ANTI-PREDATORY RESPONSE OF NICOBAR LONG-TAILED MACAQUES TOWARDS SNAKE THREATS

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Certificate of Examination

This is to certify that the dissertation titled “Anti-predatory response of Nicobar long-tailed macaques towards snake threats” submitted by Mr. Rohit Negi (Reg. No. MS15045) for the partial fulfilment of BS-MS dual degree programme of the Institute, has been examined by the thesis committee duly appointed by the Institute. The committee finds the work done by the candidate satisfactory and recommends that the report be accepted.

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		(Supervisor)	(Co-Supervisor)

Dated: June 15, 2020

Declaration

The work presented in this dissertation has been carried out by me under the guidance of Dr. Manjari Jain at the Indian Institute of Science Education and Research Mohali and Prof. Mewa Singh at University of Mysore.

This work has not been submitted in part or in full for a degree, a diploma, or a fellowship to any other university or institute. Whenever contributions of others are involved, every effort is made to indicate this clearly, with due acknowledgement of collaborative research and discussions. This thesis is a bonafide record of original work done by me and all sources listed within have been detailed in the bibliography.

Rohit Negi
Dated: June 15, 2020

In my capacity as the supervisor of the candidate's project work, I certify that the above statements by the candidate are true to the best of my knowledge.

Dr. Manjari Jain	Prof. Mewa Singh
(Thesis Supervisor)	(Thesis Co-supervisor)

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ABSTRACT –

Threat sensitivity hypothesis states that prey species assess the intensity of threat(s) from predator species and respond accordingly. An underlying assumption of the hypothesis is that prey species is able to distinguish among different threat types. Studies have equivocally established the presence of sustained stress on exposure to predator or predator cues that corroborates the hypothesis. For primate models, where 'snake detection theory' is comprehensively supported, snakes appear to be strong stimuli. Hence, primates are expected to distinguish among commensal snake species. Also, once detected keeping track of its location is a good anti-predatory strategy against snakes. This is usually intertwined with frequent vocalisations, which might give information about location of predator to the conspecifics. Hence studying anti-predator vocalisation becomes extremely important for understanding the anti-predatory behaviour in general. Through the present study, we test a corollary of snake detection hypothesis, examining the snake distinguishing capacity of Nicobar long-tailed macaques (NLoTM). NLoTM occur in 3 islands of the Nicobar archipelago, Katchal, Little Nicobar and Great Nicobar. The archipelago also supports 26 species of snakes. Based on previous studies on the subject, snake species in Katchal are categorized into three categories, predatory, venomous and non-venomous. We prepared 3-D models of one snake species from each category alongside suitable control models. The models were then presented to NLoTM and their acoustic and behavioural responses were recorded. Lastly, to test the validity of snake models, the following measures were taken a) recorded at least one naturalistic encounter with the chosen snake species from each category and b) used road-killed specimens for presentation. The study also attempts to quantify the vocal repertoire of NLoTM. Fourteen different types of calls in various contexts and four different types of anti-predatory calls against snakes by NLoTM are quantified in this study. Results indicate that NLoTM differentiate snakes as predatory, venomous and non-venomous beings.

CHAPTER 1

INTRODUCTION AND EXPERIMENTAL DESIGN

Picture Credit – Sayantan Das

1.1 BACKGROUND AND LITERATURE REVIEW –

1.1.1 Background

The basic idea of survival entails successful reproduction followed by development of the offspring till it can reproduce and henceforth continue the cycle. Among other factors that potentially curb successful survival, predation appears to be one of the major contenders. A predatory species preys over other species and may make them susceptible to extinction. In such a scenario, prey and predator may undergo a tug of war, and find themselves in a cycle of adaptions and counter-adaptations. Such a phenomena is known as a prey-predator arm race (Dawkins & Krebs, 1979). The bat - moth (Miller et al., 2001) and whelk – bivalve (Dietl, 2003) are among the few relationships which illustrate this phenomenon. However, hypothesis like 'life-dinner principle' (the cost of a mistake being death for the prey versus only a lost meal for the predator (Dawkins & Krebs, 1979)) argues that co-evolution between prey and predator is rather uncommon and a more specific antipredator defences is much more likely to show up than predator counter-strategies.

It is also well established that prey species assess the intensity of threat(s) from predator species and respond accordingly (Threat Sensitivity Hypothesis (Helfman, 1989)). Since prey species might interact with a multitude of threat species, the aforementioned hypothesis presumes the cognitive ability of the prey species to distinguish among threat types. For a solitary species, detecting a predator quickly, then discerning how threatening it might be and finally exercising a suitable anti-predator behaviour might suffice. But for a group living species, where sociality is generally adaptive (Ebensperger et al., 2012), quick detection followed by successful communication about the same to the conspecifics seems integral. Communicating information about an active threat has been argued to be altruistic behaviour (Krams et al., 2006; Wheeler, 2008), and species exhibiting such behaviours are hypothesised to potentially derive inclusive fitness out of it. Such communication can be achieved mainly via visual and acoustic signalling. Primates being social group living species are without a doubt, an epitome of such displays. Previous studies show that primates actively produce anti-predator vocalisations (Crockford et al., 2003; Stephan et al., 2008), are able to distinguish among threat types (Ramakrishnan et al., 2005) and are also able to produce threat specific vocalisations (Seyfarth et al., 1980a). As diverse life forms produce functionally referential vocalisation for specific predator types, the argument for predation being a strong selective force for such complex traits appears to be vindicated.

Similarly, it is argued that it was snakes that led to the modification of the primate visual system, especially the SC pulvinar visual system (‘Snake detection theory’ (Isbell 2006; 2009)). Also, primates have been shown to be able to detect snakes more quickly than other stimuli (like spiders etc.) under a noisy background (Soares *et* al. 2014; Kawai *et* al. 2016; Strien *et* al. 2009; Stanford *et* al. 2001; Etting *et* al. 2014). Furthermore, studies with human infants (7 to 9 months old) show that they portray an attentional bias to snakes compared to other unfamiliar animals even when they presumably have limited experience with snakes (LoBue and DeLoache, 2010). These arguments support the hypothesis of the snake being a strong stimulus (at least for primates) and also sufficient to cause an anti-predatory response. Even Darwin speaks of them in the following manner : “I put my face close to the thick glass plate in front of a puff-adder in the Zoological Gardens, with the firm determination of not starting back if the snake struck at me; but, as soon as the blow was struck, my resolution went for nothing, and I jumped a yard or two backwards with astonishing rapidity. My will and reasons were powerless against the imagination of a danger which had never been experienced” (Darwin, 1872). Now that we have established that snakes are a strong stimulus at-least for primates, one may expect primates to even possibly distinguish among snake types. Previous studies like one on bonnet macaques show that they distinguish predatory snake species from non-predatory ones (Ramakrishnan et al., 2005). Through the present study, we test a corollary of the snake detection hypothesis, examining the snake distinguishing capacity of Nicobar long-tailed macaques (NLoTM).

As mentioned above, the endeavour entails studying both visual and acoustic anti-predatory behaviour. Studies have shown that for communicating danger, vocal signals are much more effective for species inhabiting dense forests than gestures or any other type of visual signals, which may be more apt for open habitat living species (Seyfarth et al. 1980a; Alvarez 1993; Zuberbühler 1997). Since the reliance on the vocal signalling appears to be higher, it was expected to observe different vocalisations for different snake types (predatory and non-predatory). But, in order to conclusively comment on whether a species is indeed producing a threat specific vocalisation, a vocal diversity/repertoire study becomes inevitable and hence, an attempt to study and characterise the vocal repertoire of NLoTM is also made throughout the course of this study.

Finally, knowledge of animal behaviour can be an extremely useful tool in conservation (Buchholz 2007; Blumstein and Juricic 2010). Since, it is extremely important to understand how different forms of exploitation affect different species in order to predict what types of offtake are sustainable (Caro 2009), behavioural ecology becomes an important tool to give such insights. As rightly described by Bergera "An animal's behaviour lies at the centre of gene environment interactions, and, as such, it serves as a mediator between an animal's fitness and anthropogenic disturbances" (Bergera et al. 2011). Many wildlife managers clearly value this role and have been using their knowledge of animal behaviour for managing species for decades (e.g., Geist and Walther 1974; Harcourt 1999; Singh and Kaumanns, 2005). This study gives insights on the vocal diversity and anti-predatory behaviour of NLoTM.

1.1.2 Study site and focal species

The study was conducted in Katchal island. It is one of the 23 islands from the Nicobar archipelago, which is located at 7.1205° N, 93.7842° E in the Indian Ocean, between the Bay of Bengal and the Andaman sea. The climate over there is tropical with a moderate temperature (max. 36.1°C and min. 16.7°C) and high average relative humidity (75%). The islands are covered with lowland rain forests (Collins et al. 1991).

Figure 1.1 – Bird view of the study site, Katchal.

Macaca fascicularis umbrosus, the Nicobar long-tailed macaque (NLoTM) is an endemic subspecies of *M. fascicularis* and is only found in the following Nicobar islands – Little Nicobar, Great Nicobar and Katchal (Umapathy et al. 2003). NLoTM is listed by the IUCN (*International Conservation of Nature and Natural Resources*) as 'Vulnerable' and is on '**Schedule-I**' of the Indian Wildlife Protection Act (Anonymous, 1972). NLoTM has a small and isolated population (average group size = 36) which has become seriously fragmented and has therefore been recommended as a candidate for protection (Umapathy et al. 2003). Interactions between humans and monkeys across Islands also pose major threats (Umapathy et al. 2003).

1.1.3 Why NLoTM

As with most island-dwelling species, these monkeys experience very few natural predators. One of the probable natural predators is the Reticulated python (*Python reticulatus*). There has not been a single case reported in the context of python predation form Nicobar islands, but still, several studies have shown its proficiency to prey over primates including humans (Etting 2014, Headland 2011). Aside from predation by python, the monkeys may incur other costs such as snake bite-related injuries since there exists a sizable population of venomous and non-venomous snakes across islands (Vijayakumar et al. 2006). Katchal, supports both venomous (*Trimeresurus labialis, Trimeresurus cantori*) and non-venomous (*Dendrilaphis pictus pictus*) species of snakes alongside Reticulated Python (Vijayakumar et al. 2006). Our observations have shown that envenomation in monkeys by aforementioned venomous snakes lead to swelling in and around the bite area for about 2-3 days. This deters their movement as well as foraging. Since it appears as if interaction costs vary across snake species, the snake species are therefore categorized into three different classes based on the probable costs incurred by monkeys while interacting with them (Ramakrishnan et al. 2005): i) Predatory Snakes, in which the cost of interaction is the highest, ii) Venomous Snakes, and iii) Non-Venomous Snakes, which offers minimum cost. Being a social group living species which encounter snakes of different types, NLoTM of Katchal becomes an ideal population to study the snake distinguishing capacity of primates.

1.1.4 Main Objectives

The study aims at three broad objectives and they are as follows -

a) To examine the vocal repertoire of NLoTM acoustically and understand the behavioural contexts of vocalizations.

b) To quantify and compare the visual anti-predator response of NLoTM against snake threats, in order to examine the snake distinguishing capacity of NLoTM.

c) To perform acoustic characterization and examine the differences (if any) between the anti-predator vocalizations of NLoTM in response to snake threats.

1.2 EXPERIMENTAL DESIGN

1.2.1 Study group

A coastal NLoTM group, Baywatch (BW), was selected for the experiment. The group was habituated to our presence such that all individuals allowed us a proximity of less than a meter. The group comprised 48 individuals. For this study, we have only used anti-predatory responses shown by adults (> 7 years) and sub-adults (between 5-7 years). This gave us a cumulative of 23 individuals out of which 16 were adults and 7 were sub-adults.

1.2.2 Snake models

3-D models of following snake species were presented to the NLoTM to simulate a threat interaction.

Please Note: The last row refers to the dead specimen. The same were collected and presented opportunistically (road kills).

Snake Type	Species Name	Common Name
Familiar non-venomous	*Dendrelaphis pictus pictus*	Painted bronzeback
Familiar venomous snake	*Trimeresurus cantori*	Cantor’s pit viper
Familiar predatory snake	*Malayopython reticulatus*	Reticulated python
Dead venomous snake	*Trimeresurus cantori*	Cantor’s pit viper

Figure 1.2: Familiar non-venomous model. (*Dendrelaphis pictus pictus*)

Figure 1.3: Familiar venomous model. (*Trimeresurus cantori*)

	
Figure 1.4: Familiar predatory model. (*Malayopython reticulatus*)	Figure 1.5: Familiar dead specimen. (*Trimeresurus cantori*)

1.2.3 Experimental setup

- Model presentation – It was made sure that the place used for presenting the snake models had some amount of vegetation so that the models were somewhat concealed. Though, the head region was always kept such that it was clearly visible. Only those locations were chosen which were primarily used for the purpose of moving from one patch to another by the monkeys. This is done because, one may expect monkeys to avoid areas where they encounter snakes. Hence, in order to minimize such cost for monkeys, if any, we selected areas as mentioned above. Furthermore, multiple areas were selected within the home range of the focal group. The same were selected based on two things: a) previous snake sightings b) suitable habitat for respective snakes (Whitaker et al., 2004). Since monkeys might show exaggerated anti-predator response for any given location due to fear landscape (Coleman et al., 2014), snake models were presented in multiple locations.
- Snake posture – The threat sensitivity hypothesis states that prey species assess the intensity of threat(s) from predator species and respond accordingly (Helfman 1989). Also, studies have shown that the perceived threat can vary depending on the posture of the

signaller. For example – Anti-predatory response in rhesus macaques varies with change in the posture of the snake, wherein striking postures indicate maximum risk followed by coiled postures and then extended sinusoidal postures (Etting and Isbell, 2014). In this study, an **erect extended posture with an uplifted head** was used and this posture was maintained across all presentations for all trials for all models.

Figure 1.6: Cantor pit-viper model presentation highlighting the posture of the snake.

- Trial setup and data collection– Once the models were placed, we used it as a reference and kept four bamboo sticks of length 2.5 meter in four different directions such that an imaginary circle of radius 2.5 meter is created. This provided us with a high-resolution data pertaining to distance. Also, we recorded both non-vocal and vocal anti-predatory responses for individuals (methods of data collection and recording will be given in details in Chapter 3 and 4) which were interacting with the snake model and were also within this circle. Here, we recorded two types of videos for each trial.

i. With a bigger frame to cover most of the interacting individuals. This camera person was not allowed to zoom in and out. However, the lateral movement was allowed, which were used in cases where a single individual or very few were involved in the interaction and they went out of the frame while staying in the interaction.

ii. With a relatively smaller frame covering the facial expressions of the individuals actively participating in the interaction.

