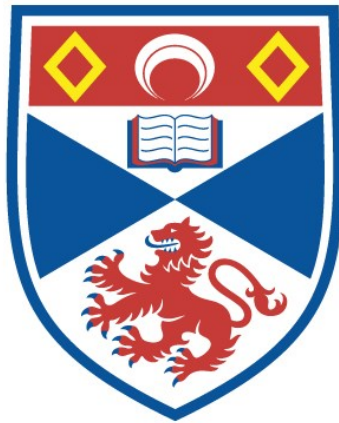


**ANTI-PREDATOR BEHAVIOUR OF BLACK-FRONTED TITI
MONKEYS (CALLICEBUS NIGRIFRONS)**

Cristiane Căsar

**A Thesis Submitted for the Degree of PhD
at the
University of St Andrews**



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**Anti-predator behaviour of black-fronted titi
monkeys (*Callicebus nigrifrons*)**

Cristiane Cäsar

**Thesis submitted to the School of Psychology
of the University of St. Andrews
for the degree of Doctor of Philosophy**

October 2011

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To those who always believed me, even when I didn't:

To my beloved husband, for all his love, support and encouragement

And to the friends I found on the way.

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“I may not have gone where I intended to go, but I think I have ended up where I needed to be.”
(Douglas Adams, 1988).

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Abstract

Titi monkeys have long been known for their complex vocal behaviour with numerous high- and low-pitched calls, which can be uttered singly or combined in more complex structures. However, up to date very little is known concerning the function, meaning and context-specific use of these vocal utterances, and virtually nothing is known about their vocalisations in the predation context.

This thesis presents a detailed description of the form and function of the anti-predator behaviour of one species of titi monkeys, the black-fronted titi monkey (*Callicebus nigrifrons*), with a specific focus on their alarm call behaviour. A second aim was to determine the exact mechanisms of alarm calling behaviour, with an emphasis on production and comprehension. Data were collected from several habituated groups in the Caraça Reserve, Minas Gerais, Brazil.

Results showed that, when detecting predator species, *C. nigrifrons* produce sequences that initially contain two types of brief, high-pitched calls with distinct frequency contours. Further evidence suggested that some of these sequences are meaningful to conspecific receivers, by indicating the general predator class and location of threat. There were also indications that, within the terrestrial threats, additional information may be encoded by acoustic and compositional differences. Analyses of call order and number of calls per sequence suggested that callers may be able to convey information on both predator type and location.

The black-fronted titi monkeys' vocal system thus provides a further example of zoo-syntax, in which acoustically fixed units of a vocal repertoire are combined into higher order sequences that are meaningful to recipients. According to current definitions, this type of calling behaviour qualifies as functionally referential, by indicating general predator class, terrestrial predator type and location. As such, this is the first empirical demonstration of a sequence-based alarm call system that conveys information on both predator category and location.

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CHAPTER 1: General Introduction

Part I: Animal Vocal Communication

1.1 Predation risk and vocal flexibility

Predation exerts a fundamental selective pressure on morphological traits (e.g. body size), behavioural (e.g. group size, group composition) and ecological characteristics (e.g. ecological niche) (Anderson 1986, Cheney and Wrangham, 1987). Anti-predator responses will depend on physiological (e.g. body size or visual acuity), ecological (such as distribution of refuges) and social factors (such as group size and collective response) that can vary significantly across species, populations, groups and even individuals (Miller and Treves, 2011).

Body size is considered one of the traits that influences the risk of predation. In general, large bodied animals have a smaller number of potential predators (Isbell, 1994); although there is evidence that this effect can be minimal, or even absent, as a consequence of different types of predators and hunting techniques (Ferrari, 2009).

Group size is another adaptation considered important in avoiding predation. Large groups are usually less susceptible to some predators as a result of higher levels of predator vigilance (van Schaik, 1983). Furthermore, individuals in larger social groups are expected to be safer than those in smaller groups because of dilution effects (Hamilton, 1971), the added vigilance of many eyes, leading to improved predator detection (Elgar, 1989) or the improved success of mobbing (Altmann, 1956, Curio, 1978).

