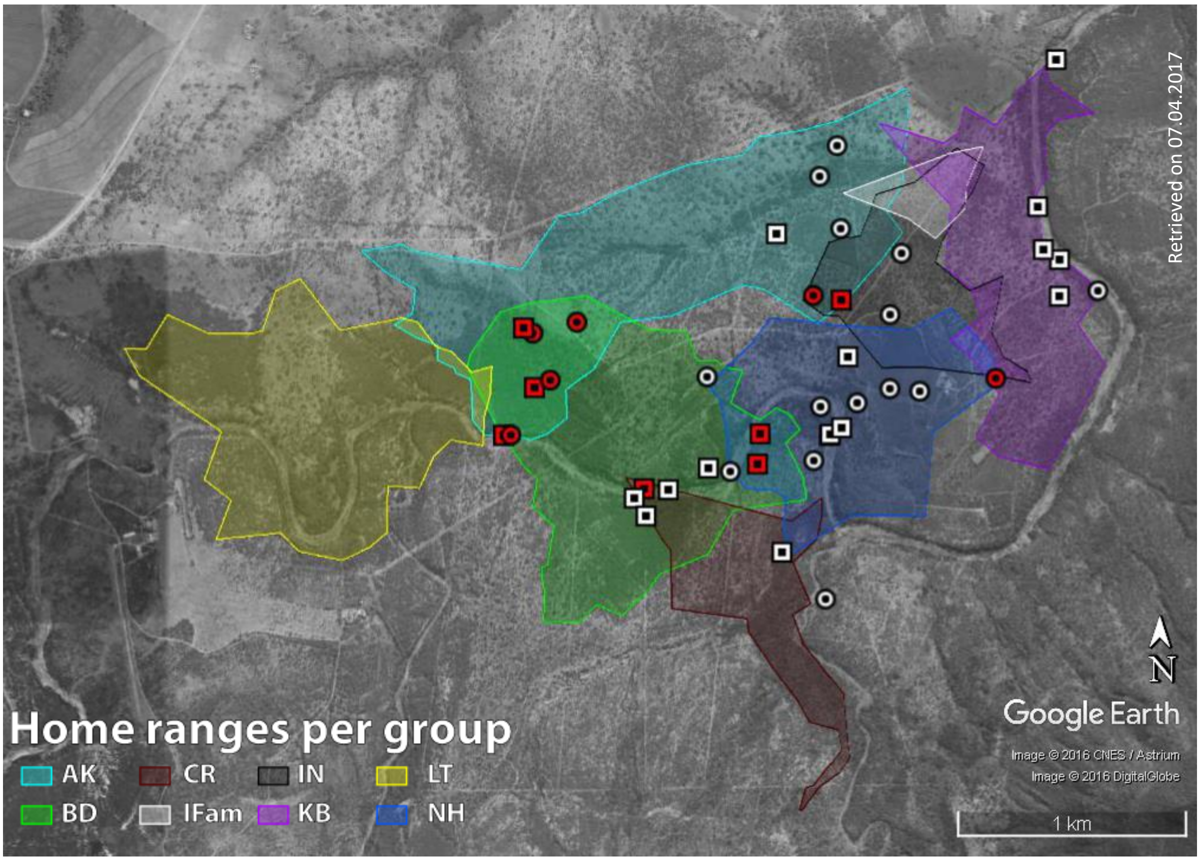

Figure 6: Map of the home ranges of the eight studied groups (AK= Ankhase, BD= Baie Dankie, CR= Crossing, IFam= I family, IN= Intaka, KB= Kubu, LT= Lemon tree, NH= Noha) showing the location of events during which bark-like alarm calls were produced either during ground predator encounters (round icons: , N= 18) or between-group-encounters (square icons: , N= 19). Calls occurring in overlapping regions of home ranges are indicated in red (ground predator encounter n= 6, between-group encounter n= 8), calls occurring in exclusive areas are in white (ground predator encounter n= 12, between-group encounter n= 11). Note that some encounters occurred in the same spot, therefore not all icons are visible on the map.

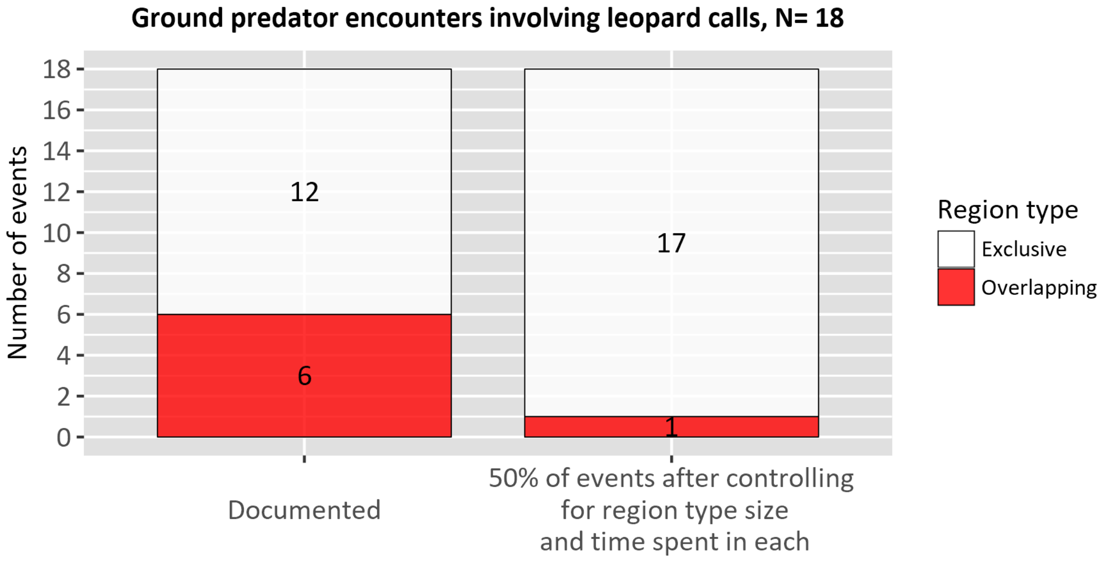

Figure 7: Leopard calls according to their relative location within their territory, N= 18 – exclusive area if used only by one group or overlapping one if multiple groups used it. Leopard calls are thought to be evenly distributed through the home range: theoretical proportions are 50/50 in overlapping/exclusive regions. Expected counts are adjusted to control for region type sizes and relative time spent observing in each area type.

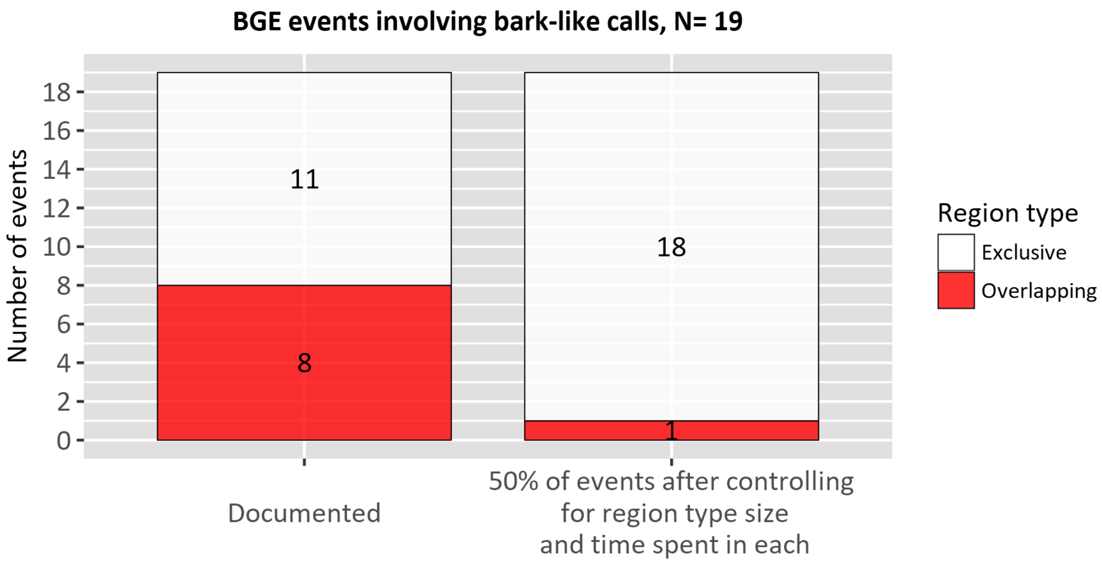

Figure 8: Between-group encounter calls according to their relative location within their territory, N= 19 – exclusive area if used only by one group or overlapping one if multiple groups used it. Between-group encounter calls should occur mostly in overlapping region: theoretical proportions are >50/<50 overlapping/exclusive regions. Expected counts are adjusted to control for region type sizes and relative time spent observing in each area type.