Lastly, one of the experimenters recorded anti-predatory vocalisations produced by monkeys during the trial. We used solid state (Marantz PMD661*MKII* frequency response: 20 Hz - 20 kHz) audio recorder with a Sennheiser shotgun microphone (Sennheiser ME66 with K6 PM; frequency response: 40 Hz to 20 kHz) intertwined with wind shield (Sennheiser MZW66) for the same. All recordings were made at a sampling rate of 44.1 kHz and 16-bit accuracy.

- Frequency of presentation – We presented the snake models with a minimum gap of 5 days to a maximum gap of 15 days (Coss et al., 2004). Overall, we performed 9 trials with venomous model and 4 trials each with non-venomous and predatory snake model**.**

1.2.4 Ethical Note

The study was approved by the Institutional Animal Ethics Committee IISER Mohali and was also approved by A&N forest department. We acknowledge the fact that field-based studies have inevitable consequences on the behaviour of wild animals and hence we strictly adhered to the ethical guidelines by International field primatology. Above that, we exercised the following measures –

i. To prevent disease transmission - We made sure that all observers used facial mask, covered their body to the fullest, and used hand sanitizer in case of indirect contact to prevent any exchange of pathogens.

ii. Snake presentation - We made sure that the monkeys have not interacted with any type of threat for at least an hour or so before presenting the snake models. In the event of an intervention by a potential threat other than the presented models, the trial was suspended right away.

iii. Data collection - The individual involved in recording acoustic data was placed at the edge of the pre-defined circle. Others i.e. those taking the video data always maintained a distance of about 10-20 metre from the snake model.

CHAPTER 2

VOCAL REPERTOIRE OF NICOBAR LONG-TAILED MACAQUE

(*Macaca fascicularis umbrosus*)

Picture Credit – Sayantan Das

2.1 INTRODUCTION

Somewhere in the struggle of survival and reproduction, life forms influence and get influenced by the behaviour of other life forms. This is sometimes referred to as communication. Communication can be achieved via the following modes: a) visual b) chemical c) tactile d) electric e) thermal and f) acoustic. All the aforementioned modalities offer their specific pros and cons. Species tend to get specialised in one or multiple forms of it, depending on the type of evolutionary force they experience and ends up possessing a complex repertoire of the same. When it comes to transmitting an immediate information, like predator whereabouts to a conspecific, vocal mode seems to be one of the best candidates. Studies have also shown that among other modes of communication, visual and acoustic modes prevail in the animal kingdom (Rosenthal et al., 2000). Vocalisation is also shown to be the oldest way of social communication in most vertebrates (Bass et al., 2008). It is often argued that the animal vocal communication is a trait found in relation to animal social behaviour (Brudzynski, 2014). Hence studying vocal diversity in social species are thus insightful as they may indicate the pressures that have likely to shaped the trait evolutionarily. Many investigators have studied the vocal repertoire in primate species (Formosan macaque, *M. cyclopis*, Hsu et al., 2005; Barbary macaque, *M. sylvanus*, Hammerschmidt and Fischer, 1998; Tonkean macaque, *M. tonkeana*, Masataka and Thierry, 1993; long-tailed macaques, *M. fascicularis*, Palombit, 1992; bonnet macaque, *M. radiata*, Hohmann, 1989; lion-tailed macaque, *M. silenus*, Hohmann & Herzog, 1985; Sugiyama, 1968; stump-tailed macaque, *M. arctoides*, Lillehei and Snowdon, 1978; Japanese macaque, *M. fuscata*, Green, 1975; Itani, 1963; rhesus macaque, M. mulatta, Rowell, 1962; Rowell and Hinde, 1962) and this is the first study to explain the vocal repertoire for the Nicobar long tailed macaque (*M. f. umbrosus*). The main objective here is to check for difference, if any, among the calls produced by NLoTM in various contexts.

2.2 METHODOLOGY

2.2.1 Data collection

We used a solid-state audio recorder (Marantz PMD661*MKII* frequency response: 20 Hz - 20 kHz) with a Sennheiser shotgun microphone (Sennheiser ME66 with K6 PM; frequency response: 40 Hz to 20 kHz) intertwined with wind shield (Sennheiser MZW66) for recording the vocalisations. As most of the cercopithecine vocalisations lie within a range of 20 kHz (Marler, 1965) the sampling rate of the acoustic recorder was set at 44.1 kHz with 16-bit accuracy. All files were saved in .wav format. Data collection was done for 63 days. Ad-libitum sampling technique was followed for collecting the acoustic data. The behavioural context of the calls was mentioned right after a call was recorded with an intention to understand what possibly might have led to the occurrence of that call. In cases where the cause of a call was specifically known, the same was mentioned in the same recording.

2.2.2 Data analysis

All the audio recordings were analysed in Raven pro 1.4 and PRAAT (Boersma and Paul, 2017) for analysis of different spectral and temporal parameters of the calls. The parameters that were employed for the quantification and comparative analysis of the calls were number of notes, call duration, fundamental frequency(F0), dominant frequency(D0) and band width of fundamental frequency. Harmonics to noise ratio (HNR) and Percentage of Unvoiced frames were also noted, using PRAAT, to quantify the quality of sound recordings (Christian et al. 2018). All the variables are defined in Table 2.1 below.

Table 2.1: Ethogram of acoustic variables used for quantification of calls.

Variables	Definition
Call duration	It is defined as the duration of the call (in seconds).
Fundamental frequency (F0)	It is described as the mean lowest frequency of a call.
Pitch pattern	It is the visual description of the fundamental frequency in a spectrogram.
Dominant frequency (D0)	It is the mean of frequencies possessing maximum energy in a call.
Band Width of F0	It is the width of the fundamental frequency. It is calculated by subtracting the maximum frequency from the smallest within fundamental frequency.
HNR	It is the function which describes the degree of acoustic periodicity of a call. It is derived using the following equation: $10*\log_{10}$ (total energy in periodic part/ total energy in noise).
No. of unvoiced frames	It is the function which describes the quality of the sound recordings.

2.3 RESULTS

Based on the visual (pitch pattern) and aural inspection of all the calls recorded during this study, 14 different types of calls were identified which were produced by the NLoTM in various social contexts (Figure 2.2 – 2.5). Furthermore, 4 different types of anti-predatory calls were also found, which were specifically produced against snakes. Therefore, a total number of 18 calls are described in this study. The calls produced against snake models will be discussed in Chapter 4 in detail. 14 different calls were sub-divided into two categories based on the probable context in which these calls were produced i.e. affiliative and agonistic. Hence, there were 9 calls under affiliative category and the remaining 5 under agonistic.

Calls **a, b, c, d** and **e** were produced by infants (<1.5 years). Since the organs involved in the vocal production might not be fully developed in infants (Lieberman et al., 1972), the above-mentioned calls are likely to be subject to change. All calls were produced when the infant's mother was not around and such calls would mostly be followed by mothers approaching their calling infants and carrying them away (Table 2.2, Figure 2.1 a, b, c, d and e). Calls **f** and **g** were produced by sub-adult and adults while foraging (Table 2.2, Figure 2.1 f and g). Call **h** (onomatopoeic description – coo) was produced by all age/sex individuals (Table 2.2, Figure 2.1 h). Mostly this call was produced when there was a spatial segregation between individuals of the same group. Call **i** (onomatopoeic description – crack-co) was only produced by the alpha male of the group and was usually produced in events of chaos, for example – during inter-group interaction (Figure 2.1 i). Call **j, k** and **l** were produced during intra and inter-group interaction. Call **j** and **k** were produced against humans and dogs respectively (Table 2.2, Figure 2.2 j and k) but would entail threatening posture like pointing behaviour, hand slap etc. Calls **m** and **n** were only produced against humans and dogs (Table 2.2, Figure 2.2 m and n).

Table 2.2: Different types of calls produced by NLoTM in different behavioural context showing mean ± std of 6 different acoustic parameters based the visual (pitch pattern) and aural inspection.

Unvoiced frames %	**HNR (dB)**	**Band Width (Hz)**	**Dominant Frequency D0 (Hz)**	**Fundamental frequency F0 (Hz)**	**Call/note duration (s)**	**No. of calls (n)**	**Probable Behavioural context**	**Call Type**	**I D**
8.42 ± 13.30	9.49 ± 2.21	1106.14 ± 365.3	2540 ± 274.6	1389 ± 119.3	0.37 ± 0.05	06	Mother not around	Distress	**a**
5.35 ± 6.18	9.27 ± 5.35	226.34 ± 89.55	4024.15 ± 2150.98	963.07 ± 94.85	0.38 ± .12	13	Mother not around	Distress	**b**
-	-	-	6455.63 ± 1502.29	-	0.45 ± 0.24	8	Mother not around	Distress	**c**
9.50 ± 7.81	8.05 ± 2.36	5098.88 ± 1793.34	7202.04 ± 1523.78	6108.79±1564.88	0.30 ± 0.09	28	Mother not around	Distress	**d**
3.75 ± 4.21	10.93 ± 3.45	4762.47 ± 1586.19	9464.07 ± 1763.50	7117.71 ± 1701.5	0.74 ± 0.31	26	Mother not around	Distress	**e**
-	-	-	5076 ± 1174.27	-	0.79 ± 0.17	6	While foraging	Contact	**f**
-	-	-	5163.98 ± 2471.48	-	0.56 ± 0.64	29	While foraging	Contact	**g**
-	-	-	3403.95 ± 1119.47	-	0.49 ± 0.13	22	Group not around	Contact	**h**
-	-	-	1429.09 ± 316.66	-	0.52 ± 0.11	17	Chaos	Group Integration	**I**
-	-	-	3430.19 ± 753.49	-	0.29 ± 0.13	47	Human, Intra & Inter-group conflicts	Threat	**j**
-	-	-	3519.69 ± 385.16	-	0.30 ± 0.09	28	For Dog, Intra & Inter-group conflicts	Threat	**k**
-	-	-	3694.30 ± 999.10	-	0.25 ± 0.05	16	In Intra & Inter-group conflicts	Threat	**l**
-	-	-	3186.99 ± 935.04	-	0.32 ± 0.11	13	For Human & Dog	Alarm	**m**
12.33 ± 9.61	8.13 ± 3.73	643.88 ± 296.12	3965.81 ± 465.53	1905.46 ± 393.12	0.18 ± 0.03	21	For Human & Dog	Alarm	**n**

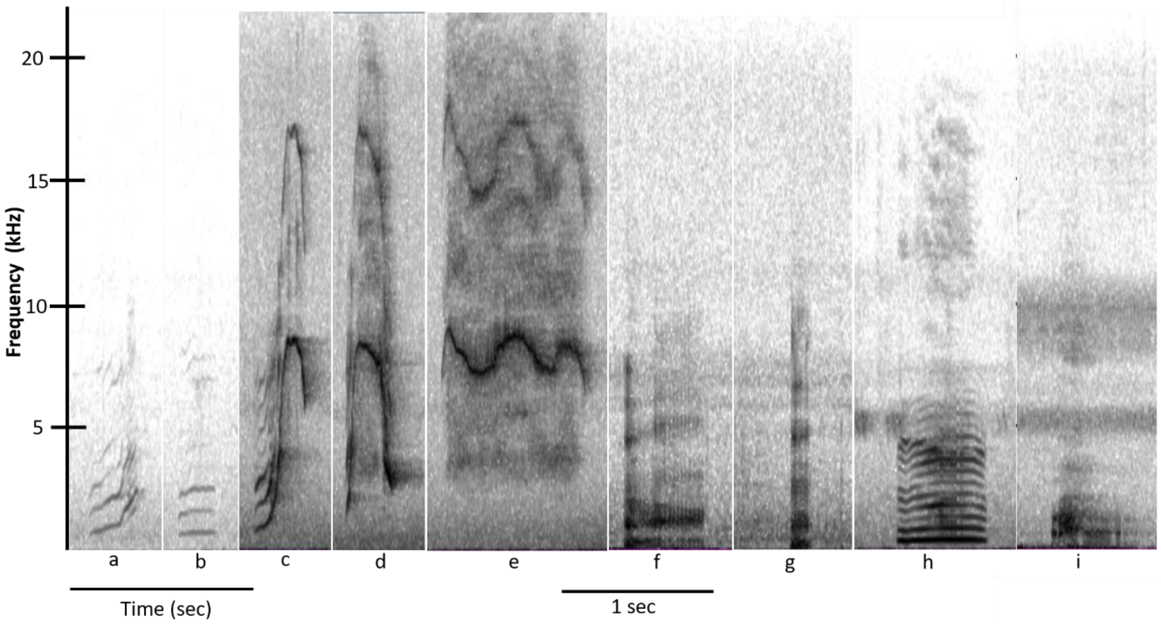


Figure 2.1: Spectrogram of 9 types of affiliative calls. Calls a,b,c,d and e are distress calls produced by infants. Calls f, g and h are contact calls produced by individuals of all age/sex class. Call i is an integration call, only produced by the alpha male of the group.