Cognition is also considered to have evolved under predation pressure, for instance where species are able to produce and understand predator specific alarm calls (Zuberbühler, 2007). The ability to understand the alarm calls of conspecific, and even

of heterospecific, primates and non-primates shows vocal flexibility (Seyfarth and Cheney, 1990, Zuberbühler, 2000a, Zuberbühler 2000b). Predation has been suggested to increase flexibility in primate cognitive and vocal capacities (Zuberbühler, 2000a, Zuberbühler and Jenny, 2002). Vervet monkeys (*Chlorocebus aethiops*), for instance, respond with their own anti-predator behaviour in response to the predator calls of a bird that inhabits the same area: the Superb starling (Cheney and Seyfarth, 1985). Similarly, Diana monkeys (*Cercopithecus Diana*) react with their corresponding predator alarm calls after hearing playbacks of guinea fowl alarm calls (Zuberbühler, 2000d). Moreover, Diana monkeys can also use the predator information conveyed in male Campbell's monkeys' alarm calls to adjust their anti-predator behaviour (Zuberbühler, 2000a). The production and understanding of predator specific alarm calls will be described in the following sections.

1.1.1 Behavioural strategies or anti-predator responses

Recent studies have illustrated that diverse primate taxa are preyed upon by a variety of predators: especially raptors (Falconiformes), mammals (Carnivora) and reptiles (Squamata) (review in Ferrari, 2009 and Miller and Treves, 2011). Along with a variety of types of prey-predator interaction there is an enormous array of anti-predator adaptations, and primates have evolved a wide repertoire of morphologies and behaviour to avoid, escape and otherwise elude their predators (Miller and Treves, 2011). Behavioural responses to predators vary considerably in primate species. In broad terms, reactions are either passive (e.g. avoidance, hiding or fleeing) or active (e.g. monitoring or mobbing) and they vary systematically within species depending on the type of predator (Ferrari, 2009, Zuberbühler, 2007).

The most fundamental anti-predator behaviour is to **avoid** the initial encounter. Miller and Treves (2011) suggest that predator avoidance may be improved by cryptic habits, including nocturnality, forming smaller and quieter groups, and foraging alone; but few

studies have examined these as anti-predator strategies because experimental controls are very difficult to establish.

Some species use the **early detection** of predators to escape or signal their detection. To escape from predators, terrestrial species seek refuge either in trees and cliffs, whereas arboreal species rapidly change levels within the canopy (reviewed in Treves, 2002). In several primate species, individuals signal the detection of a predator, while listeners very often use the semantic information encoded in the signals to respond appropriately (e.g. Seyfarth et al 1980).

Some vocal signals are directed to predators instead of, or in addition to, conspecifics. These may function to warn predators that they have been detected, thereby encouraging ambush predators to abort the predation attempt (Zuberbühler et al, 1997, Zuberbühler, 2000b). Several species of primate also mob their predators (Cros and Rogers 2006, Cheney and Seyfarth, 2007, Clara et al 2008, Ferrari, 2009). Mobbing involves one or more prey animals making repeated and aggressive advances on a predator, usually while vocalizing and displaying in a conspicuous manner. These conspicuous and persistent approaches usually distract or repel the predator (e.g. Schel et al 2010).

Another trait that varies during anti-predator responses is the specificity of alarm calls. Prey species with many potential predators may have developed either an extensive repertoire of specific antipredator behaviours (for instance, different alarm calls in response to leopards and snakes) or a few generalised responses that are effective against a variety of predators (e.g. one alarm call to different species of terrestrial predators). In general, alarm calls given to dangerous raptors are usually more specific than alarm calls given to disturbances on the ground, which sometimes are also given during non-predatory events (Fichtel and Kappeler, 2002, Digweed et al., 2005, Fichtel and van Schaik, 2006, Wheeler, 2010). Whether or not such systems qualify as

functioning referentially is a matter of ongoing debate (Arnold and Zuberbühler, submitted).

Anti-predator responses also depend, in part, on characteristics of the predator's attack pattern; for example: a prey may respond differentially to avoid an aerial raptor as opposed to a large, terrestrial felid (Macedonia & Evans, 1993). Vervet monkeys, for instance, dive down into dense vegetation after hearing a conspecific give an eagle alarm call, but climb into nearby trees after hearing alarm calls indicating the presence of a leopard (Seyfarth et al 1980).

Some anti-predator responses are more flexible than others. For instance, alarm calling can be used when effective and omitted when ineffective; however, a rapid change of group size is generally less readily accomplished (Miller and Treves, 2011).