Discussion

The first aim of this study was to investigate whether the notion of functional reference is warranted for vervet leopard alarms, given that they produce acoustically similar calls to neighbouring groups during agonistic encounters, thus violating the production criterion proposed by Macedonia and Evans (1993). Secondly, to examine if those calls occurred randomly throughout the home ranges of the vervet monkeys, or if they followed a specific pattern.

Acoustically, I did not find that the leopard and the between-group encounter calls were significantly different, suggesting that the vervet monkeys use additional contextual cues to assess each situation and respond appropriately. When examining the geographical distribution of leopard and between-group encounter calls throughout the home ranges of this population of vervet monkeys, I noted that the two types of calls occurred more often in regions shared by more than one group than in regions used solely by one group. Although this was expected for the between-group encounter calls, the unbalanced distribution of leopard calls might correlate with the home ranges of the predators of the monkeys.

Acoustic analysis could not discriminate between the two calls

Acoustic analysis could not differentiate between the two similar bark-like calls that were given in the two contexts, namely between-group encounters and ground predator encounters. This could mean that between-group encounter calls and leopard calls are in fact the same. This would constitute an infringement of Macedonia and Evans' (1993) production criterion, which states that a functionally referential signal must be produced specifically in response to its corresponding stimulus, thus this acoustic signal might not qualify as functionally referential as per their definition. It also suggest that the vervet monkeys probably use other cues than the acoustic features of the call to determine in which context it is produced and how to respond appropriately. Indeed, on the one hand, the presence of a ground predator requires the vervet monkeys to seek refuge in tall trees as to avoid the predator, one the other, encounters with other groups entails a variety of behaviours from friendly inspection to fleet to fighting. In both cases, the monkeys only have an instant to assess the context in which a call is uttered and react accordingly, or else they might not survive.

What contextual cues can monkeys use to disambiguate calls given to predators and calls given to a neighbouring group? Here, I propose a few contextual cues that monkeys could use to properly evaluate each context and respond properly. Evidently, bystanders might see the predator themselves, which would allow them to react unequivocally. If they have the caller in sight, they can gather information from his demeanour and posture. Other species can come in handy through their own alarms and help the vervet monkeys to assess the situation. It has been shown that vervet monkeys can recognise the alarm calls of the superb starlings (*Spreo superbus*) (Cheney and Seyfarth, 1985; Hauser, 1988; Seyfarth and Cheney, 1990) to different predators and eavesdropping seems to be rather widespread practice among other species too (see Magrath *et al.*, 2015 for a review). And although vervet monkeys seem unable to use visual secondary cues, such as python tracks or carcasses from leopards' meals (Cheney and Seyfarth, 1985), to infer presence of a predator, they could use scents (Townsend *et al.*, 2012) left by predators or neighbouring groups to gauge their presence or travelling path. This type of information could allow them to have some kind of a representation of their localisation within the boundaries of their home range and where danger might be higher. It is most likely that vervet monkeys use more than one cue to evaluate their environment and process all type of information (visual, auditory, olfactory, geographical) altogether in order to get an accurate evaluation of the situation at all times.

In addition to supporting the idea that vervet monkeys use contextual cues besides the acoustical ones of the call itself to assess what threat they are facing, the fact that the between-group encounter call and the leopard call might be only one call could challenge our definition of between-group encounter and leopard contexts. Indeed, what we, human observers, consider to be two contexts might simply be one to the vervet monkeys and therefore justify the use of the same call. We (human beings) assigned a meaning, a category according to our own understanding of what we observed. When we realised that vervet monkeys produced specific alarm calls for large ground predators, we reasonably concluded, thanks to playback experiments, that some specific alarm calls referred to ground predators (Seyfarth *et al.*, 1980a). On another occasion, when we heard them producing similar alarm calls when they encountered another group of vervet monkeys, we assumed that these calls were directed to another category of objects: other vervet monkeys. But what if the monkeys consider their neighbours as dangerous as ground predators? Neighbouring vervet groups might even be considered as higher threats than ground predators because in addition to the risk of potential lethal injuries, they might also steal part of the territory, and valuable resources such as food, water or potential mates. After all, they have large teeth, they are well at ease both on the ground and in trees, are very muscular (Bolter and Zihlman, 2006), and can occasionally put up real fights. Females can be very aggressive too, especially during between-group encounters, as they can even kill other females or juveniles (Hauser *et al.*, 1986). With this in mind, it is not surprising then that the alarm calls produced during agonistic encounters with neighbouring groups are more similar to the ones produced during encounters with ground predators, as dangers might be more similar in those two conditions than during encounters with snakes hidden in tall grasses or eagles cruising in the sky. Hence, our definition of "context" might be too narrow and if other vervet monkeys were encompassed within the "predatory context" then the between-group encounter/leopard call would in fact be produced in one specific context and could still be deemed functionally referential.

Leopard and between-group encounter calls occur mostly in overlapping regions of the home ranges

Overlapping regions are parts of a home range that are shared with other groups and as a result, one would expect encounters and relevant calls to be correlated with the higher chance of meeting conspecifics. Unsurprisingly, I did find that between-group encounter calls occurred significantly more in overlapping regions than exclusive ones. However, leopard calls were not randomly distributed as expected, but instead, vervet monkeys produced significantly more leopard alarm calls in overlapping regions. That the monkeys do not encounter predators at similar rates everywhere in the home range suggests that the predators themselves also share some parts of their territories more than others with the vervet monkeys. There could be more predators in those regions because they constitute prey-rich environments. Regions shared by multiple groups of monkeys will contain more potential preys and as a result, draw more predators to that region (Zuberbühler and Jenny, 2002). Consequently, the presence of more predators will inevitably also increase the number of ground predator alarm events. This predator-rich environment theory is also supported by a study on the greeting calls of vervet monkeys from the same studied groups that showed that predator encounters were more likely near rivers (Mercier *et al*, 2017, *in press*). Since rivers are an important resource for the vervet monkeys, it is expected that most of the overlapping areas include at least part of the river, contributing to a higher rate of predator encounters. In order to verify if the distribution of leopard calls is correlated with that of predators, one could conduct a detailed survey of predators' living habits (Zuberbühler and Jenny, 2002), studying their hunting strategies, territoriality and diet using radio-tracking systems and trace analysis (such as markings, faeces or prints). Alternatively, monkeys might also be more alert in overlapping regions of their home ranges and therefore be more likely to alarm call, also to minor disturbances or non-threatening animals, potentially increasing their rate of mistakes but at the benefit of being rather more safe than sorry.

Another explanation could be that our sample does not reflect the reality of occurrences of both types of alarm calls. As previously cautioned, the number of between-group and predators encounters might have been biased (Isbell and Young, 1993) by the mere presence of researchers. By following the monkeys, they could have frighten away some neighbouring groups or predators. Furthermore, group spread being sometimes over hundreds of meters, some encounters might have been unnoticed despite the presence of researchers with part of the group. This bias might be mitigated by increasing the sample size and using data from a longer period of time.

POPULATION BIAS

Of course, these findings might be applicable only to this specific population of South African vervet monkeys of the IVP. Most studies on this species have been conducted on East African vervet monkeys, in the Amboseli National Park in Kenya. Different populations of monkeys will not have the exact same habitat, nor sympatric fauna. Especially the predator fauna, the Amboseli National Park has a large population of leopards commonly preying upon the monkeys as well as baboons, as opposed to the IVP in South Africa, where leopards have not been documented for many years and baboons live outside of the reserve. At the IVP, the vervet monkeys' most common threat seems to be jackals (Table 3) and although monkeys there are not directly preyed upon by poachers, the latter come into the reserve regularly with their dogs to hunt grazing mammals such as impalas or wildebeests. As predator experience can influence the development of alarm calling (Stephan and Zuberbühler, 2008), these results might be due to some specificity of this population of vervet monkeys and might not be generalised to other populations living in other areas. Nonetheless, more studies on this population of vervet monkeys and comparative studies with other populations could bring more insight on how they acquire information from their environment, further enlightening us on what contextual cues they might be using to determine their predator response.