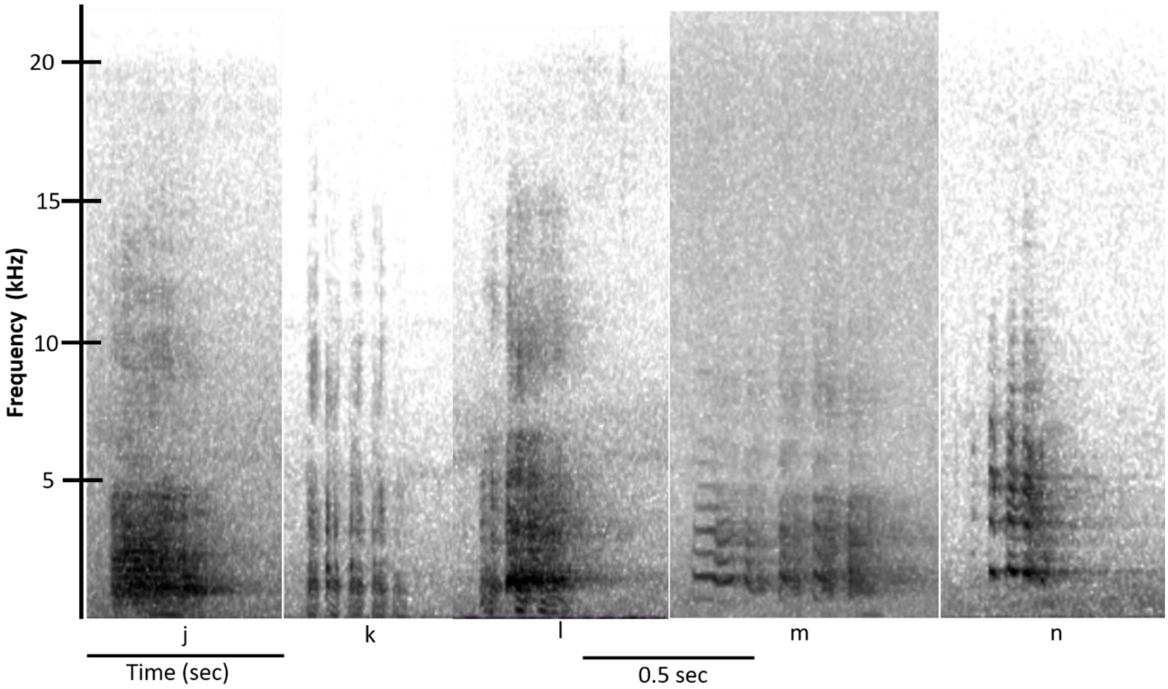
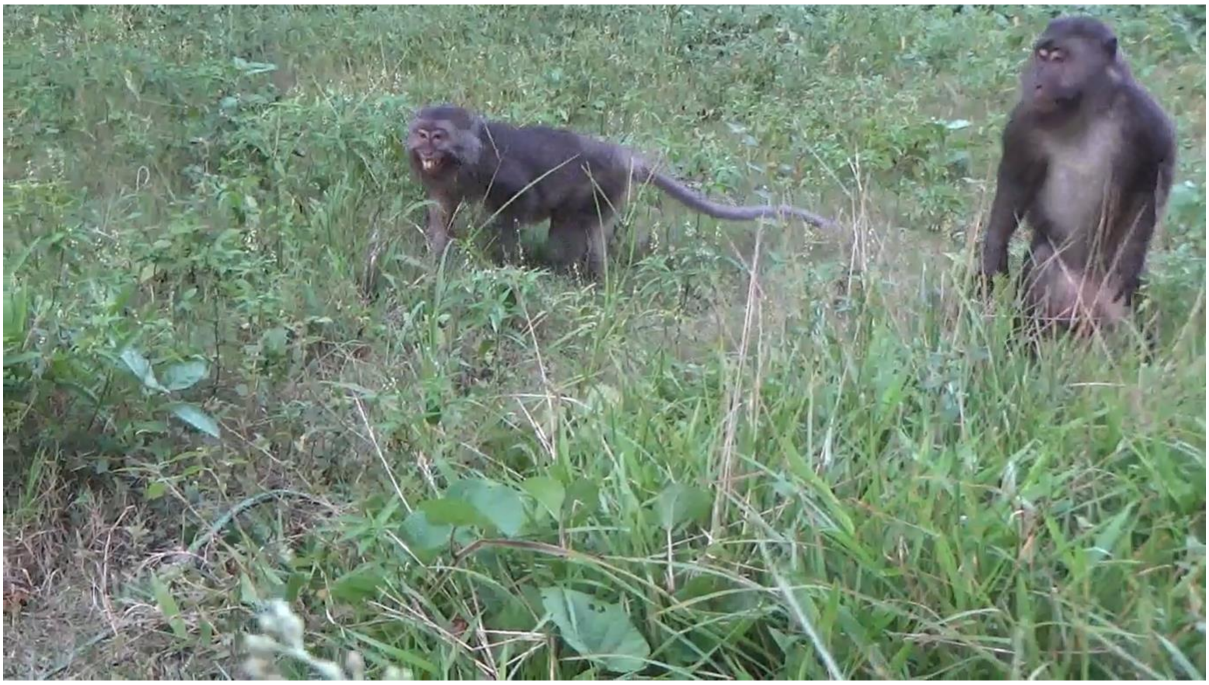


Figure 2.2: Spectrogram of 5 types of agonistic calls. Calls j, k and l are threat calls produce by individuals from all age/sex class. Calls m and n are alarm calls produced by individuals from all age/sex class against humans and dogs.

CHAPTER 3

TO QUANTIFY AND COMPARE THE VISUAL ANTI-PREDATOR RESPONSE OF NLoTM AGAINST SNAKE THREATS, IN ORDER TO EXAMINE THE SNAKE DISTINGUISHING CAPACITY OF NLoTM.



Picture Credit – Sayantan Das

3.1 INTRODUCTION

Preliminary observations showed that Nicobar long-tailed macaques have a particularly distinguishing behaviour in a situation entailing threat. Dogs are one of the major threats for Nicobar long-tailed macaques (Umapathy et al. 2003) and they show behaviour associated to high vigilance and stress (for example: frequent and loud vocalisations, tail up-posture etc) in their presence. A somewhat similar behaviour was also observed when these macaques interacted with snakes. As, one of the major focuses of the study was to investigate whether NLoTM distinguishes between snakes and studies have also shown that among other ways of communication, visual and acoustic methods prevail in the animal kingdom (Rosenthal et al., 2000) it became essential to study the non-vocal/gestural anti-predatory behaviour alongside vocal behaviour in the same context. For the same, following was done a) differences, if any, in approach of monkeys towards familiar venomous, non-venomous and predatory snake model b) compare physical indicators of, stress and vigilance due to snake exposure. An ethogram (catalogue of behaviours) of the associated behaviour (Table 3.1) was made and differences among them across snake types were investigated.

Table 3.1: Behavioural ethogram of the focal variables extracted from the videos.

Variable	Behaviour	Definition
Approach	Flight Response (FR)	Flight response is the presence of a backward motion as a first response shown by the primary detector. Here, the primary detector is the one who detects the snake model for the first time in a trial. Recording flight response inevitably entails recording it just for the primary detector hence ideally the variable should be recorded just once per trial, except for the cases where a single trial has multiple primary detectors.
	Closest Proximity (CP)	It is the minimum distance attained by an individual monkey while interacting with the snake model.
	Passing Distance (PD)	Assuming the snake model to be a straight line, we marked the centre of the snake. Then, we extended an imaginary line perpendicular to the snake model indefinitely. The, passing distance would be the distance at which a monkey crosses this line while passing the snake model.

Stress	Fear grimace (FG)	It is defined as the showing of teeth. This is usually directed towards the threat (Mineka et al. 1980).
	Self-scratching (SS)	Whenever an individual monkey scratched itself, we noted that as an individual event of self- scratching.
Vigilance	Bipedal Standing (BS)	An individual monkey was marked as bipedal when it was standing on its two hind limbs.
	Gaze percentage (GP)	It is defined as the proportion of time spent looking at the snake model while staying within the pre-defined circle to the total time spent inside the circle, post-detection.

3.2 METHODOLOGY

3.2.1 Control

To validate our snake models, we a) presented dead specimens of Cantor's pit viper and b) recorded at least one naturalistic snake - monkey interaction for each snake type. Testing the similarity between the anti-predatory response shown to the dead, live Cantor's pit viper and the model snakes would show how the models were actually perceived by the monkeys.

3.2.2 Data collection

We recorded digital videos of the individuals participating in the interaction, using a Nikon Coolpix B500 (16 MP, 40X optical zoom and 4X digital zoom). We performed 9 trials with Cantor's pit viper model and 4 trial each with Painted Bronze-back and Python model. Recording for each trial started whenever any individuals from the focal group came within 5 meters to the snake model. We allowed monkeys to interact with the model as long as they continued. The trial ended when the last individual ended its interaction with the model. The same was decided once the last interacting individual/s moved about 10 meters from the snake model. After this, a cloth was used to cover the model first, followed by removing it from its location.

3.2.3 Data Analysis

Since the identity of all the individuals from the focal group was known and multiple angles for all of the interactions were available, all the gestural behaviours were scored manually on Microsoft Excel ‘2019’ (Table 3.1). Any variable which entails recording time period was done using a stopwatch alongside calculating the number of frames.

3.2.4 Statistical Analysis

All tests were performed using scipy library (Virtanen et al., 2020) in python (Van et al., 2011) programming language. One sample Kolmogorov-Smirnov test was employed to check for the normality of the data set. Since this test assumes the raw data to be standardised, the data was first standardised manually before running the test. For the same all values were subtracted from their respective mean and were divided by their standard deviation. As many of the variables were not following a normal distribution, non-parametric, two tailed Mann – Whitney U test, was employed to check the validity of our hypothesis. The confidence level for significance was 95%.

3.3 RESULTS

3.3.1 TEST THE VALIDITY OF SNAKE MODELS: **LIVE VS MODEL PIT VIPER**

The passing distance was not found to be statistically different for live pit viper (mean ± std. = 145.16 ± 8.95 cm) and for model pit viper (mean = 121.91 ± 86.44 cm) (Figure 3.1, U =103.50, p =0.24). Frequency of fear grimace shown to live pit viper (1.50 ± 1.51) was significantly higher than that shown to model pit viper (0.05 ± 0.09) (Figure 3.2, U=70.00, p=0.02). Frequency of self-scratching shown to live pit viper (0.33 ± 0.51) and to the model pit viper (0.02 ± 0.04) were not different (Figure 3.3, U=67.00, p=0.64). The frequency of bi-pedal standing shown to live pit viper (0.83 ± 0.75) was significantly higher than that to model pit viper (0.02 ± 0.05) (Figure 3.4, U=67.00, p=0.01). Finally, the gaze percentage for live pit viper (69.09 ± 17.96 sec) was significantly higher than that to model pit viper (42.89 ± 18.24 sec) (Figure 3.5, U=52.00, p=0.01).

Here, Number of responding individuals (N): Live Pit Viper = 07; Model Pit Viper = 49.

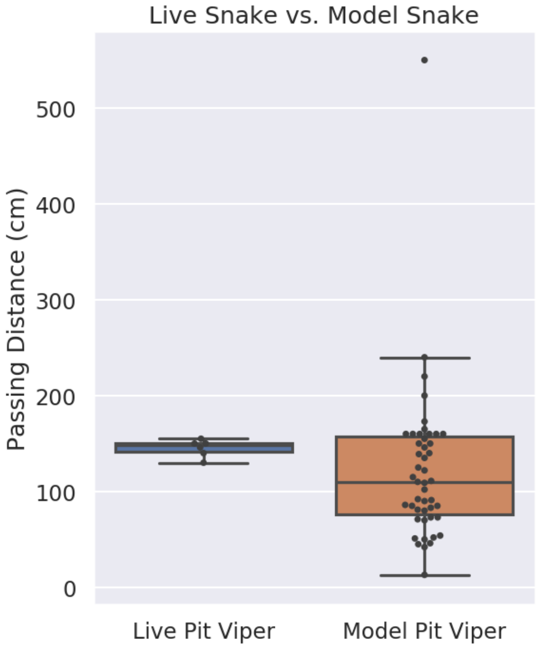


Figure 3.1: Distance maintained by monkeys while passing a model snake and a live snake.

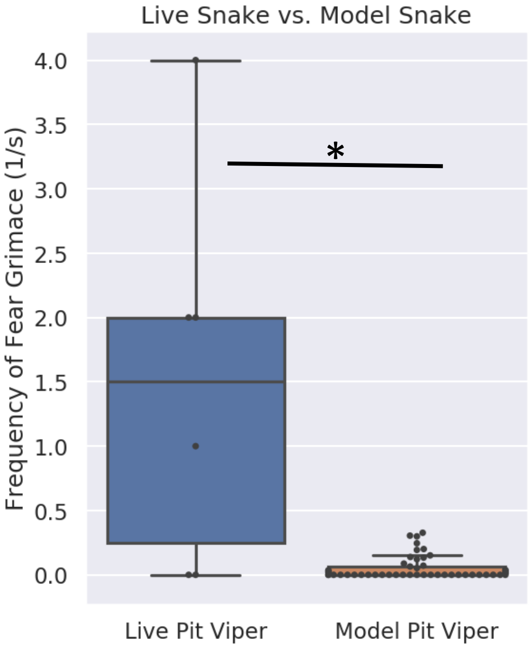


Figure 3.2: Frequency of fear grimace shown towards live and model Pit Viper. * indicates significant differences (p<0.05).

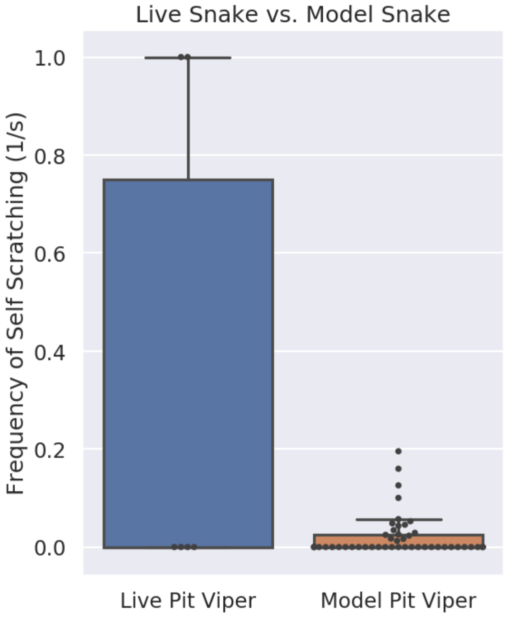


Figure 3.3: Frequency of self-scratching shown towards live and model pit viper.

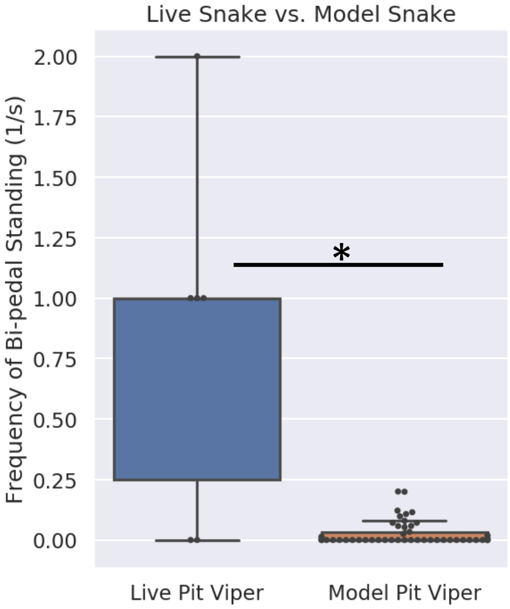


Figure 3.4: Frequency of bi-pedal standing for live and model pit viper. * indicates significant differences (p<0.05)

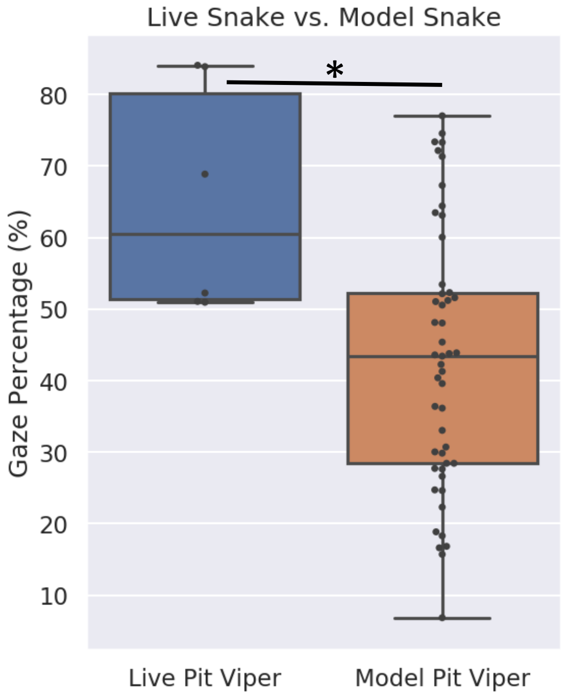


Figure 3.5: Gaze percentage for live and model pit viper.