Several mammal and bird species produce alarm calls that typically function to signal the presence of predators to conspecifics and/or communicate to the predator that it has been detected (Caro, 2005a). Where calls depend on the context in which they are produced, the structure of calls, the number of calls given, and/or the intensity of calls can be highly specific (e.g. Seyfarth et al 1980, Blumstein, 1999a). Such context-dependent calls can potentially evoke reactions in call receivers that are appropriate for the context in which the calls were given (e.g. Seyfarth et al 1980, Blumstein, 1999b). Among those species that produce context dependent alarm calls, two distinct types of call systems have been identified: (1) a “functionally referential” alarm call system, where call structure varies based on threat type (e.g. eagle versus leopard, Seyfarth et al 1980) and (2) an “urgency-based” alarm call system, that varies based on the degree of threat from a predator perceived by a caller (e.g. high versus low, Blumstein 1999b). Moreover, there are also alarm call systems that combine both functionally referential and urgency-based systems simultaneously (Marler et al., 1992, Manser, 2001).

1.2. Alarm call systems

1.2.1 Referential alarm call systems

Some primate species produce different alarm calls that are acoustically distinct in response to different predator types and these calls evoke accurate and adaptive responses in recipients (Seyfarth et al., 1980ab; Zuberbühler et al, 1997; Zuberbühler, 2001). The classic example is the alarm calling system of Vervet monkeys, *Chlorocebus aethiops* (Struhsaker, 1967, Seyfarth et al 1980). These primates give distinct alarm call types to each one of their most dangerous predators, such as leopards, eagles and pythons (Struhsaker, 1967). Playback studies have shown that receivers responded to these predator-specific alarm calls by taking evasive reactions appropriate to the hunting technique of the predator that elicited the call, without any other evidence of the presence of the predator (Seyfarth et al 1980). On hearing an eagle alarm call, for instance, monkeys dive down into dense vegetation, whereas they climb into nearby trees after hearing leopard alarm calls and stand bipedally and scan the ground after hearing python alarm calls.

Such signals are usually referred to as ‘functionally’ referential signals. Functionally referential calls must show both context specificity of call production (the ‘production criterion’), where the signal is produced in a context-specific way, and perception specificity (‘perception criterion’), where the signal alone is sufficient to evoke an appropriate response from listeners in the absence of the eliciting stimulus (Macedonia and Evans, 1993). Similar findings have been reported for several other primate species, such as ring-tailed lemurs (*Lemur catta*; Macedonia 1990; Pereira and Macedonia 1991), Diana monkeys (*Cercopithecus diana*; Zuberbühler, et al. 1999b), and Campbell's monkeys (*Cercopithecus campbelli*; Zuberbühler 2001), moustached tamarins (*Saguinus mystax*, Kirchhof and Hammerschmidt 2006), blue monkeys (*Cercopithecus mitis stuhlmanni*, Papworth et al 2008), and tufted capuchin monkeys (*Cebus apella nigrinus*, Wheeler 2010).

The use of such functionally referential, or semantic, signals may be limited to primate species, especially the arboreal or semi-arboreal ones, that make use of highly distinct escape techniques when confronted with different predator types (Fichtel & Kappeler, 2002). Living in three dimensional environments, along with being exposed to a wide range of predators (which require a variety of potential escape options adapted to the predators' hunting techniques), are considered important factors that influenced the diversification of anti-predator vocalizations and responses (Macedonia & Evans, 1993).

1.2.2 Risk-based or Urgency-based alarm call system

In other animal species, however, alarm calls indicate level or position of threat, instead of, or in addition to, predator type. These vary in terms of immediacy, degree or urgency in a predator encounter and can be caused by the size of a predator (e.g. Templeton et al 2005), proximity of the predator (e.g. Leger et al 1980) or by internal factors that affect caller's fear level or perception of urgency (e.g. Baker and Becker 2002). For instance, the alarm calls in the California ground squirrels (Owings & Virginia, 1978) usually convey information about distance or fear experienced by the caller, rather than predator type information. These animals give 'whistles' to raptors and 'chatter-chats' to terrestrial predators; however, whistles were also given to ground predators that suddenly attacked the squirrels and conversely, chatter-chats were also given to distant eagles (Leger et al., 1980). Marmots also produce alarm calls where different aspects of call structure reflect differences in the degree of urgency (e.g. distance and type of stimulus) and playbacks of such calls elicited different responses (e.g. higher vigilance to high-urgency calls, Blumstein, 1999b). However, since there were no stimuli-dependent vocalizations, marmots' alarm calls are best seen as communicating different risks of predation (Blumstein, 1999b). These examples show that alarm calls in some species do not denote different predator categories but simply reflect different types or levels of danger.