Perspectives

The focus of this study was the caller. I analysed what type of vocalisation male vervet monkeys gave and where. Further research should investigate these calls from the point of view of the receiver. By using playbacks of those calls for example, we could explore how listeners perceive the calls. We could observe if they hear them differently and consequently respond differently, meaning that there could still be using additional contextual cues to respond appropriately but they could also be using some subtle acoustic features that we were unable to detect. For example, the state of the caller (Seyfarth *et al.*, 2010) might influence the properties of alarm calls. That arousal level might be specific to each situation, depending on the size of the predator, its pace and direction of movement, or its behaviour (moving *vs*. hunting). Similarly, during encounters with neighbouring groups, the level of danger will vary according to the size of the neighbouring group, its composition (mainly number of males), or the aggressiveness of the other group members (as encounters between two groups can also be "friendly"). Again, monkeys might be more aggressive during the breeding season as to secure their access to females. Therefore, the tracks used to run the playbacks should be recorded in environments as controlled as possible in order to take into account all those contextual factors and allow an accurate comparison between the responses to the two calls.

Furthermore, we could investigate if vervet monkeys consider conspecifics as predators. We could present to them stuffed vervet monkeys in exclusive and overlapping areas as well as in a "neutral" area, such as in a laboratory. We would record the monkeys' response and vocalisations and see if they correlate with the location. The neutral setting would allow determining if vervet monkeys alone were considered a potential threat. The exclusive and overlapping setups would tell us if the vervet monkeys take geographical (and other) cues to judge if they are facing a predator or a rival. These fake vervet models should be of various age-class and sex as a juvenile might not be considered as big a threat as an adult male.

These type of experiments can give us insight into the cognitive processes that allow vervet monkeys to gather and treat information and respond in different situations as well as how they categorise external objects. In term, this knowledge could be transposed to human beings, as we are primates too and might have used the same type of processes at the beginning of the evolution of language, bringing us closer to the *when*, *how* and *why* we can speak.

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APPENDIXES

A1. LIST OF STAFF MEMBERS WHO COLLECTED DATA FROM 1ST MAY 2015 TO 30TH APRIL 2016

In alphabetical order.

Bergerat	Charlotte
Besson	Emmanuelle
Bodin	Manon
Bono	Axelle
Borgeaud	Christèle
Botting	Jenny
Brocard	Sarah
Cantoni	Jacopo
Carré	Severyne
Clerc	Maxime
Dongre	Pooja
Eichenberger	Franca
Gareta	Miguel
Gordon	Kim
Grampp	Mathilde
Holden	Eve
Lamprecht	Annerie
Laurent	Zoe
Mandra	Simona
Mercier	Stéphanie
Nierat	Virginie
O'Hearn	William
Reverchon-Billot	Lola
Sobrino	Alvaro
Stoebener	Pauline
van Blerk	Arend

A2. Scan form

Form entry	Explanation
Date	Date of the day we collected scan data
Group	The name of the observed group
Time	Timeframe of the scan (10 minutes every 30 minutes), so every hours at 00' or 30' minutes
GPSSouth_decimaldegrees	GPS location using the latitude and longitude of the vervet monkey group, with researchers trying to be at the centre point of the group
GPSEast_decimaldegrees	
GroupSpread	Evaluation of how spread out the group is
Observing	Name of the researcher(s) observing the monkeys
PersonEnteringData	Name of researcher entering the data
Weather	The weather at the time of the scan (Breezy, Cloudy, Misty, Raining, Stormy, Sunny, Windy)
Individual	The identity of the focal individual during the scan
Infant	Location of the focal's infant if applicable (Does not apply, Holding/Clinging, Contact, Nearby (<10m), Around (<5m), Not Nearby (>10m), Unknown)
Height	Height of the focal individual (On ground (0m), <2m, 2-5m, 5-10m, 10-15m, 15-20m, >20m)
Refuge	Distance between the focal and a refuge (Does Not Apply, <2m, 2-5m, 5-10m, 10-15m, More Than 15m). A refuge here is defined as a tree of at least 5 meters high.
PositionInGroup	Position of focal individual relative to the group (Front (Moving), Centre, Back (Moving), Periphery, Unknown)
Activity	Main activity of the focal (Resting, Moving, Feeding, Social)
NearestNeighbour	Identity and distance of the focal's nearest neighbour (Contact, Arm Length (0.5m), 1m, 2m, 3m, 4m, 5m, 6-10m, >10m, Unknown)
DistanceToNeighbour	
NumberNeighboursIn10mCat	Number of neighbours of the focal in a 10m radius (0, 1-2, 3-5, 6-10, 11-15, 16-20, >20)
AdultsIn1m	Identities of adults, juveniles and 1 year olds in a 1m radius from the focal
JuvsIn1m	
1yoIn1m	
AdultsIn5m	Identities of adults, juveniles and 1 year olds in a 5m radius from the focal
JuvsIn5m	
1yoIn5m	
NumberContactCallingBouts	Number of contact calls, conflicts and grunts during the entire 10 minutes scan frame
NumberConflicts	
NumberOfGruntsDuringScan	
OtherPeoplePresent	Whoever was accompanying but was not observing or entering the data
Remarks	A place to record anything that was not featured in the form, out of the ordinary or complementary information

A3. Alarm form

Form entry	Explanation
Date	Date of the alarm event
StartTime	Starting time of the alarm event
Group	Name of the observed group
GpSpread	Estimate of the group spread
Context	The context during which the alarm occurred (Experiment, Baiting/Capture, Feeding, Focal, Habituation/Recognition, Identification Test, Moving, Resting, Scan, Social, Unknown).
GPSS_decimaldegrees	GPS location of the event using the latitude and longitude
GPSE_decimaldegrees	
HabitatType	The habitat type where the event occurred (Mixed, Close, Open, Unknown)
VocAlarm	If there was a vocalisation, indicating the type of alarm call produced when researchers could identify it (Human call, Eagle call, Leopard call, Other call, Snake call, Unknown call)
Focal	The focal individual used to describe the event, usually the first adult in sight at the time of alarm event
Infant	Location of the focal's infant if applicable (Does not apply, Holding/Clinging, Contact, Nearby (<10m), Around (<5m), Not Nearby (>10m), Unknown)
FocalDetector	Whether the focal was the detector (*i.e.* the first to react) to the threat (Yes/No)
VocProd	Whether vocalisations were produced (Yes/No)
Duration	Duration of the vocalisations if any
ResumeCalling	Whether the focal stopped for more than 30 sec and then resumed calling (Yes/No)
FocalBehaviours	The focal's behaviour (not detailed here)
NearestNeighbour	Identity and distance of the focal's nearest neighbour (Contact, Arm Length (0.5m), 1m, 2m, 3m, 4m, 5m, 6-10m, >10m, Unknown)
DistanceNN	
Neighbours1m	Number and identities of individuals in a 1m/5m/10m/ "in sight" radius from the focal
Neighbours5m	
Neighbours10m	
NeighboursVisible	
DistToPred	Distance between the focal and the predator
DistCaller	Distance between the focal and the first caller (if applicable)
SubgroupResponse	Response of the subgroup (*i.e.* visible monkeys)
PercentSubgroupResponding	Percentage of the subgroup responding
IDFirstCaller	Identity of the first caller if known
TotalNumberCallers	Total number of callers if applicable
IDOthers	Identity of the other callers
Intensity	Overall intensity of the event (Weak, Medium, Strong)
PredatorSight	Whether the predator was sighted by human observer (Yes/No) and the species of animal if seen
WhatAnimal	
OtherGroupSighted	Whether another vervet monkey group was sighted (Yes/No)
EndTime	Ending time of the event, i.e. when the monkeys resume their previous behaviour, without any alarm calls being produced during at least 30sec
VocalizationsRec	Whether the vocalisations were recorded (Yes/No) and on which track number
TrackNb	
Description1	Description of the event