***** indicates significant differences ($p<0.05$).

3.5.2 TEST THE VALIDITY OF SNAKE MODELS: **DEAD VS MODEL PIT VIPER**

The closest proximity maintained for the dead viper's specimen (38.00 ± 27.49 cm) and model viper (60.42 ± 81.09 cm) was not found to be significantly different (Figure 3.6, U=172.50, p = 0.49). Passing distance was significantly smaller for dead pit viper's specimen (mean = 58.83 ± 30.61 cm) than for model pit viper (mean = 121.91 ± 86.44 cm). (Figure 3.7, U=245.50, p <0.05). Frequency of fear grimace shown to dead pit viper's specimen (2.33 ± 1.75) was higher than that shown to model pit viper (0.05 ± 0.09) (Figure 3.8, U=35.50, p < 0.05) Frequency of self-scratching shown to dead pit viper's specimen (1.16 ± 1.83) and to model pit viper (0.02 ± 0.04) was not found to be significantly different (Figure 3.9, U=132.00, p=0.64). The frequency of bi-pedal standing shown to dead pit viper's specimen (0.33 ± 0.51) was significantly higher than that to model pit viper (0.02 ± 0.05) (Figure 3.10, U=167.50, p=0.52). The gaze percentage for model pit viper (42.89 ± 18.24 sec) was not significantly different that to the dead specimen (31.25 ± 11.34 sec) (Figure 3.11, U=194.00, p=0.20).

Number of responding individuals (N): Dead Pit Viper = 06; Model Pit Viper = 49.

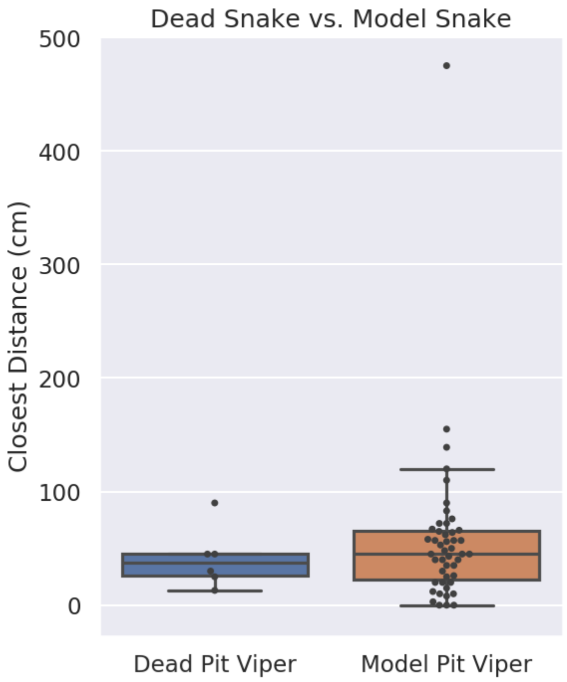


Figure 3.6: Closest distance (cm) maintained by monkeys from live and model pit viper.

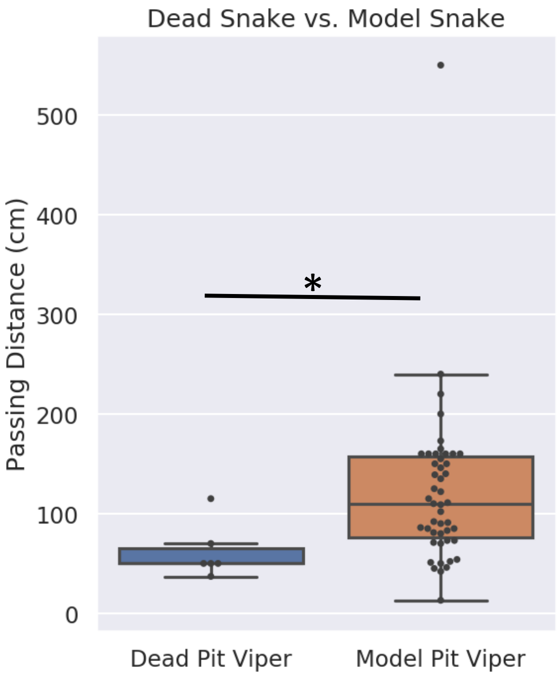


Figure 3.7: Distance maintained while passing a model snake and a dead snake.

* indicate significant difference (p<0.05)

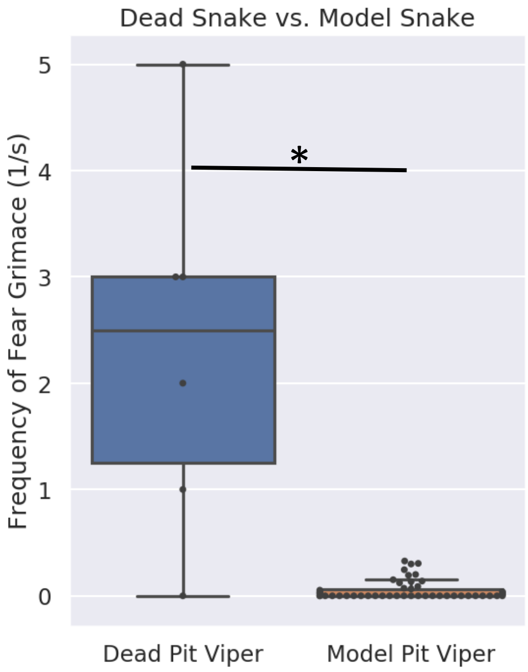


Figure 3.8: Frequency of fear grimace shown towards dead and model pit viper.

* indicate significant difference (p<0.05)

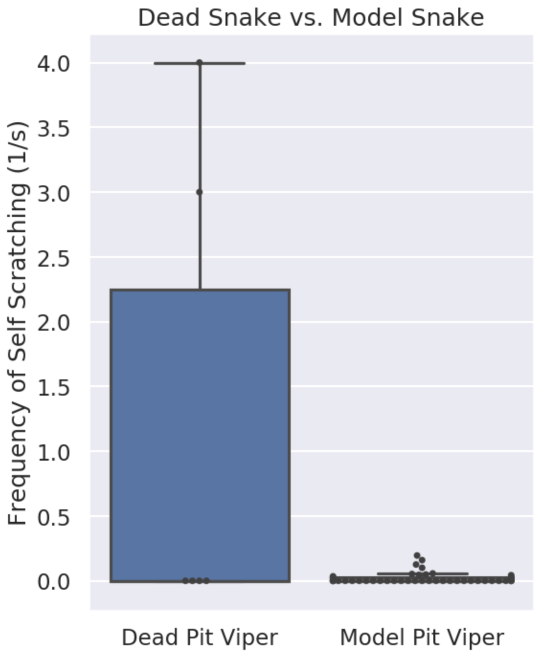


Figure 3.9: Frequency of self-scratching shown towards dead and model pit viper.

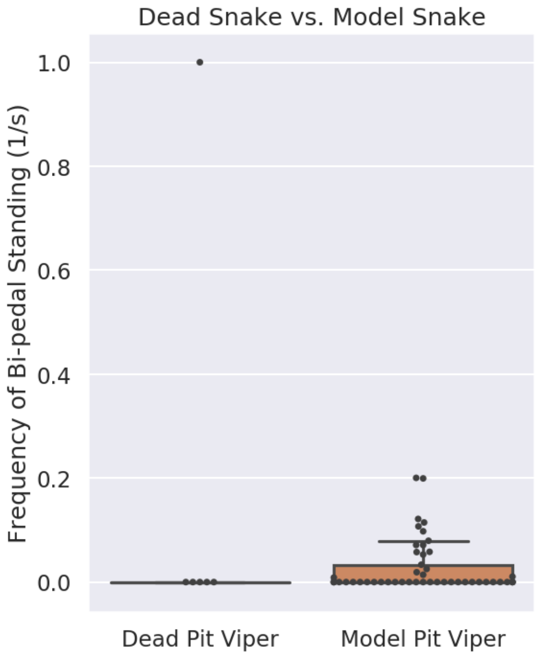


Figure 3.10: Frequency of bi-pedal standing shown towards dead and model pit viper.

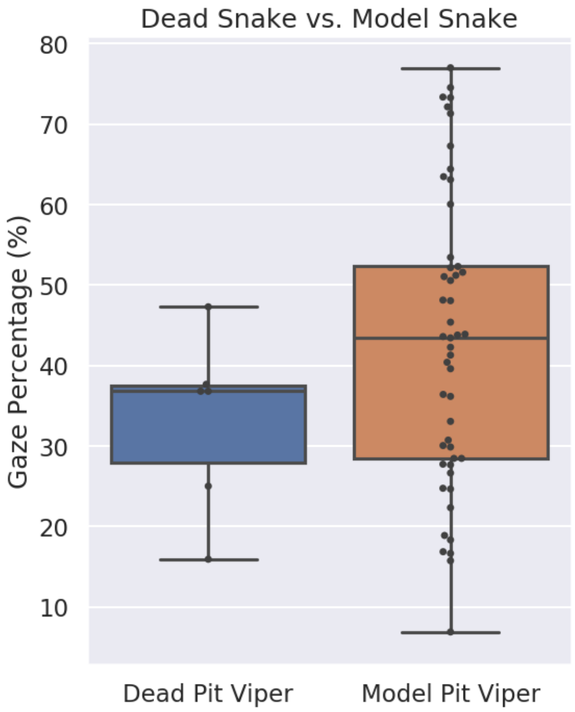


Figure 3.11: Gaze percentage shown towards dead and model pit viper.

3.5.3 TEST OF HYPOTHESIS: **SNAKE MODELS**

It was investigated whether the flight response, depended on the type of snake or on the distance of detection. Here, the distance of detection is defined as the distance at which snake models are detected by the primary detector. There was no flight response observed for the Python model at all. The percentage of flight response was significantly higher for Pit viper (66.66%) than for Bronze-back (33.33%) (Figure 3.12). The individuals detecting the snake model within 0.7 meter (12 out of 26) were much more likely to show a flight response, regardless of the snake type, than those who detect the same beyond that (14 out of 26) (Figure 3.13, U=60.49, p=7.78 X e^{-15}). The closest proximity maintained across snake models differed significantly for Bronzeback (74.50 ± 42.89 cm) – Python (100.25 ± 59.48 cm) (Figure 3.14, p=0.01, U=194.00) and for Python - Pit Viper (60.42 ± 81.09 cm) (Figure 3.14, p=0.0001, U=906.00). There was no significant difference for proximity between Bronzeback - Pit Viper (Figure 3.14, p=0.21, U=777.00, appendix 3A, N for Bronze-back= 27; Python = 24 and for Pit Viper = 47). The passing distance was significantly different across all snake types (U, p<0.05). Average distance maintained while passing the snake model was maximum for Python (159.85 ± 50.02

cm) followed by Pit viper (121.91 ± 86.44 cm) and bronze-back (91.88 ± 38.42 cm) ($p<0.05$; appendix 3B, N for Bronze-back= 27; Python = 24 and for Pit Viper = 47). The frequency of fear grimace was not found to be significantly different across all snake classes ($p>0.05$; appendix 3C, N for Bronze-back = 27; Python = 24 and for Pit Viper = 49). The frequency of self-scratching was found to be significantly different for Bonzeback (0.007 ± 0.01) – Python (0.02 ± 0.02) (Figure3.17**,** p=0.0002, U=145.00) and for Python - Pit viper (0.02 ± 0.04) (Figure 3.17, p=0.02, U=767.00), whereas, it was not significantly different for Brozeback - Pit viper (Figure 3.17, p=16, U=556, appendix 3D; N for Bronze-back = 27; Python = 24 and for Pit Viper = 49). The frequency of bipedal standing was found to be significantly different for Bronzeback (0) – Python (0.01 ± 0.01) (Figure 3.18, $p=6.06 \times 10^{-06}$, U=135.00) and for Bronzeback (0) - Pit viper (0.02 ± 0.05) (Figure 3.18, p=0.0004, U=418.50). It was not significantly different for Python - Pit viper (Figure 3.18, p=0.68, U=620.00, appendix 3E; N for Bronze-back = 27; Python = 24 and for Pit Viper = 49). The gaze percentage was significantly different across all snake models (Figure 3.19, $p < 0.05$; appendix 3F, N for Bronze-back = 27; Python = 24 and for Pit Viper = 49). The same was maximum for Python followed by Pit viper and by Bronze-back.

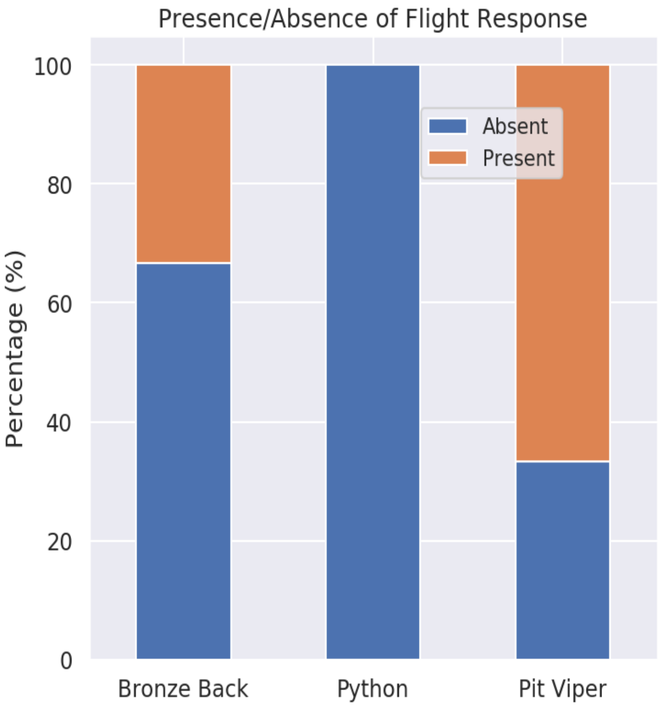


Figure 3.12: Percentage cases of flight response shown by monkeys for Bronze-back, Python and Pit Viper.