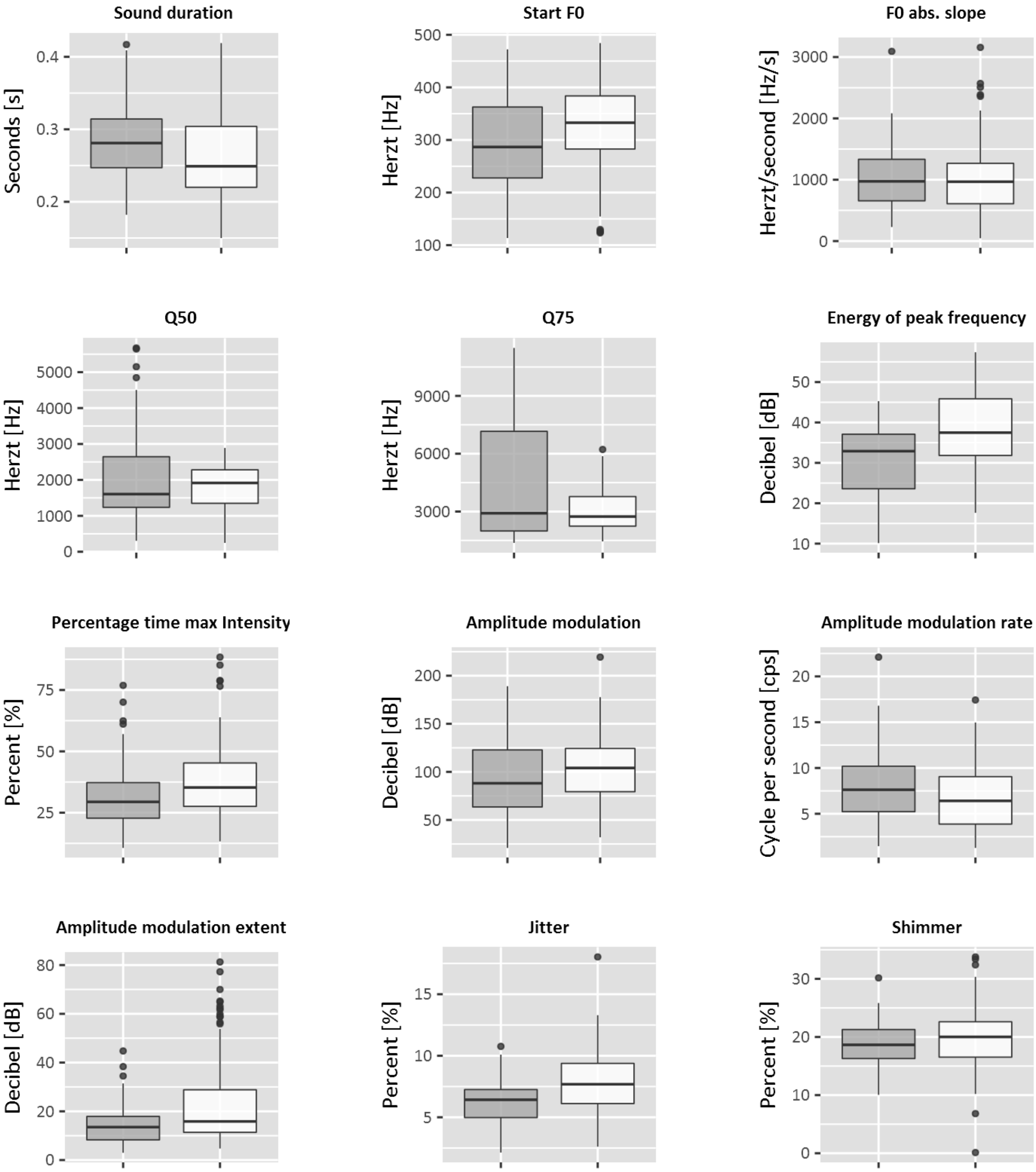
A4. Between-group encounter form

Form entry	Explanation
Date	Date of the between group encounter
StartTime	Starting time of the between-group encounter event
StartLocS_decimaldegrees	Latitude and longitude at the beginning of the event
StartLocE_decimaldegrees	
Observers	Name of researcher observing the monkeys
FocalGroup	Name of the group followed by researchers
FocalGroupCohesion	Evaluation of how spread out the group is
FocalBehaviourOnset	Focal group behaviour at onset of event (Moving, Feeding, Resting, Social, Unknown)
EncounterGroup	Name of the encountered group
EncGroupCohesion	The encountered group spread
EncBehaviourOnset	The encountered group's behaviour at onset of event (Moving, Feeding, Resting, Social, Unknown)
GroupLevelEncounterType	Type of encounter (Affiliative, Aggressive, Avoid, Face Offs, Ignore, Inspecting, Neutral, One group displacing the other, Vigilant, Vocal).
EndTime	Ending time of the between-group encounter event
EndLocS_decimaldegrees	Latitude and longitude at the end of the event
EndLocE_decimaldegrees	
Winner	Whether there was a clear winner of the encounter (Yes/No) and its identity
WinnerID	
FocalGroupBehaviour	Focal group and encountered group's behaviour after the encounter (Move <50m Away, Cross River, Move >50m Away, Remain in Area, Remain in Area and Feed, Remain in Area and Rest, Unknown)
EncGroupBehaviour	
DetailedDescription	Detailed description of the event

A5. Boxplots of the parameters used for the pDFA

Boxplots of the 12 parameters used in the acoustic analysis showing the median and first and third quartiles of the alarm calls produced in the two contexts (in grey the alarm calls produced during between-group encounter while in white the alarm calls produced during predator encounters).

Context: grey box = between-group encounter | white box = leopard



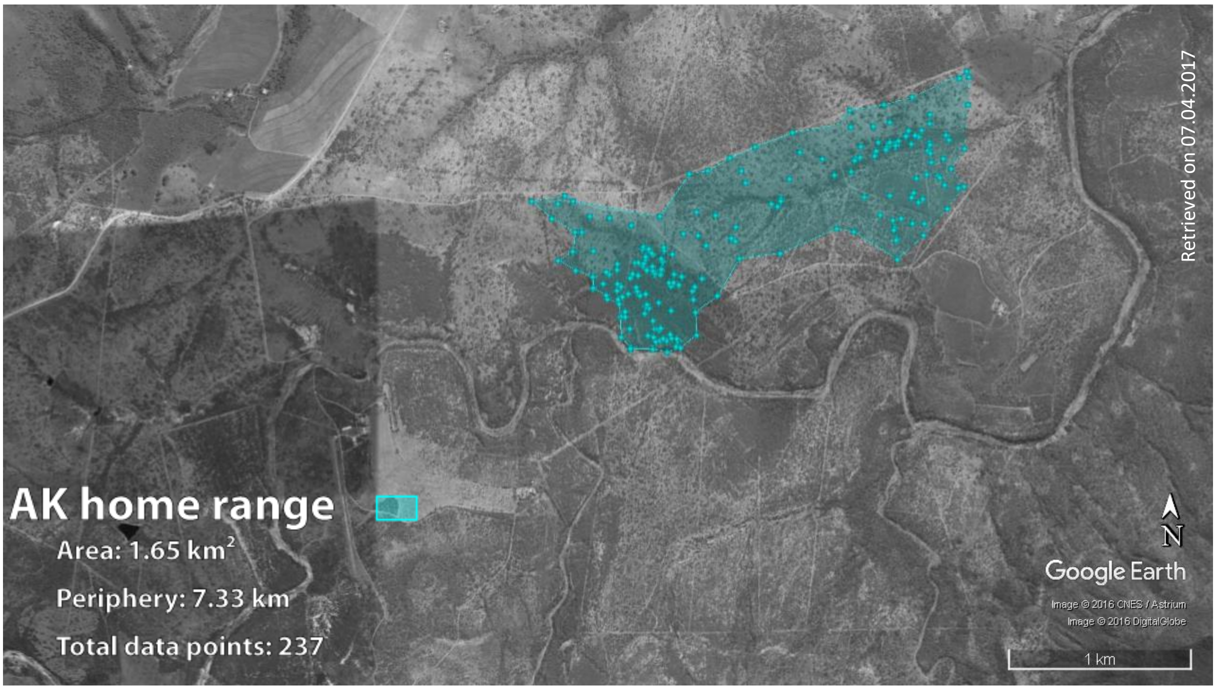
A6. Parameters excluded from acoustics analysis

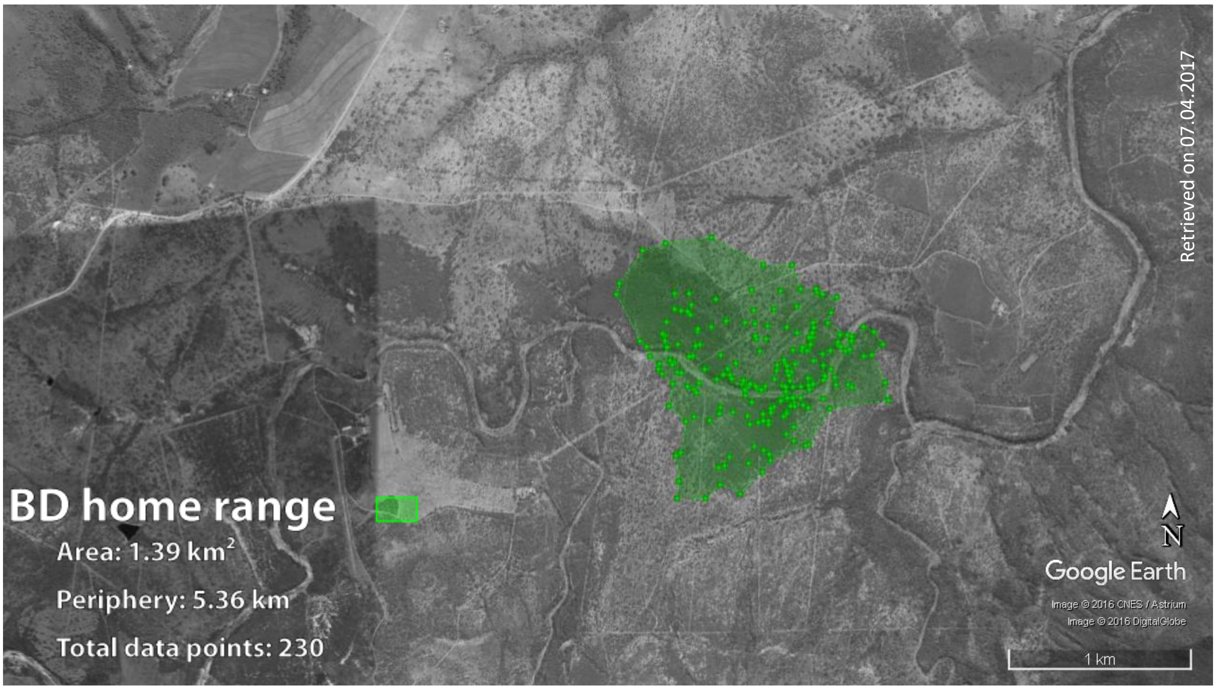
Table 4: The following parameters were discarded because: (†) contained to many missing values, (‡) were too highly correlated (Pearson's correlation r > 0.8) and (⁺) were too far from normality of residuals despite transformations.

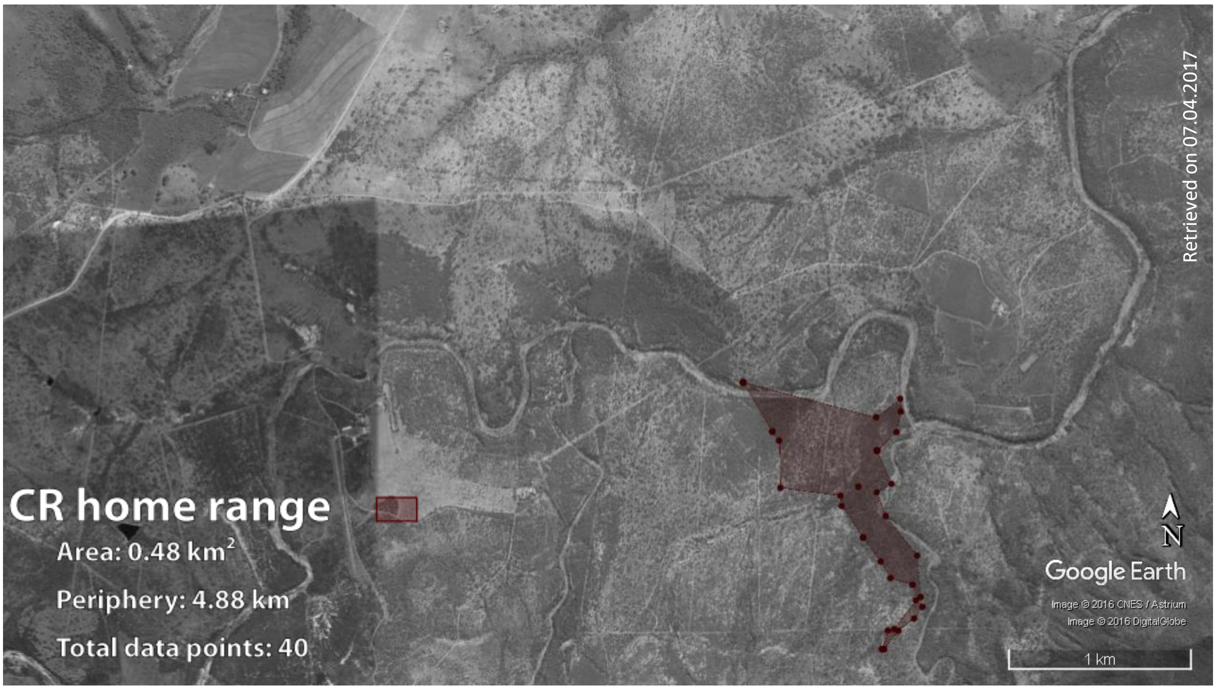
Parameter	Unit	Description
Mean F0 ‡	Hz	Mean of the fundamental frequency (F0) of the entire call unit
F0 end ⁺	Hz	Frequency of F0 at the end of the call unit
Max F0 ⁺	Hz	Maximum value of F0 across the call unit
Percentage time max F0 ⁺	%	Time point of the maximum value of F0 expressed as a percentage of the total duration of the call unit
Min F0 ⁺	Hz	Minimum value of F0 across the call unit
F0 variation ⁺	Hz/s	Mean variation of F0 per second
Frequency modulation rate ⁺	cps	Number of complete cycles of frequency modulation per second
Frequency modulation extent †	Hz	Mean peak-to-peak variation of each frequency modulation of the F0 contour of the call unit
Q25 ⁺	Hz	Frequency quartile dividing the call unit into two intervals of energy containing 25% and 75% of the energy calculated over the entire call unit
Fpeak ⁺	Hz	Frequency of maximum amplitude of the spectrum
Percentage energy EFpeak ‡	%	Energy of Fpeak expressed as a percentage of the total energy of the call unit

A7. Home ranges

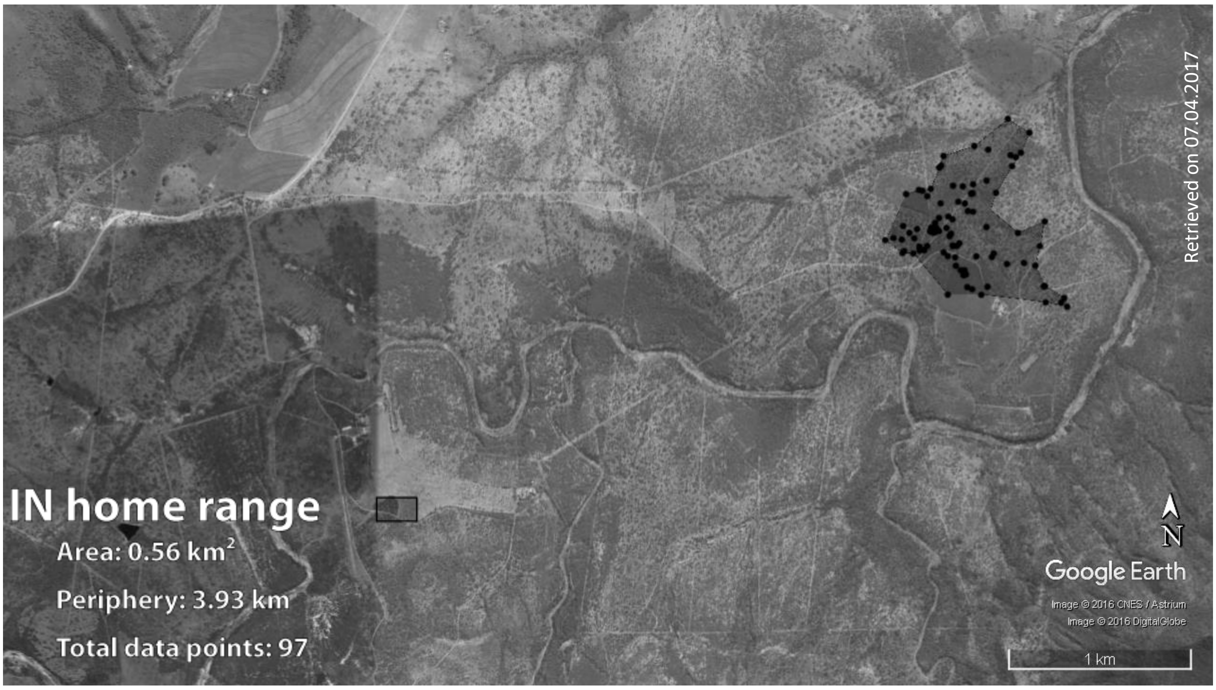
Maps of the home ranges of the eight studied groups of vervet monkeys in alphabetical order: AK (Ankhase), BD (Baie Dankie), CR (Crossing), IFam (I Family), IN (Intaka), KB (Kubu), LT (Lemon Tree) and NH (Noha). We used the GPS locations collected during scan days to delimitate the external polygon of each studied group.