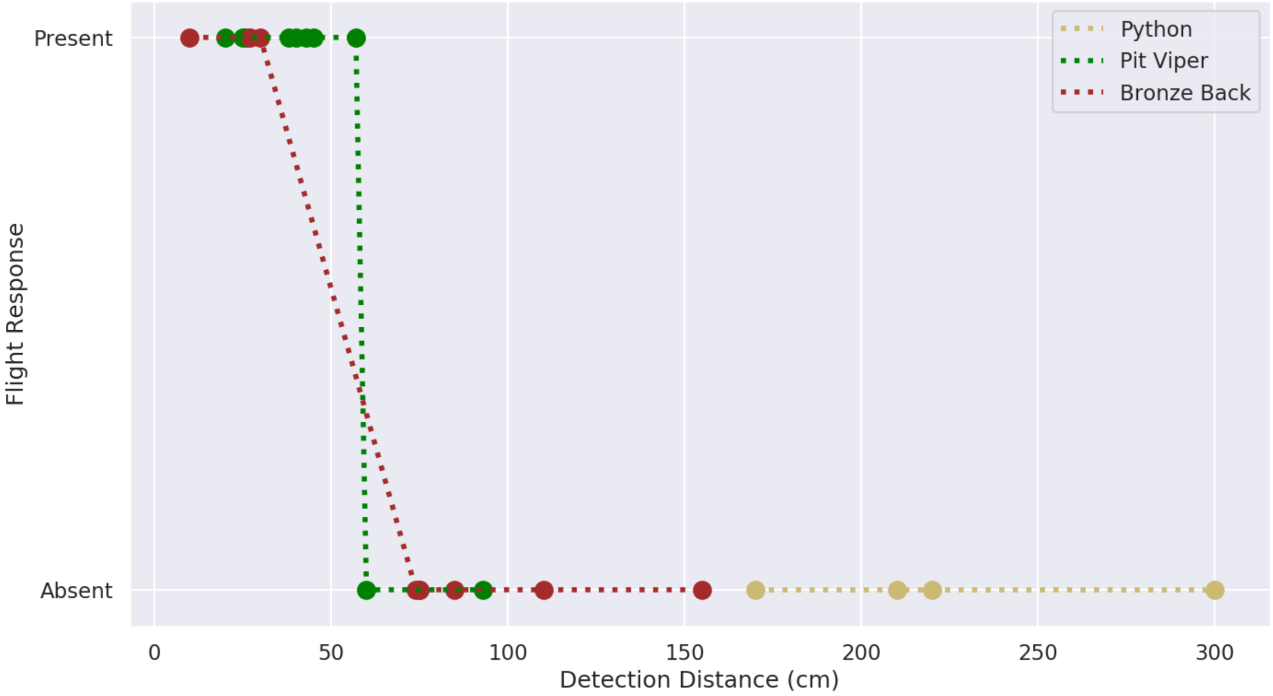


Figure 3.13: Presence/Absence of flight response by monkeys for Bronze-back, Python and Pit Viper. The individual dots represent the unit response i.e. either presence or absence of FR from individual monkeys.

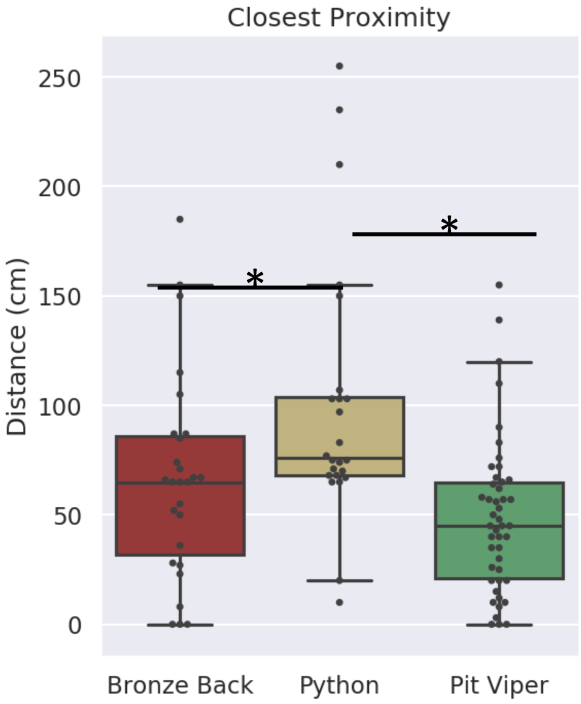


Figure 3.14: Closest proximity maintained towards Bronze-back, Python and Pit Viper. *indicates the significant difference ($p<0.05$).

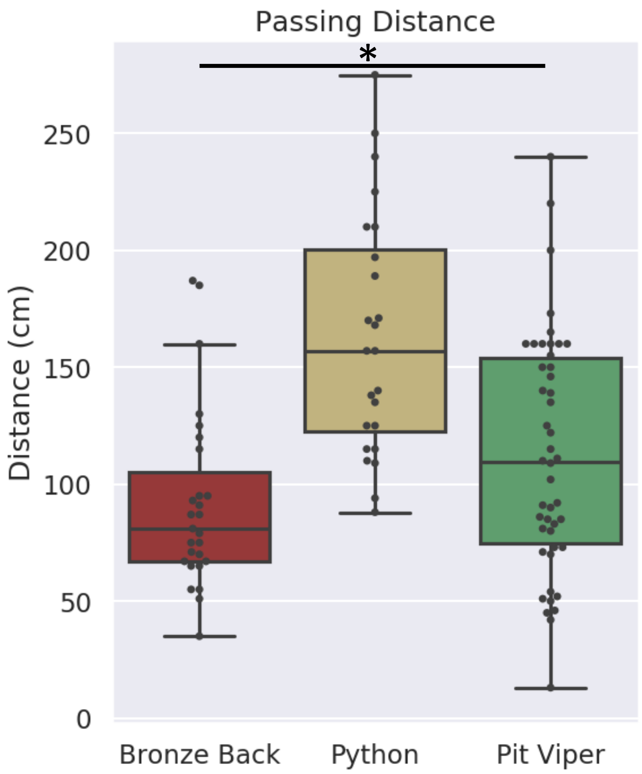


Figure 3.15: Distance maintained while crossing the aforementioned snake models. * indicates the significant difference ($p<0.05$).

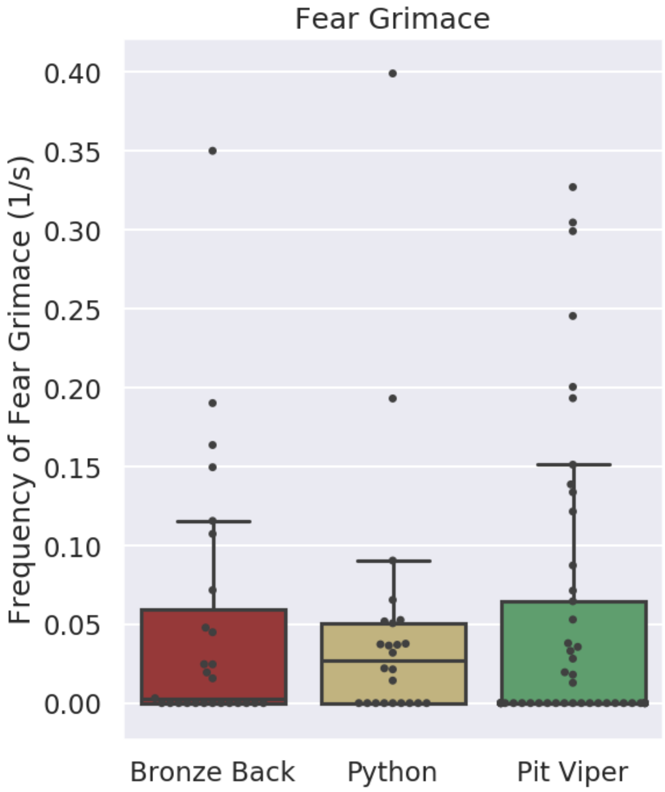


Figure 3.16: Frequency of fear grimace for Bronze-back, Python and Pit Viper model.

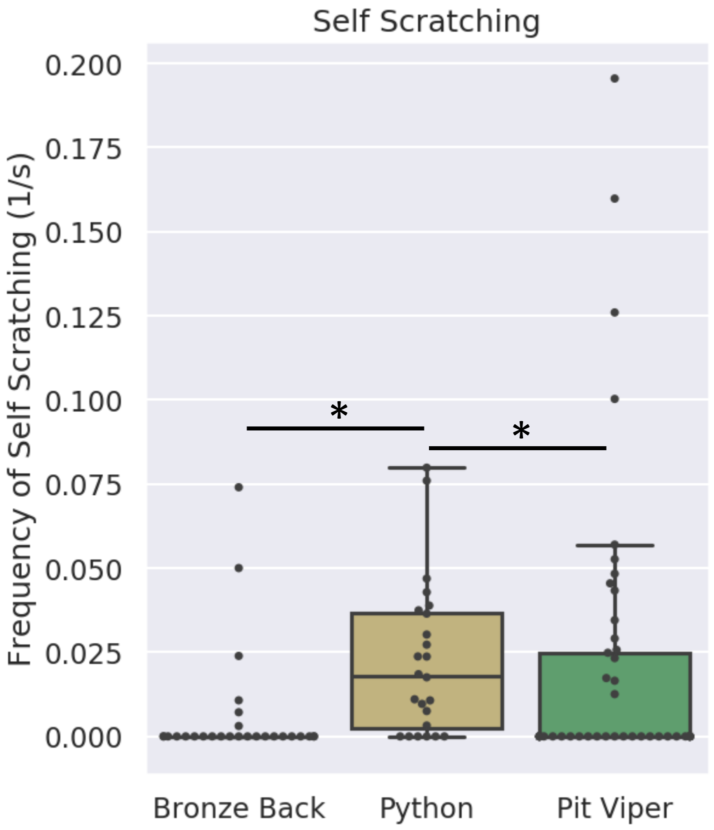


Figure 3.17: Frequency of Self-Scratching for Bronze-back, Python and Pit Viper model.

* indicates significant differences ($p<0.05$).

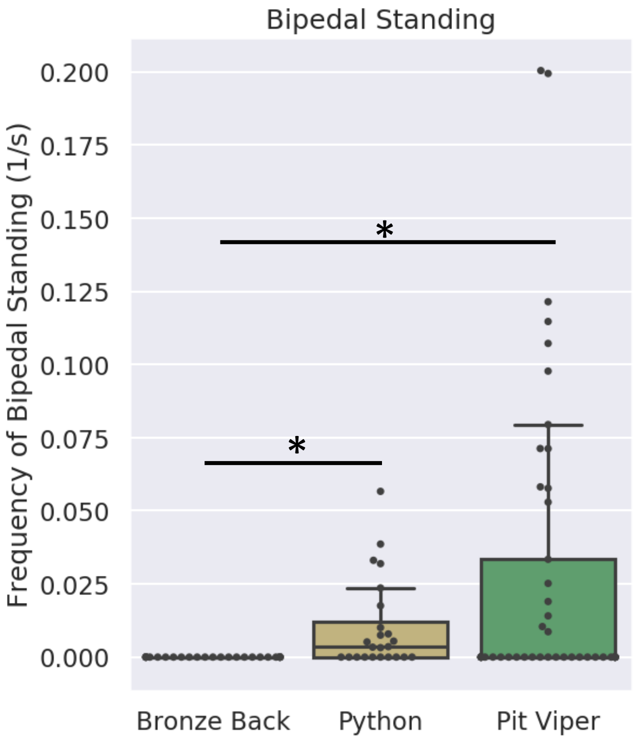


Figure 3.18: Frequency of Bipedal standing for Bronze-back, Python and Pit Viper model.

* indicates significant differences ($p<0.05$).

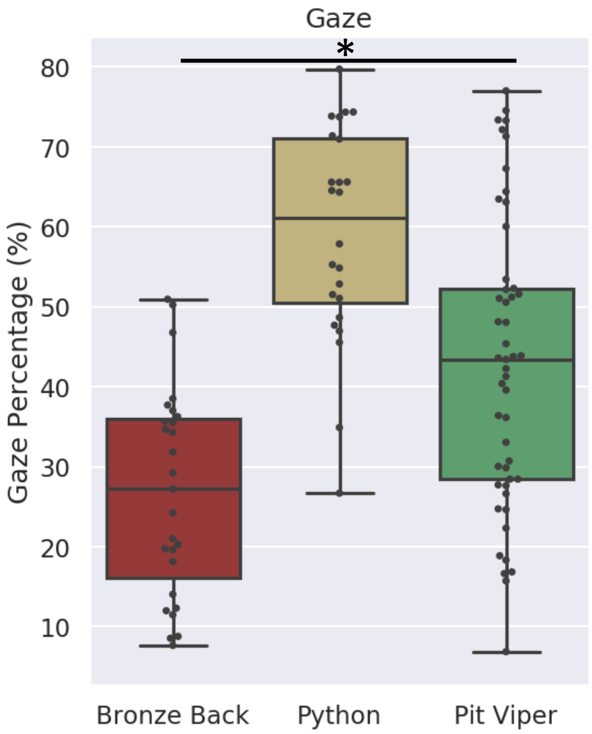


Figure 3.19: Gaze percentage for Bronze-back, Python and Pit Viper model.

***** indicates significant differences ($p<0.05$).

CHAPTER 4

TO PERFORM ACOUSTIC CHARACTERIZATION AND EXAMINE THE DIFFERENCES (IF ANY) BETWEEN THE ANTI-PREDATORY VOCALISATIONS OF NLoTM IN RESPONSE TO SNAKE THREATS

Picture Credit – Sayantan Das

4.1 INTRODUCTION

An anti-predatory response might entail a suitable evolutionarily acquired behaviour shown by the prey species against the predator species. Such a response, in general, should then be threat specific. Studies have shown that primates, in particular, can produce certain type of alarm vocalisations for specific types of predators, thereby, eliciting pertinent response from its respective receivers (Seyfarth et al., 1980; Crockford et al., 2003; Stephan et al., 2008). Preliminary field observations of NLoTM also support the hypothesis that an anti-predator response can be threat specific as in, the type of anti-predatory response shown toward a dog does not appear to be identical to an anti-predatory response for a snake. As mentioned earlier dogs pose one of the major threats to NLoTM (Umapathy et al. 2003) and hence, in response, NLoTM show intense anti-predatory behaviour against them. This entails emission of behaviour associated to stress and vigilance like frequent, loud calling and climbing trees etc. But, an anti-predatory response for a snake can be different in the sense that given the nature of the threat type, keeping track of the location of the snake and emitting the same information frequently should suffice. Therefore, one may expect monkeys to invest more on the calling behaviour for threats like snakes. As mentioned above, snakes appear to be a strong stimulus for causing fear (Isbell 2006; 2009) and calling behaviour appears to be a key aspect in its response, therefore, one may except to observe a difference in call types for different types of snakes. Hence, this study investigates whether NLoTM produce different/specific types of anti-predatory vocalisations for snakes belonging to the aforementioned classes. The main objective for the same is to check for difference, if any, among the anti-predatory calls produced against aforementioned snake models.

4.2 METHODOLOGY

4.2.1 Data Collection

The movement pattern of the focal group was anticipated and snake models were kept in place such that monkeys encounter them while moving. Once an individual had detected the snake model, focal behavioural sampling technique was followed to collect the anti-predatory vocalisation data. Vocalisations were recorded using a solid-state audio recorder (Marantz PMD661*MKII* frequency response: 20 Hz - 20 kHz) with a Sennheiser shotgun microphone (Sennheiser ME66 with K6 PM; frequency response: 40 Hz to 20 kHz) intertwined with wind shield (Sennheiser MZW66) for recording the vocalisations. The sampling rate of the recorder was kept at 44.1 kHz with 16-bit accuracy. All audio files were saved in .wav format. The total number of trials done using cantor's pit viper model were nine and four each with bronze-back and python model. This made a cumulative of seventeen trials of snake model presentation with a gap ranging between 5-15 days between subsequent trials (Coss et al.2004). Analysis of only those vocalisations are done which are produced by either the adults (>7 years) or sub-adults (5-7 years).

4.2.2 Data Analysis

All the audio recordings were analysed in Raven pro 1.4 (Cornell lab of ornithology, USA) and PRAAT (Boersma and Paul, 2017) for analysis of different spectral and temporal parameters of the calls. The parameters that were employed for the quantification and comparative analysis of the calls were number of notes, call duration (CD), fundamental frequency(F0), dominant frequency(D0) and band width of fundamental frequency (BW). To quantify frequency modulation, a score of band width of F0 (BW)/ call duration (CD) was used (Palombit, 1991). Harmonics to noise ratio (HNR) and percentage of unvoiced frames were also calculated using PRAAT, to quantify the quality of sound recordings (Christian et al., 2018). All of the variables are defined in Table 2.1 above.

4.2.3 Statistical Analysis

All tests were performed using scipy library (Virtanen et al., 2020) in python (Van et al., 2011) programming language. Shapiro -Wilk test was employed to check for the normality of the data set. The p values for many of the variables of interest were found to be < 0.05 (Appendix 4L). As many of the variables did not follow a normal distribution, Kruskal – Wallis ANOVA was performed followed by non-parametric, post-hoc test i.e. Mann – Whitney U test to check the validity of our hypothesis. The confidence level for significance was 95%.

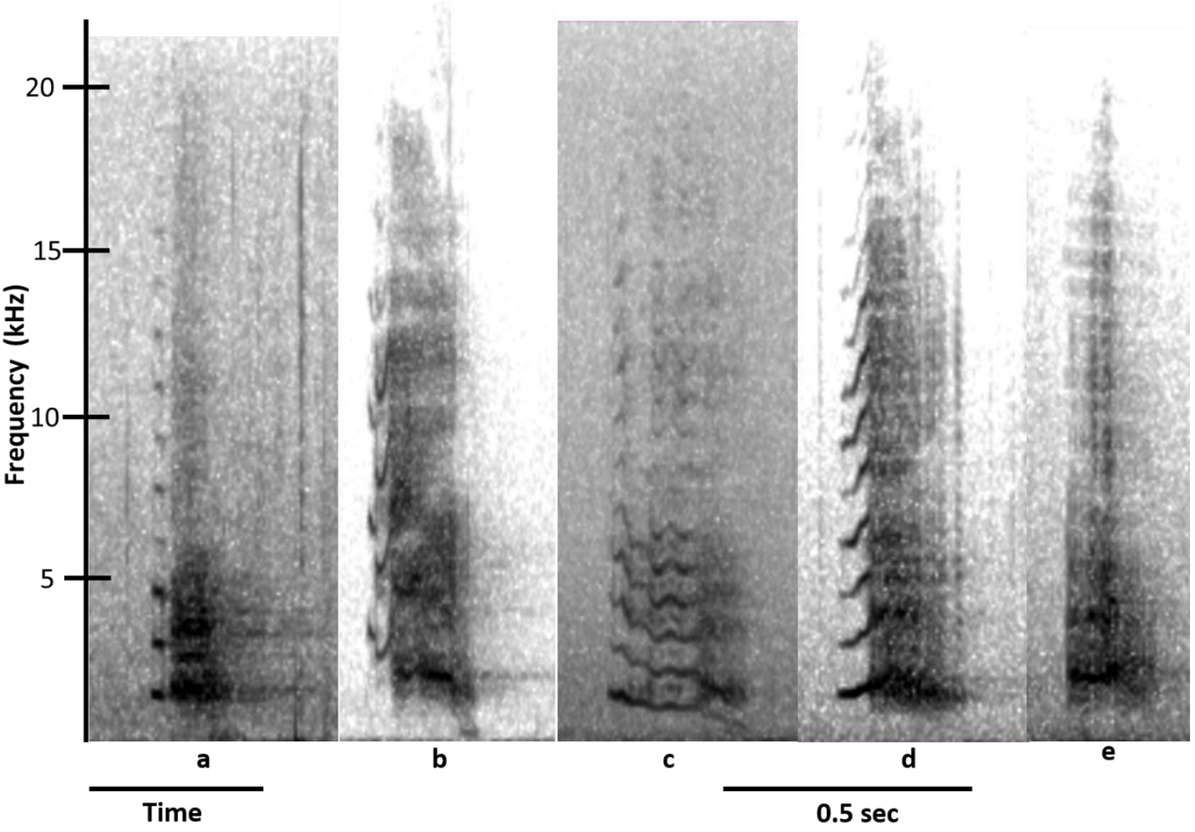
4.3 RESULTS

Based on the visual (pitch pattern) and aural inspection of the calls, 18 different types of anti-predatory calls were obtained which were produced by the NLoTM against above-mentioned snake models (Figure 4.1). From the aforementioned 18 calls **four calls** were found to be statistically different by at-least one parameter (K-W ANOVA, Mann-Whitney U test, $p<0.05$). These four calls were 1) **III** 2) **IV** 3) **VI-BB** and 4) **IX** (Figure 4.10, 4.11, 4.12 and 4.13

respectively). Also, the Nicobar long-tailed macaques produced call VI-BB (39.47 %) for the maximum number of times while vocalising against bronze-back model whereas call IV (26.74 %) was produced for the maximum number of times while vocalising against python model. Lastly, the power spectrum of call **III, IV, VI-BB** and **IX** are shown in Figure 4.10, 4.11,4.12 and 4.13 respectively. None of the call has clear harmonics.

Table 4.1: Different anti-predatory call types visual (pitch pattern) and aural inspection produced by NLoTM for aforementioned snake models (mean and std of 7 acoustic parameters). * represents the calls that are significantly different by at-least one parameter. N denotes number of different respondents (true replicates).

Unvoiced frames %	**HNR (dB)**	**Frequency modulation = BW/CD**	**Band Width (Hz)**	**Dominant Frequency D0 (Hz)**	**Fundamental frequency F0 (Hz)**	**Call/note duration (s)**	**No. of notes**	**N**	**No. of calls (n)**	**Alarm call against _____model.**	**ID**
-	-	-	-	4231.36 ± 644.79	-	0.17 ± 0.01	1 ± 0	3	7	Pit Viper	**I**
-	-	-	-	6177.34 ± 584.26	-	0.23 ± 0.01	1 ± 0	1	6	Pit Viper	**II**
-	-	-	-	3697.41 ± 752.58	-	0.26 ± 0.08	1 ± 0	4	16	Python	**III***
-	-	-	-	4031.559 ± 742.63	-	0.23 ± 0.06	1.17 ± 0.57	6	23	Python	**IV***
19.90 ± 12.92	7.84 ± 2.92	2534.06 ± 1712.00	373.11 ± 205.81	5358.53 ± 760.13	1223.11 ± 120.02	0.20 ± 0.15	1.5 ± 0.92	2	8	Bronze-back	**V-BB**
8.43 ± 13.04	12.68 ± 5.76	4747.48 ± 3373.37	281.73 ± 225.51	4238.48 ± 1318.07	1508.72 ± 435.02	0.07 ± 0.05	1.15 ± 0.37	3	13	Pit Viper	**V-CV**
13.75 ± 13.50	17.18 ± 2.86	2831.28 ± 3783.20	337.39 ± 143.92	3756.08 ± 620.44	1602.01 ± 195.91	0.13 ± 0.06	1.4 ± 0.54	4	5	Python	**V-PY (a)**
-	-	-	-	4085.97 ± 542.63	-	0.15 ± 0.05	1.15 ± 0.55	5	13	Python	**V-PY (b)**
11.52 ± 12.04	11.80 ± 4.05	8777.07 ± 3212.81	525.19 ± 196.257	4226.31 ± 525.19	1087.92 ± 187.29	0.06 ± 0.01	1 ± 0	5	15	Bronze-back	**VI-BB***
6.62 ±6.72	14.23 ±3.45	11424.40 ± 4625.27	878.97 ±366.26	3969.32 ± 677.62	1586.50 ± 372.27	0.07 ± 0.02	1.10 ± 0.31	7	28	Pit Viper	**VI-CV**
6.32 ± 5.51	13.31 ± 3.96	7334.13 ± 2814.47	616.20 ± 260.95	3125.053 ± 780.40	1272.33 ± 329.88	0.09 ± 0.05	1 ± 0	5	19	Python	**VI-PY**
7.68 ± 7.70	11.10 ± 2.43	11814.71 ± 8965.31	1099.69 ± 631.75	4681.56 ± 787.76	1245.98 ± 253.43	0.13 ± 0.09	1 ± 0	2	4	Bronze-back	**VII-BB**
3.74 ± 3.39	10.22 ± 2.91	13804.52 ± 4391.69	807.05 ± 322.32	4495.17 ±662.67	1045.40 ± 324.09	0.06 ± 0.02	1 ± 0	3	6	Pit Viper	**VII-CV**
18.00 ± 10.08	11.54 ± 3.76	5728.67 ± 3008.01	576.59 ± 256.05	3373.67 ±524.62	1272.91 ±384.76	0.11 ± 0.03	2.16 ± 0.40	2	6	Pit Viper	**VIII-CV**
11.38 ± 8.30	14.59 ± 4.02	4536.06 ± 1912.38	666.77 ± 239.34	3749.71 ± 625.98	1586 ± 211.77	0.15 ± 0.04	1.83 ± 0.40	3	6	Python	**VIII-PY**
3.84 ±2.46	10.27 ±1.19	5902.01 ± 1471.653564	540.07 ±231.31	4690.31 ± 519.14	1110.80 ±184.15	0.09 ± 0.02	1.20 ± 0.44	2	5	Bronze-back	**IX***
8.10 ±7.95	12.62 ±3.55	9286.06 ± 5081.33	1236.52 ± 659.57	4533.40 ± 867.08	1612.44 ±360.51	0.13 ±0.02	1.4 ±0.89	2	5	Bronze-back	**X**
16.09 ± 5.50	12.79 ± 2.53	6160.02 ± 4191.08	589.30 ± 356.17	3553.56 ± 475.04	1033.98 ± 248.11	0.10 ± 0.02	2 ± 0	4	7	All	**XI**