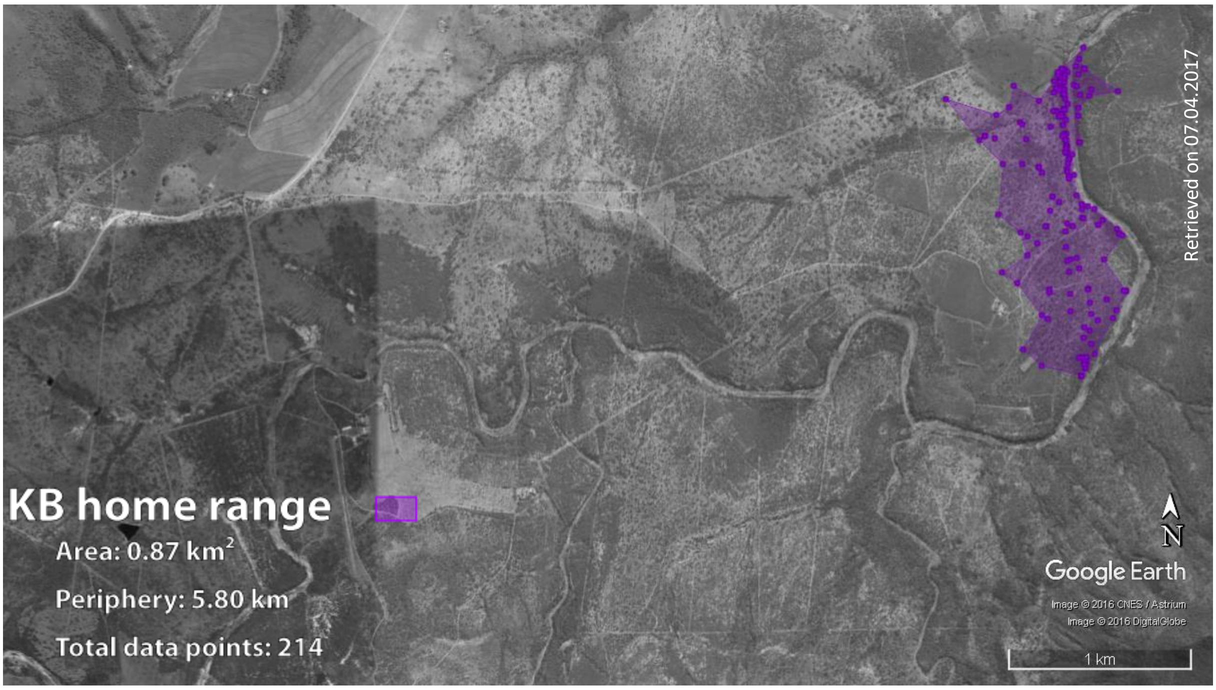


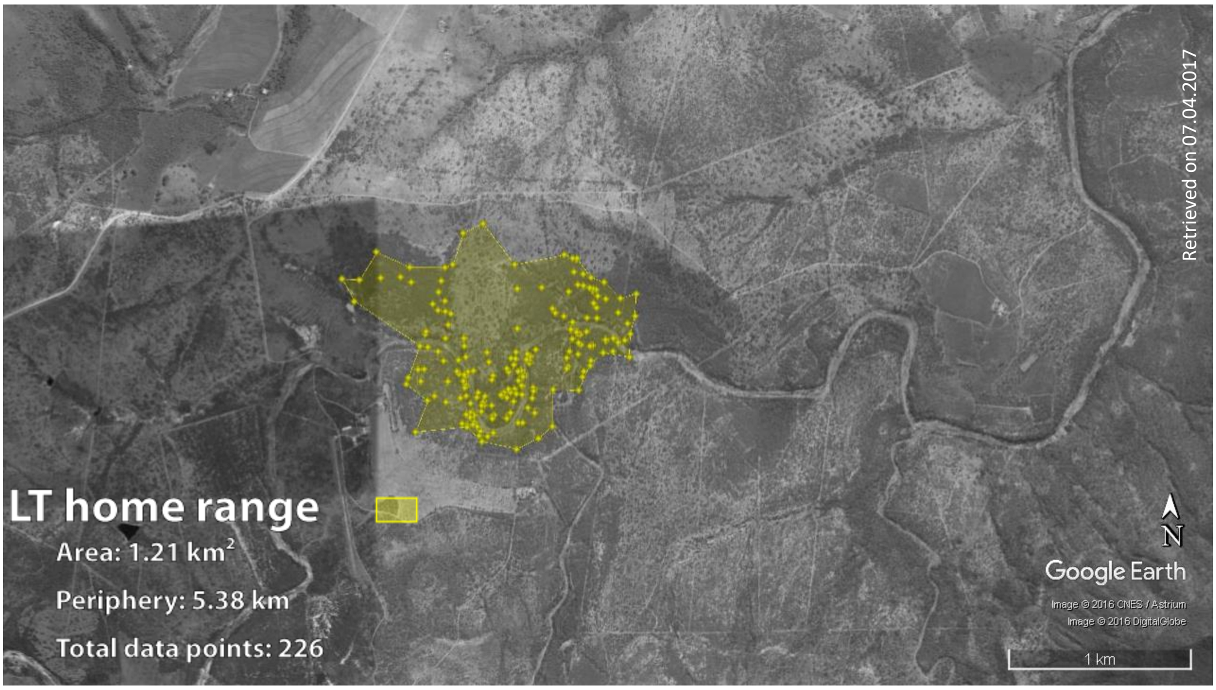


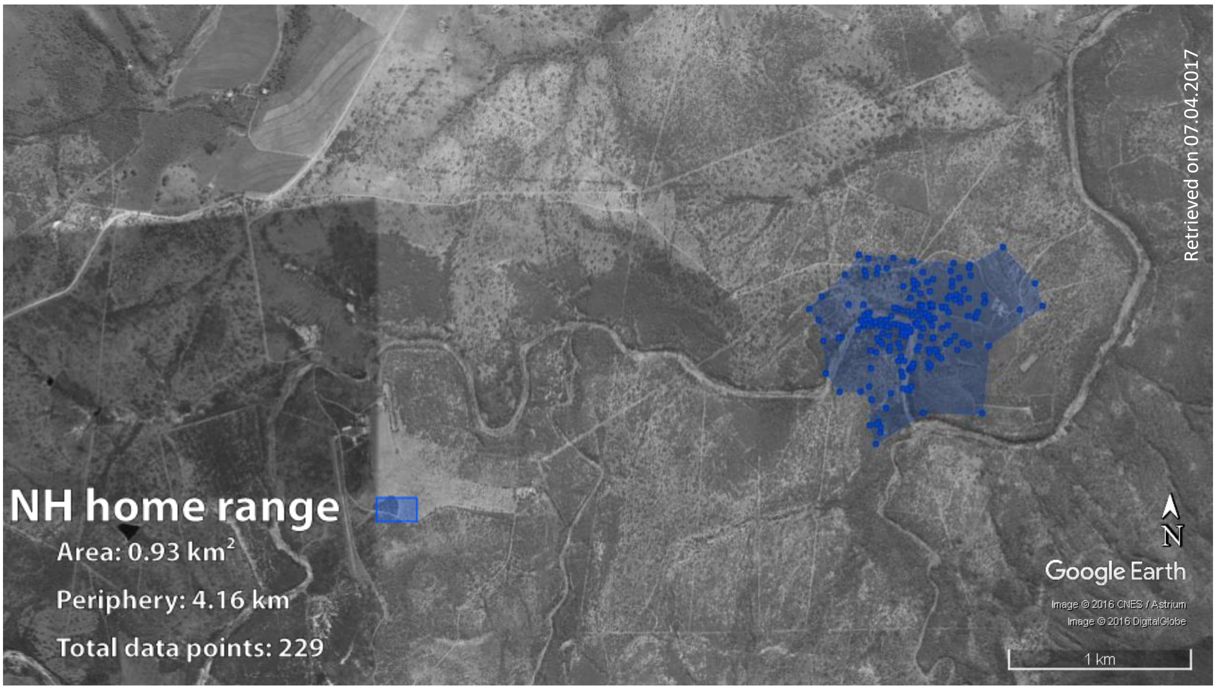

CR home range
Area: 0.48 km²
Periphery: 4.88 km
Total data points: 40
Retrieved on 07.04.2017
N
Google Earth
Image © 2016 CNES / Astrium
Image © 2016 DigitalGlobe
1 km