Frequency (kHz)
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Time
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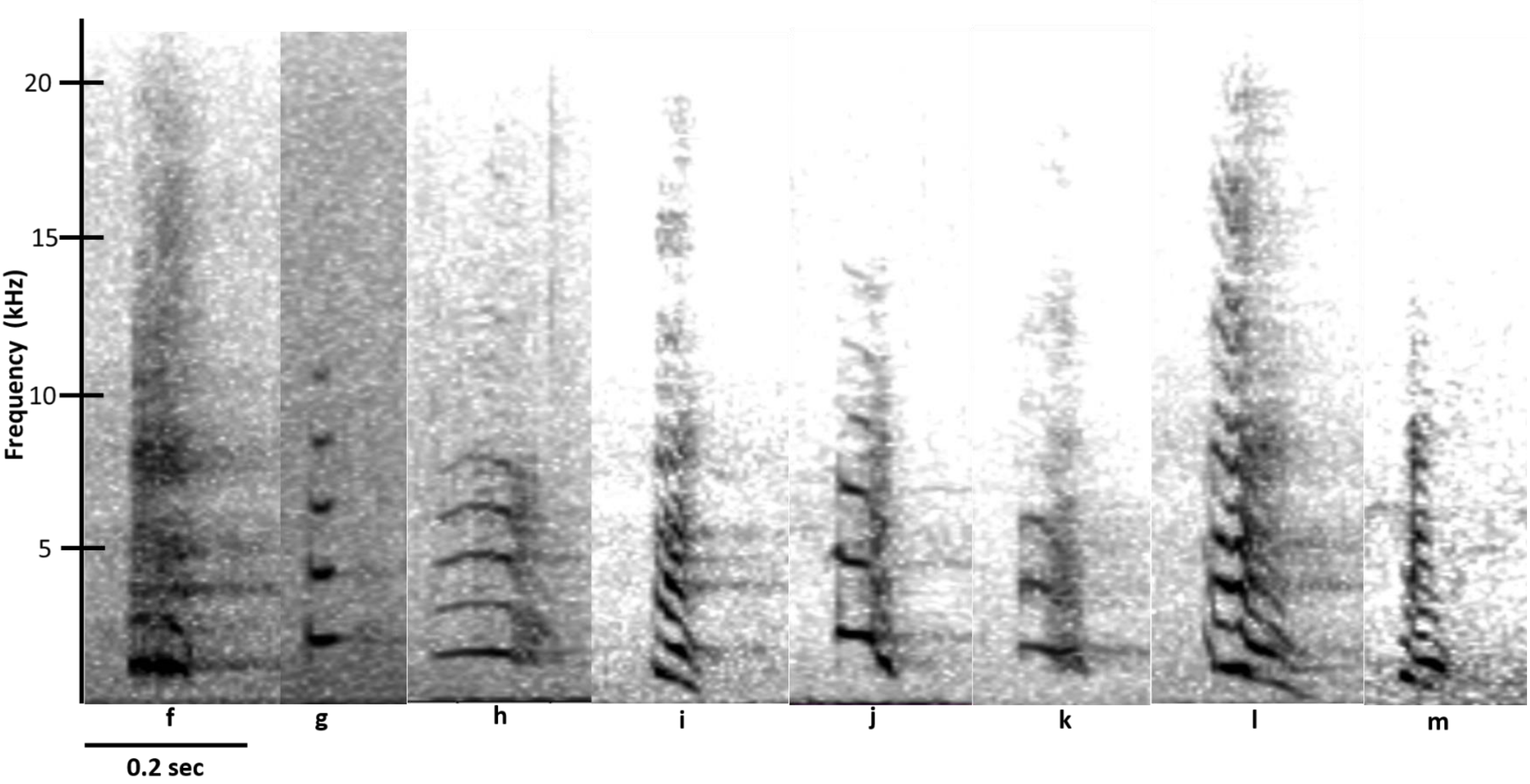
Frequency (kHz)
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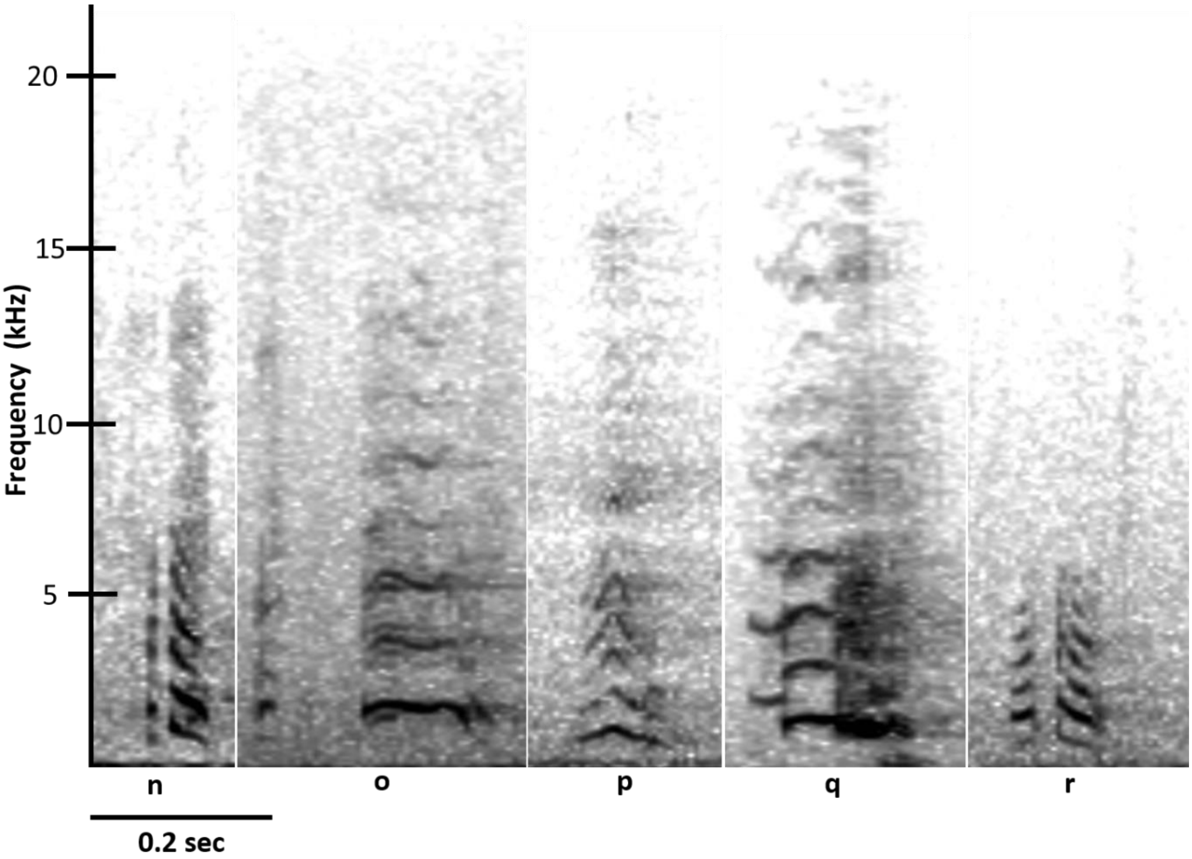

Figure 4.1: Spectrogram of anti-predator vocalisations produced by NLoTM against snake threats based on visual and aural inspection. a - call I, produced against pit-viper model, b - call II, produced against pit-viper model, c - call III, produced against python model, d - call IV, produced against python model, e - call V-PY(b), produced against python model, f - call V-BB, produced against bronze-back model, g - call V-CV, produced against pit-viper model, h - call V-PY(a), produced against python model, i - call VI-BB, produced against bronze-back model, j - call VI-CV, produced against pit-viper model, k - call VI-PY, produced against python model, l - call VII-BB, produced against bronze-back model, m - call VII-CV, produced against pit-viper model, n - call VIII-CV, produced against pit-viper model, o - call VIII-PY, produced against python model, p - call IX, produced against bronze-back model, q - call X, produced against bronze-back model and r – call XI produced against all types of snake models.

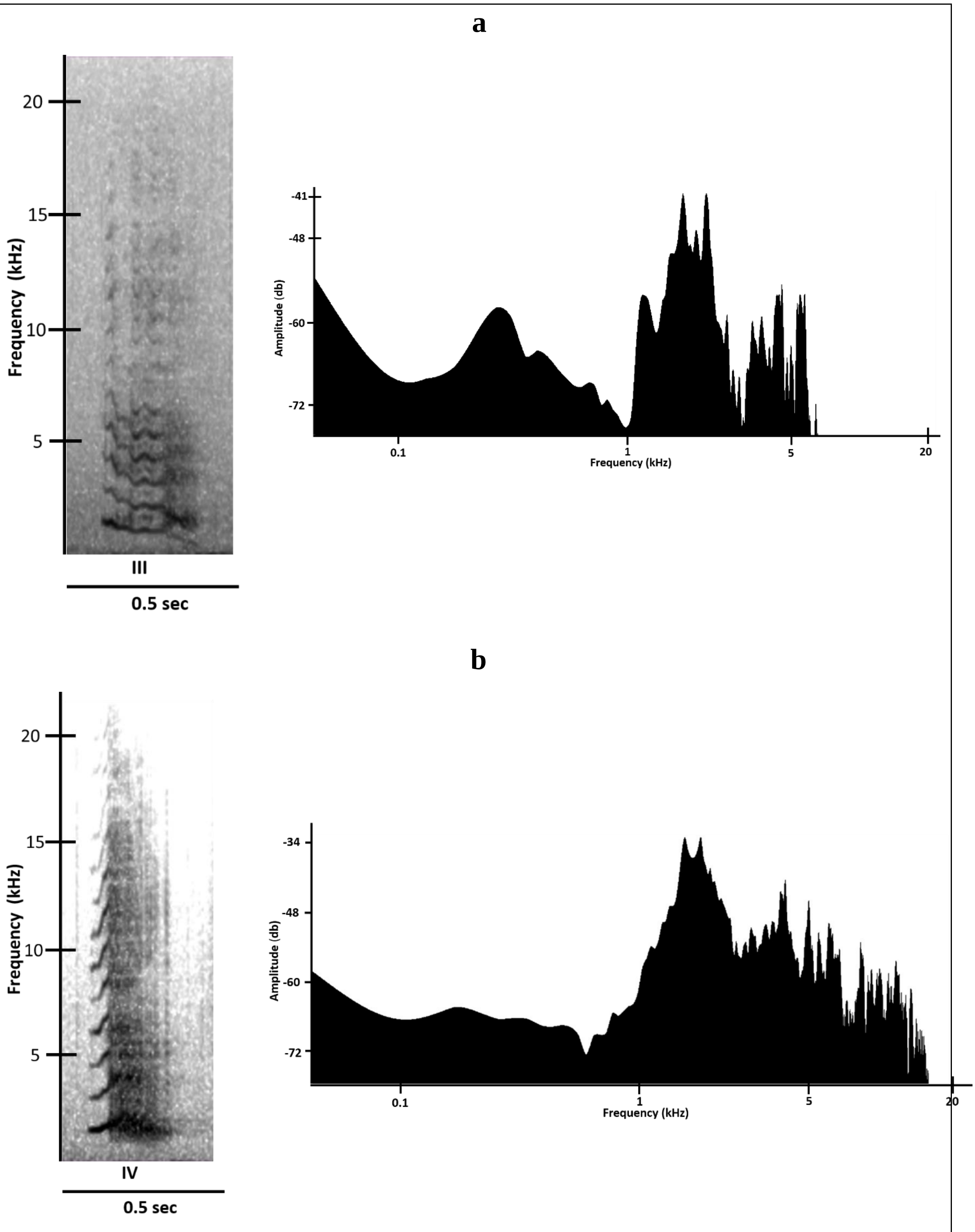

Figure 4.2: Spectrogram (left) and the power spectrum (right) of two calls which were significantly different by at-least one parameter and were produced against python model. a – refers to call III and b – refers to call IV.

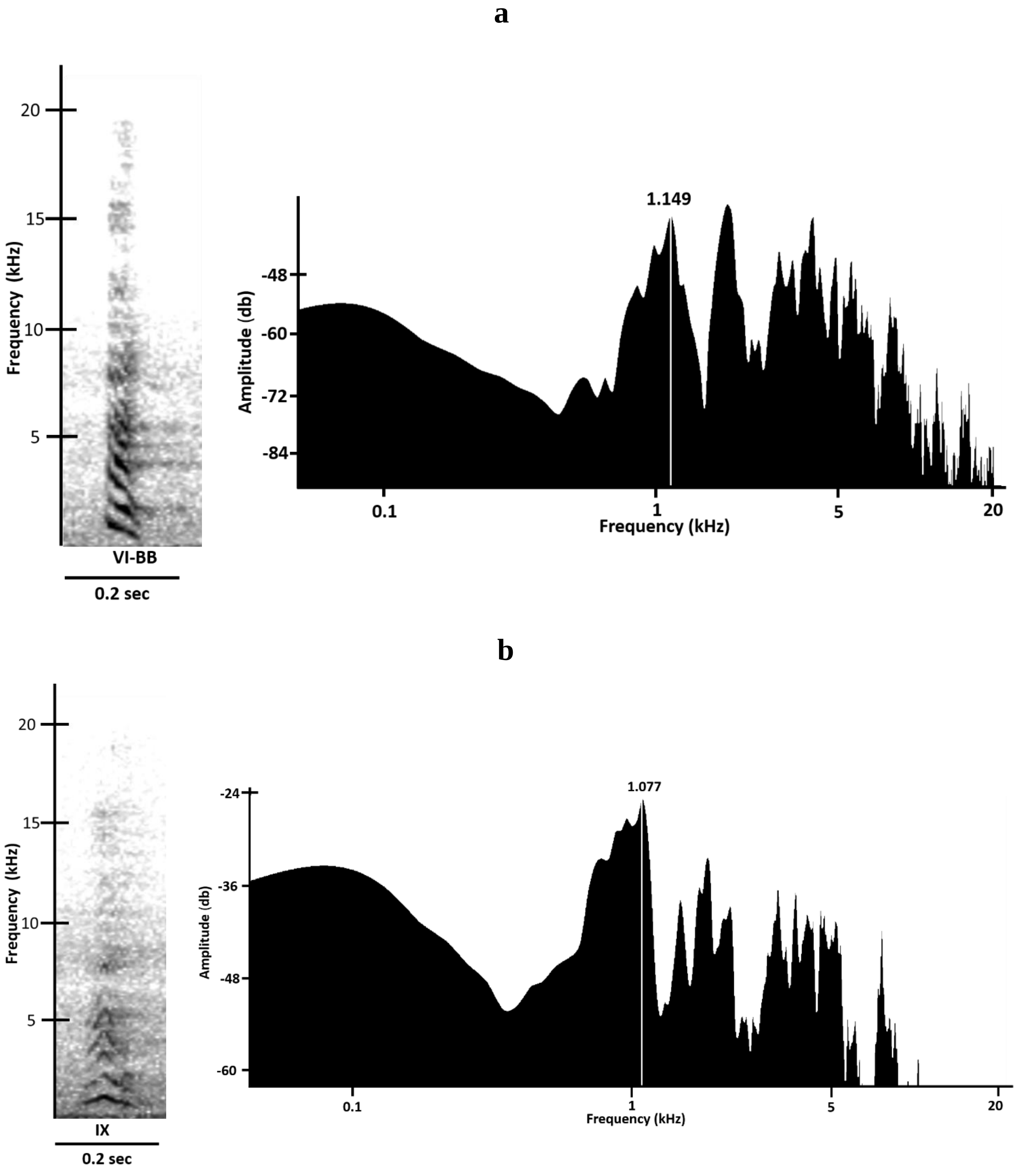

Figure 4:3 – Spectrogram (left) and the power spectrum (right) of the other two calls which were significantly different by at-least one parameter and were produced against bronze-back model. a – refers to call VI-BB and b – refers to call IX.

CHAPTER 5

DISCUSSION

Picture Credit - Saurabh

5.1 OBJECTIVE 1

The NLoTM seemed to be producing several different types of vocalisation in various contexts. A repertoire study on wild population of long tailed macaques from Indonesia show presence of 13 different types of harsh calls in them (Palombit, 1991). This study identifies (visual and aural inspection) 18 different types of calls which were produced by NLoTM in different contexts. Out of the abovementioned 18 calls, 4 calls looked similar (in terms of their onomatopoeic description and spectrogram) to calls described by Palombit for long-tailed macaques of Indonesia. These calls were: call **b** which looked similar to “L.S coo”, call **d** which looked similar to “khreet screech”, call **k** similar to “kra-a” and finally call **i** similar to “krahoo” (Palombit, 1991). Furthermore, studies from other macaque species show that call **d** resembles “arched scream” (Gouzoules et al., 1984) or “screech” (Rowell, 1962) of rhesus macaque, *M. mulatta* as well. Similarly, calls **j** and **k** had different similar looking variants of shrill barks in barbary macaque, *M. sylvanus*, which were produced in response to different predators (Manser,2001).

Call **i** by NLoTM appears to be only produced by the alpha male of the group and is unambiguously distinguishable to a human ear from the rest of the calls. It also appears to be one of the loudest calls from the repertoire as well. The repertoire study by Palombit, describes “karhoo” (call only produced by adult males) made more than other calls. The same call is mentioned to be the loudest among all the others calls produced by long-tailed macaques. The author also mentions that social hierarchy seems to be playing a role in terms of who can produce a krahoo. Low ranking adult males only produce krahoo when the highest-ranking adult male is not present in the same sub-group. Previous literature points to the direction that a probable function of the call could be to maintain the intra-group spacing (Palombit, 1991) since long-tailed macaques follow fission-fusion of subgroup (groups subdivide and later re-group) (van Schaik et al., 1983). Also, it is described as a probable honest signal too. Males could be using the high energetic call to reinforce the dominance hierarchy within the group (Palombit, 1991). According to the preliminary observation on NLoTMs, they do not seem to follow the fission-fusion subgroup strategy i.e. phenomena like ‘pushing forward’ effect (van Schaik et al., 1983) does not split a single group into multiple small sub-groups while foraging. Since, the whole group spends most of the time somewhat together, it allows the alpha male to monopolise the krahoo/**i** call and use it as an honest indicator of fitness. Further experiments to decipher the probable function/s of the krahoo/ **i** call can give insights on its functionality.