IFam home range
Area: 0.13 km²
Periphery: 1.69 km
Total data points: 8
Retrieved on 07.04.2017
N
Google Earth
Image © 2016 CNES / Astrium
Image © 2016 DigitalGlobe
1 km


IN home range
Area: 0.56 km^2
Periphery: 3.93 km
Total data points: 97
Retrieved on 07.04.2017
N
Google Earth
Image © 2016 CNES / Astrium
Image © 2016 DigitalGlobe
1 km


KB home range
Area: 0.87 km^2
Periphery: 5.80 km
Total data points: 214
Retrieved on 07.04.2017
N
Google Earth
Image © 2016 CNES / Astrium
Image © 2016 DigitalGlobe
1 km


LT home range
Area: 1.21 km2
Periphery: 5.38 km
Total data points: 226
Retrieved on 07.04.2017
N
Google Earth
Image © 2016 CNES / Astrium
Image © 2016 DigitalGlobe
1 km


NH home range
Area: 0.93 km2
Periphery: 4.16 km
Total data points: 229
Retrieved on 07.04.2017
N
Google Earth
Image © 2016 CNES / Astrium
Image © 2016 DigitalGlobe
1 km

A8. Leopard alarms data

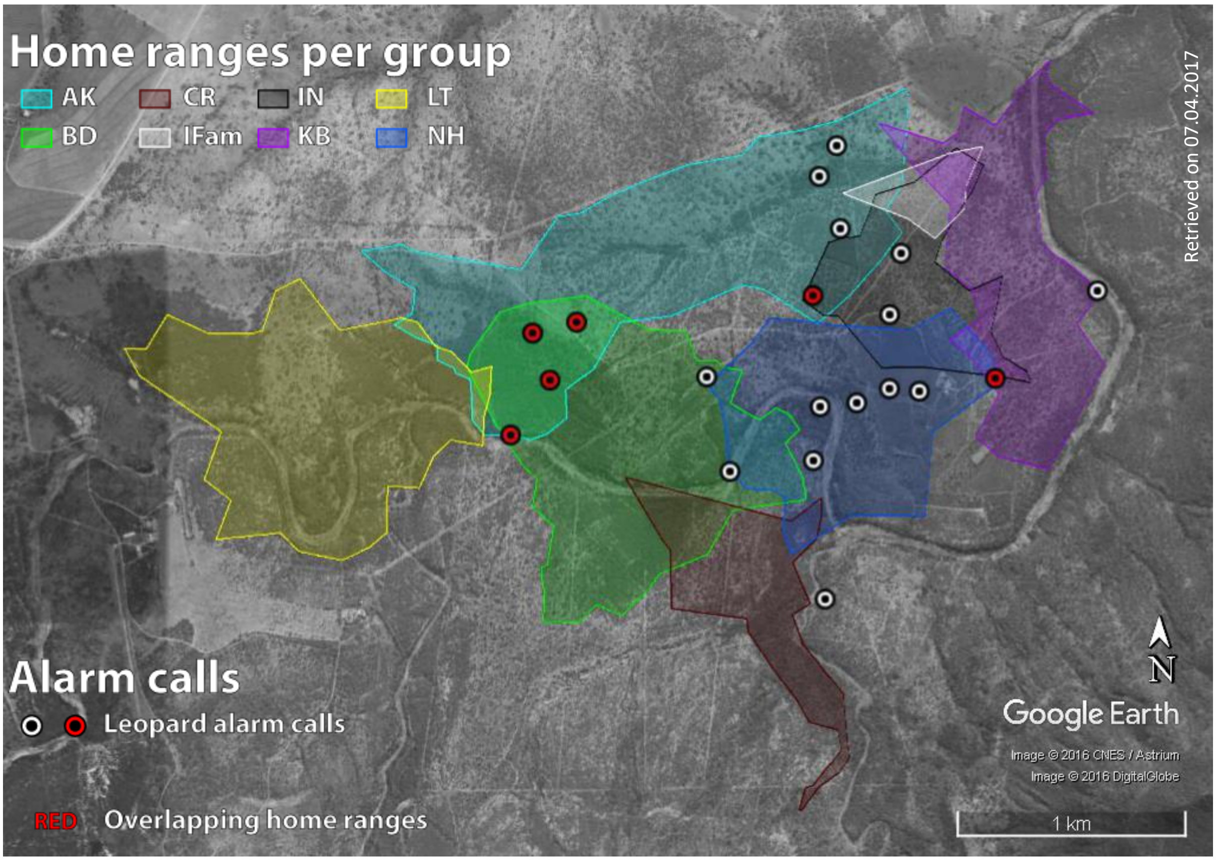


Figure 9: Map showing the GPS location of each predator encounter for which leopard alarm calls have been produced. Colours indicate the regions of the home ranges where they occurred: white corresponding to exclusive areas while red are the overlapping areas.

A9. Between-group encounter alarms data

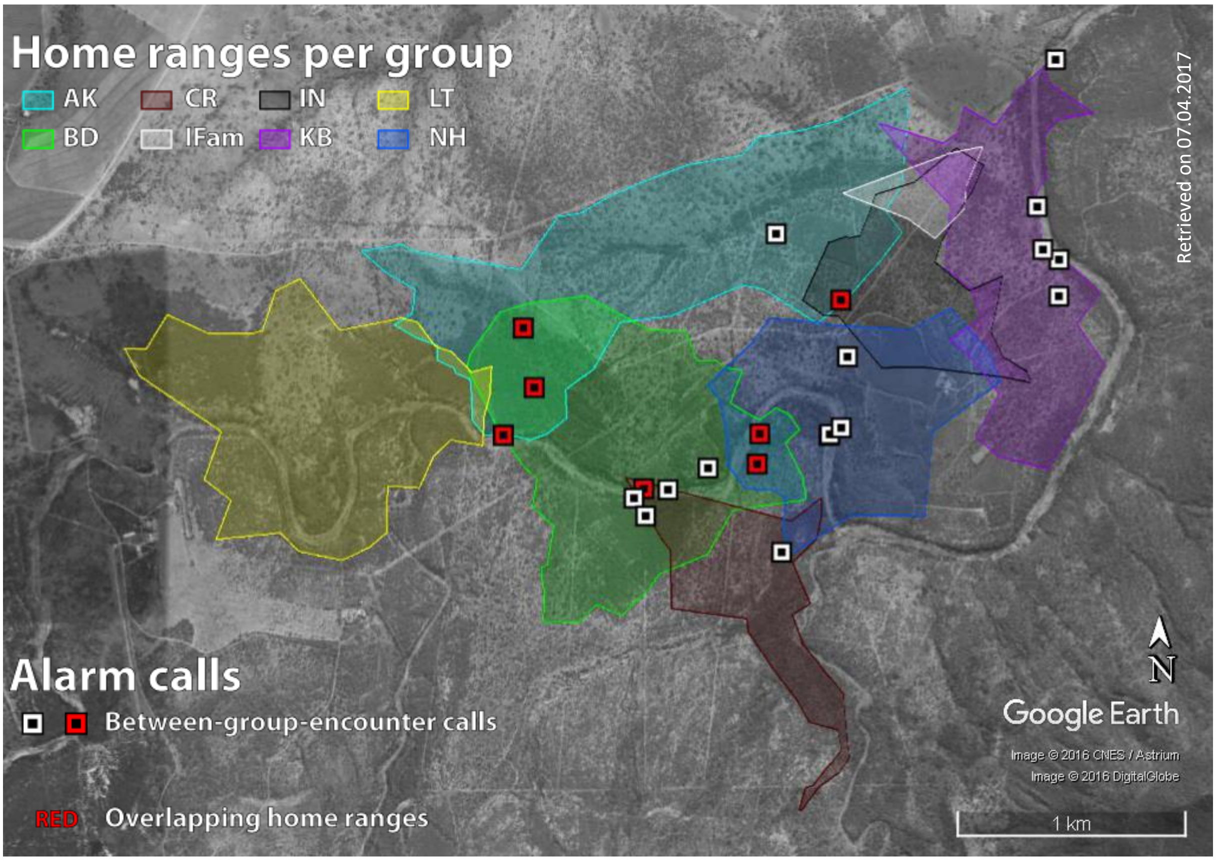


Figure 10: Map showing the GPS location of each between-group encounter for which between-group encounter alarm calls have been produced. Colours indicate the regions of the home ranges where they occurred: white corresponding to exclusive areas while red are the overlapping areas.

A10. TERRITORY UTILISATION

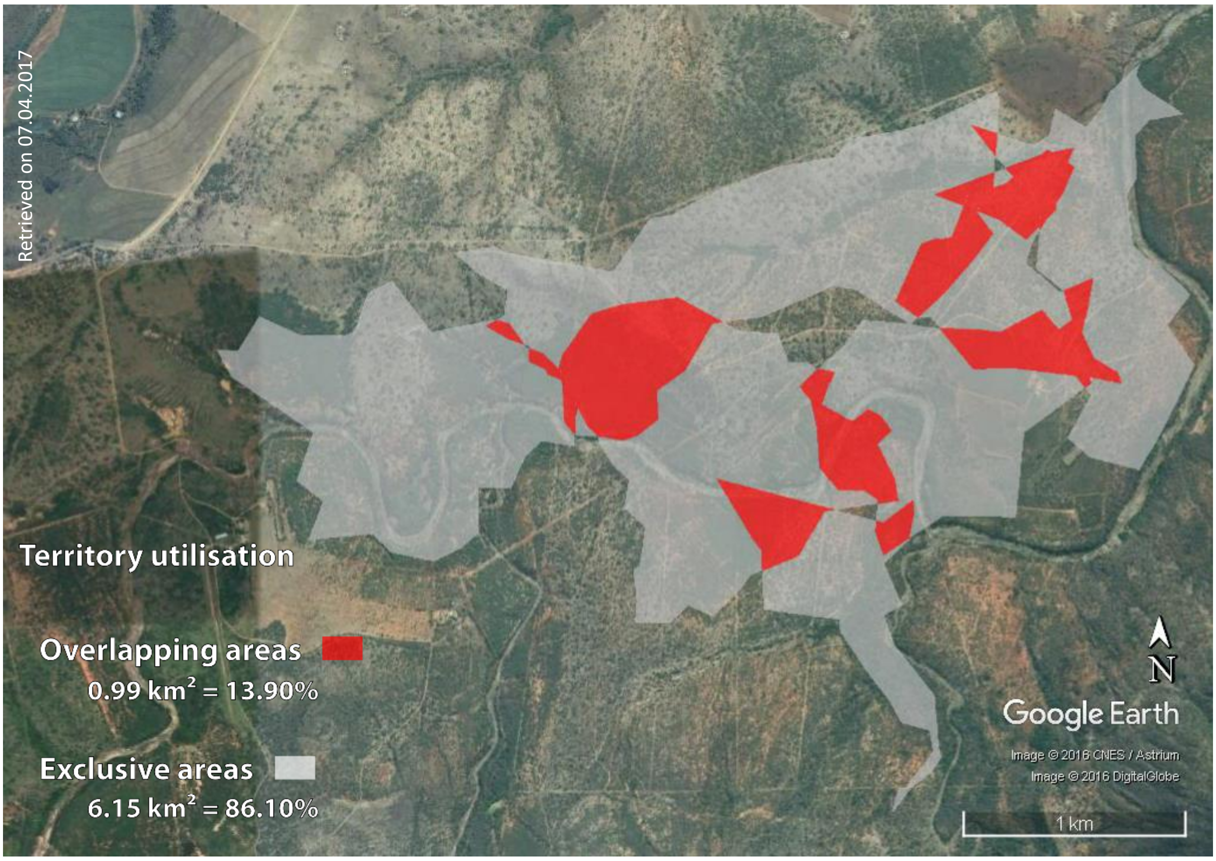


Figure 11: Map showing the delimitation of the different areas within the home ranges of vervet monkeys. Grey areas correspond to exclusive regions, used only by one group while red ones correspond to overlapping areas, used by at least two different neighbouring groups.

A11. EXCLUDED LEOPARD AND BETWEEN-GROUP ENCOUNTER CALLS

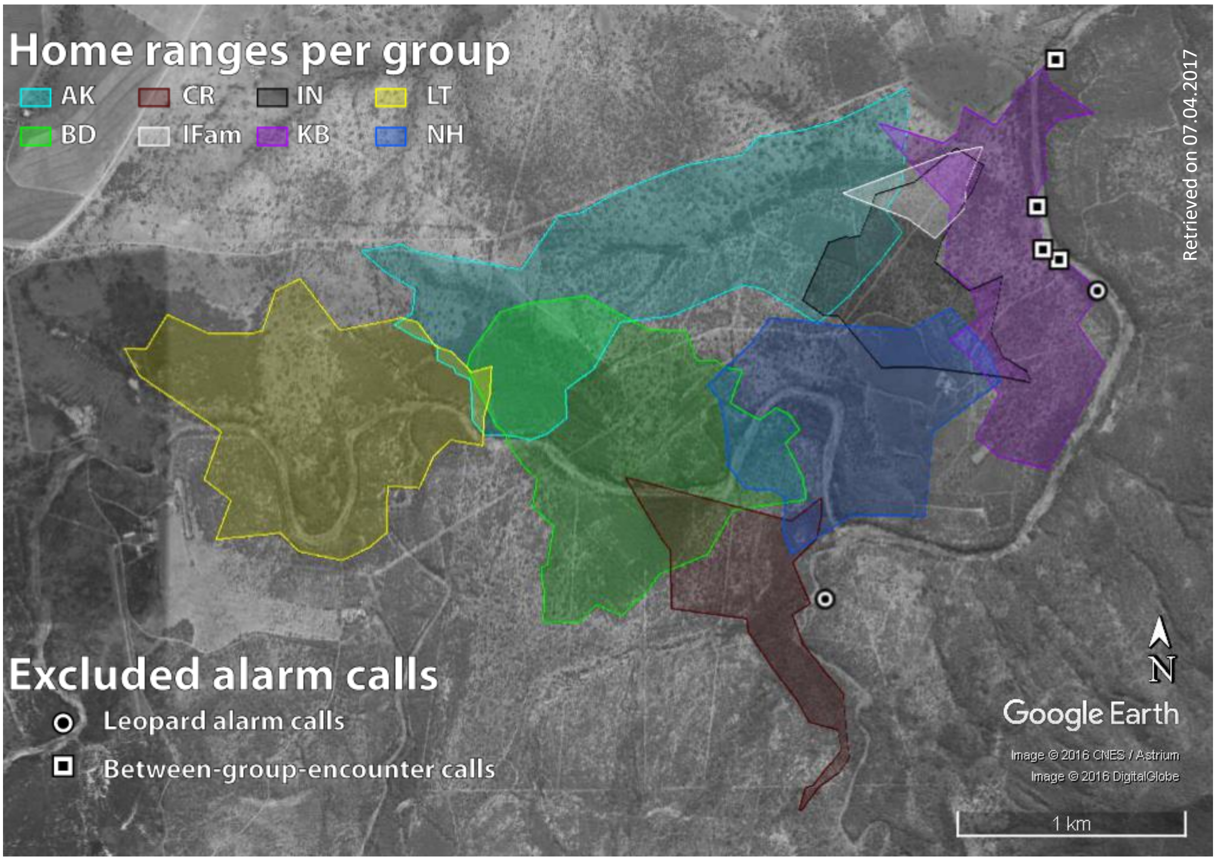


Figure 12: Map showing the GPS location of vocal encounter that have been excluded from analysis because of their ambiguous situations (near groups that are not monitored by researchers but have been seen and heard).