Also, if it is established that only the alpha male of the NLoTM groups produce the krahoo's, then this can give insights on the evolution of the homologous calls.

5.2 OBJECTIVE 2

Preliminary observations of natural snake-monkey interactions in Katchal showed that NLoTMs might be differentiating snakes based on the probable cost of interaction. A similar study on bonnet macaques suggest that they distinguish predatory snakes from non-predatory (Ramakrishnan et al., 2005). This study also suggests that NLoTM differentiate snakes based on the probable cost of interaction. Upon comparing the variables encoding stress and vigilance, across snake types we found that only six out of eighteen comparisons were significantly similar i.e. monkeys did not show different response towards those two snake models for the respective variable. The closest proximity maintained for bronze-back and for pit viper were not different, probably because the monkeys were used to a certain proximity for pit viper. Being nocturnal (Whitaker et al., 2004) pit vipers are coiled up during the day-time and pose least threat (Helfman 1989; Stephanie and Lynne 2014). This might have allowed the macaques to maintain relatively close proximity to pit viper in general. And bronze-back being non-venomous, allows the freedom to maintain a relatively close proximity. Hence distance maintained was somewhat similar for both the snakes. Frequency of fear grimace was similar for all snake types. The same was unexpected and could have happened due to inadequate inter-trial interval leading to behavioural extinction. Again, frequency of self-scratching was significantly similar for Bronze-back and Pit viper. This also points towards the direction that macaques might have been getting habituated and hence experiencing less stress. The values were different for python and this could have been the case because 1) it's a predatory type and hence cost of habituation for such a stimulus could be extremely high, and 2) inter-trail duration for python was at-least 15 days. Furthermore, the gaze percentage was significantly different across all snake models and the mean value was maximum for python followed by pit-viper and by bronze-back. Lastly, bipedal standing was significantly similar for Python and pit viper. The values for python and pit viper were significantly greater than Bronzeback's. Both the variables of vigilance show that even if the macaques were getting habituated, they exercised greater vigilance for pit viper than bronze-back. Lastly, this study uses snake models and a comparison was made between the anti-predatory behaviour shown by NLoTM for model snake and for live and dead snakes. The comparison between live pit viper and a model pit viper showed that three out of five variables i.e. frequency of fear grimace, frequency of bi-pedal standing and gaze percentage were not similar. The mean value was higher for live snake than model snake for all the variables. All the above-mentioned variables encode for stress and vigilance, and one may also expect macaques to experience more of it when the threat is not stationary. Again, while comparing the anti-predatory response shown by NLoTM to a dead pit viper and to a model snake, 2 out of 6 variables i.e. passing distance and frequency of fear grimace were not significantly similar. The passing distance was significantly greater for model snake than dead snake. As mentioned above the macaques usually encounter pit vipers in a coiled state and the dead specimens were also presented in somewhat coiled posture, thereby posing least threat and hence allowing a certain proximity to the macaque. One the other hand, snake models were always kept in an extended erect posture. The same poses greater threat than coiled (Helfman 1989; Stephanie and Lynne 2014) and hence forcing the macaques to exercise greater precaution. For frequency of fear grimace, as expected, the mean value was significantly higher for dead snake than model snake. Since, most of the variables were similar in the aforementioned comparison, we can safely assume that the models successfully mimicked the respective snake species.

5.3 OBJECTIVE 3

Preliminary observations of natural snake-monkey interactions in Katchal showed that NLoTM might also be producing different vocalisations for different snake type. A much clearer observation was that the macaques appeared distinctively more aroused i.e. frequent, louder calling, greater participation and maximum interaction time, while interacting with a predatory snake type than a non-predatory snake type. A preliminary study on wild long-tailed macaques also suggest presence of semantic vocal discrimination of predator types in them (Palombit, 1991). Similar studies pertaining to the topic also suggests that primates are able to distinguish and produce threat specific vocalisations. Vervet monkeys (*Chlorocebus pygerythrus*) produce three different types of vocalisation based on the type of predator (Struhsaker, 1967; Seyfarth et al., 1980a), White and black colobus monkey (*Colobus guereza*) produce two acoustically distinguished alarm call variants for different predator classes (Schel et al. 2009, 2010). In this study all the call recorded from NLoTM against above-mentioned snake models were winnowed down using visual (pitch pattern) and aural inspection. 18 different types of anti-predatory calls were achieved. Statistical tests (ANOVA followed by post hoc, Mann Whitney

U test) were then applied on the same and 4 calls were found which were significantly different from the rest in at-least one parameter. Interestingly, all the 4 different types of calls were exclusively produced for a specific type of snake model. Here, call III and IV were only produced against python model whereas call VI-BB and IX were only produced against bronze-back model. The fact that NLoTM might possibly possess different types of snake specific calls i.e. explicit vocalisations for a predatory snake and a non-venomous snake, depicts that NLoTM are able to cognize predatory and non-venomous snakes distinctively. Furthermore, call IV and VI-BB were also produced by the macaques for the maximum proportion of time while vocalizing against python and bronze-back model respectively and hence depicting that they might very well be distinguishing predatory snake models from non-predatory ones. Lastly, in order to comment on what does the aforementioned vocalisations exactly depict i.e. are they just encoding the amount of threat or are they functionally referential too, one has to perform appropriate playback experiments alongside suitable controls.

CHAPTER 6

CONCLUSION AND FUTUTE DIRECTION

Picture Credit – Sayantan Das

6.1 THESIS CONCLUSION:

This study shows that Nicobar long-tailed macaques emit multiple types of vocalisations in various contexts. The results portray the ability of macaques to cognize different contexts and hence behave accordingly. The study also shows specifically that macaques cognize snakes as predatory, venomous and non-venomous beings. Major findings of the study chapters are as follows –

6.1.1 Chapter 1

- 18 different types of vocalisation were found which were produced by NLoTM in various contexts.
- 4 out of the 18 calls, were produced specifically against snakes and are discussed in Chapter 3.
- 5 different types of infant distress vocalisations (call - **a, b, c, d** and **e**) were found.
- A group integration call (call - **i**) was found which appears to be only produced by the alpha male of the group.

6.1.2 Chapter 2

- Distance maintained by monkeys while crossing the snake model and percentage time spent looking at the model were significantly different for all snake models. Here, the same was maximum for predatory type than venomous and then non-venomous type.
- The closest proximity maintained by the monkeys while interacting with the python model was significantly higher than Pit-viper and bronze-back model.
- Frequency of self-scratching by the monkeys while interacting with the python model was significantly higher than Pit-viper and bronze-back model.
- Frequency of bipedal standing by the monkeys while interacting with the bronze-back model was significantly lower than Pit-viper and python model. There was no significant difference in the same between Pit-viper and python model.
- Frequency of fear grimace shown by the monkeys were not significantly different for any of the snake models.

6.1.3 Chapter 3

- 4 different types of anti-predatory calls were produced by the NLoTM against snake models.

- Call III and IV were specifically produced for Python model.
- Call VI-BB and IX were specifically produced for Bronze-back model.

6.2 FUTURE DIRECTION –

Our preliminary observations show that in NLoTM the krahoo/**i** call is only produced by the alpha male of the group. It will be interesting to see if alpha males of NLoTM really show monopolisation of this call. This can be tested by performing focal behavioural sampling with multiple groups of NLoTM with multimale - multifemale societies. Once the monopolisation of 'krahoo' by the alpha males' is established, playback experiments can be performed in order to distinguish the probable function/s of the call. Since the 'krahoo' is produced by all the adult males (of all rank order) in wild long-tailed macaques (Palombit, 1991) the same study has a potential of giving insights on the evolution of homologous calls as well.

This study was done on Nicobar long-tailed macaques of Katchal island, Nicobar. The same islands support snakes belonging to predatory, venomous and non-venomous category (Vijaykumar et al., 2006). The results of the study clearly show that Nicobar long-tailed macaques differentiate snakes as predatory, venomous and non-venomous beings. Now, an allopatric population of the same species is also present in Great Nicobar island, Nicobar. Interestingly, this island only supports snakes belonging to predatory and non-venomous category (Vijaykumar et al., 2006). One can repeat the same experiment with the macaque population of Great Nicobar and can find out how do they respond to an ancestral/bygone threat. Such a study has a potential to provide insights on the retention of cognitive template for ancestral threat type in primate species.

The visual and aural inspection clearly shows that there are a greater number of distinct calls produced by NLoTM than what I have found. There is a need to include more parameters for further acoustic analysis. Those parameters can be included which depicts temporal change in pitch pattern more precisely (mean fundamental frequency at each quartile). Also, parameters like maximum frequency, number of harmonics, call band-width and inter-harmonic distance can also be included.

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Appendix 3

3 A: Closest proximity

Classes	**P - value**
BB – PY*	0.014
PY – CV*	0.0001
CV - BB	0.211

3 B: Passing distance

Classes	**P - value**
BB – PY*	3.264×10^{-6}
PY – CV*	0.004
CV - BB*	0.039

3 C: Frequency of fear grimace

Classes	**P - value**
BB – PY	0.636
PY – CV	0.381
CV - BB	0.705

3 G – LIVE VS MODEL

Variable	P – value
PD	0.24526013041995354
FG	0.024046765243482007
SS	0.6444739995314395
BS	0.015349609358666845

3 D: Frequency of self-scratching

Classes	**P - value**
BB – PY*	0.0002
PY – CV*	0.023
CV – BB	0.160

3 E: Frequency of bipedal standing.

Classes	**P - value**
BB – PY*	6.068×10^{-6}
PY – CV	0.683
CV - BB*	0.004

3 F: Gaze percentage

Classes	**P - value**
BB – PY*	3.776×10^{-8}
PY – CV*	0.0002
CV – BB*	0.0002

3 H – DEAD VS MODEL

Variable	P – value
Pr	0.4993908883750581
PD	0.008093583637374597
FG	0.0011206654693062246
SS	0.6444822953983315
BS	0.5244699710210101

GP	0.010733416102997193

GP	0.20933190427008763

3 I: Normality scores for gestural anti-predatory behaviour.

P - Values	Bronze-back	Cantor’s Pit Viper	Python
Fear grimace	0.020	0.0003	0.015
Self - scratching	7.868	1.408	0.511
Bipedal standing	-	1.438	0.048
Gaze proportion	0.792	0.781	0.605
Closest proximity	0.599	0.004	0.088
Passing distance	0.165	0.054	0.812

Appendix 4

4 A: Mann-Whitney U test between mentioned calls.

(F0)	V - BB	V - CV	V - PY
V - BB			
V - CV	0.18		0.27
V - PY	0.27		

(D0)	V - BB	V - CV	V - PY
V - BB			
V - CV	0.07		0.27
V - PY	0.006*		

(BW)	V - BB	V - CV	V - PY
V - BB			
V - CV	0.29		0.0004*
V - PY	0.60		

(CD)	V - BB	V - CV	V - PY
V - BB			
V - CV	0.02*		0.06
V - PY	0.60		

4 B: Mann-Whitney U test between mentioned calls.

(F0)	VI - BB		VI - PY
VI - BB			
VI - CV	0.00003*		0.0049*
VI - PY	0.16		

(D0)	VI - BB		VI - PY
VI - BB			
VI - CV	0.35		0.0002*
VI - PY	0.003*		

P – Value (BW)	VI - BB		VI - PY
VI - BB			
VI - CV	0.001*		0.005*
VI - PY	0.44		

P – Value (CD)	VI - BB		VI - PY
VI - BB			
VI - CV	0.009*		0.39
VI - PY	0.008*		

4 C: Mann-Whitney U test between mentioned calls.

DO	II
I	0.005*

CD	II
I	0.003*

4D: Mann-Whitney U test between mentioned calls.

(F0)	VII - BB	VII - CV
VII - BB		
VII - CV	0.24	

(D0)	VII - BB	VII - CV
VII - BB		
VII - CV	0.59	

P – Value (BW)	VII - BB	VII - CV
VII - BB		
VII - CV	0.455	

P – Value (CD)	VII - BB	VII - CV
VII - BB		
VII - CV	0.06	

4E: Mann-Whitney U test between mentioned calls.

(F0)	VIII - CV	VIII - PY
VIII - CV		

(D0)	VIII - CV	VIII - PY
VIII - CV		

VIII - PY	0.092	

P – Value (BW)	VIII - CV	VIII - PY
VIII - CV		
VIII - PY	0.57	

VIII - PY	0.29	

P – Value (CD)	VIII - CV	VIII - PY
VIII - CV		
VIII - PY	0.005*	

4F: Mann-Whitney U test between mentioned calls.

(F0)	VII
VIII-CV	0.22

(D0)	VII
VIII-CV	0.03*

(BW)	VII
VIII-CV	0.24

CD	VII
VIII-CV	0.03*

4G: Mann-Whitney U test between mentioned calls.

(D0)	IX
IV	0.11

(CD)	IX
IV	0.001*

4H: Mann-Whitney U test between mentioned calls.

(DO)	IV
I	0.37

(CD)	IV
I	0.008*

4I: Mann-Whitney U test between mentioned calls.

(DO)	V-BB
V-PY (b)	0.001*

(CD)	V-BB
V-PY (b)	0.91

4J: Mann-Whitney U test between mentioned calls.

DO	V-CV
V-PY (b)	0.79

CD	V-CV
V-PY (b)	0.004*

4K: Mann-Whitney U test between mentioned calls.

DO	V-PY
V-PY (b)	0.09

CD	V-PY
V-PY (b)	0.37

4L: Normality scores (Shapiro -Wilk test) of focal variables for all the calls.

Call Type	P - Values			
	Fundamental frequency (F0)	Dominant frequency (D0)	Call duration	Band width
I	>0.05	>0.05	>0.05	>0.05
II	>0.05	>0.05	>0.05	>0.05
III	>0.05	<0.05	<0.05	>0.05
IV	<0.05	>0.05	>0.05	>0.05
V-BB	<0.05	<0.05	>0.05	>0.05
V-CV	-	>0.05	>0.05	-
V-PY	-	<0.05	<<0.05	-
VI-BB	-	<0.05	>0.05	-
VI-CV	-	<0.05	>0.05	-
VI-PY	-	<0.05	>0.05	-
VII-BB	-	<0.05	<0.05	-
VII-CV	-	>0.05	>0.05	-
VIII-CV	-	>0.05	>0.05	-
VIII-CV	<0.05	>0.05	>0.05	<0.05
IX	>0.05	<0.05	>0.05	<0.05
X	>0.05	>0.05	>0.05	<0.05
XI	>0.05	>0.05	>0.05	>0.05
XII	-	<0.05	>0.05	-