Urgency-dependent alarm calling appears to work well for species that rely on a single escape strategy, such as running into a hole, to deal with all potential threats of predation. In these species, the level of threat is the only information required for an appropriate escape response (Macedonia and Evans, 1993). Thus, in urgency-dependent alarm call systems, one call type is given when a predator is in a position to attack, and another is given when the predator is far away and perhaps only requires monitoring. Evidence of urgency-dependent alarm calling in primate species has been suggested for a few species: bonnet macaques, *Macaca radiata* (Coss et al 2007), redfronted lemurs, *Eulemur fulvus*, and Verreaux's sifakas, *Propithecus verreauxi* (Fichtel and Kappeler, 2002, Fichtel and Hammerschmidt, 2002). The authors argued that the terrestrial predator associated alarm calls of red-fronted lemurs and Verreaux's sifakas may reflect the caller's perceived threat urgency because these calls were also given in nonpredatory contexts characterized by high arousal. The problem with such studies is that arousal (or affect) is difficult to quantify as we can simply never know what is going on inside of an animal's brain (Zuberbühler 2003). Nonetheless, it has been suggested that affect intensity influences call production, e.g. through changes in respiration, facial musculature, and vocal folds, influencing amplitude, resonance and fundamental frequency (Morton, 1977). Some studies have attempted to investigate the intensity of affect in species such as baboons (Rendall, 2003) and squirrel monkeys (Fichtel et al., 2001). In general, measures of affect, such as aggressiveness, aversion and fearfulness, usually were found to be correlated with, and influenced by, signalers' number of calls, noisiness, fundamental and peak frequency, frequency range and formant frequencies. Interestingly, the production of high amount of calls may also reduce cortisol levels (Clara et al, 2008, Cross and Rogers, 2008).

Another example of an alarm-call system that is not closely dependent on predator type comes from the domestic chicken, *Gallus gallus domesticus*. These animals produce two acoustically distinct alarm calls, one for aerial and one for ground predators; subsequent playbacks of each call type were sufficient to evoke responses of listeners

that were appropriate to the visual stimulus that elicited the call originally (Gyger et al., 1987, Evans & Marler, 1995). To further test if the chickens simply responded with aerial alarm calls to anything ‘above’ them, Evans & Marler (1995) altered the ‘location of danger’ by displaying a video of a ground predator (for instance, a raccoon) from above and the video of an aerial predator (a hawk) from the ground. They found that signallers produce aerial alarm calls and ground alarm calls, respectively, in response to these two stimuli, suggesting that chickens respond to the **spatial position** of the threat instead of the predator category (Evans et al 1993).

1.2.3 Alarm call systems using different strategies

Species with a particular alarm call for raptors and another call type for disturbances on the ground, which is frequently used during non-predatory events (Fichtel and Kappeler, 2002, Digweed et al., 2005, Fichtel and van Schaik, 2006), are considered to have a **mixed alarm call** system (Fichtel & Kappeler, 2002), mainly because one call does not meet both criteria of referentiality proposed by Macedonia and Evans (1993).

Other species use the same basic call type for various predator species or situations, but vary the acoustic fine structure in context-specific ways (e.g. Ouattara et al., 2009a). Nonetheless, experimental studies have showed that receivers associate different events with the acoustically **graded signals**, suggesting that discrete call types are not a prerequisite for encoding specific external events (Fischer et al., 2001b).

A third pattern observed in primates is to use more complex utterances, in which they assemble a small number of call types into different combinations of **call sequences**. For instance, male putty-nosed monkeys (*Cercopithecus nictitans*) produce series of loud and conspicuous calls combined in predator- and context-specific ways (Arnold and Zuberbühler, 2006ab). Campbell’s monkeys indicate low levels of threat, or signals aimed at competitors, by adding a pair of “boom” calls to subsequent loud call series, which are regularly given to predators (Zuberbühler, 2002). White handed gibbons use

different ordering of song units when singing as part of their regular morning ‘routine’ or when singing in response to terrestrial predators (Clarke et al., 2006). Likewise, titi monkeys were described as producing different call sequences according to differences in time and distance between neighbouring groups (Robinson, 1979a); however, no evidence was found of use of these or other calls/sequences in response to predator encounters.

Finally, one study has described a sequence-based alarm call system based on number of calls. Guereza colobus monkeys, *Colobus guereza*, produce many roaring sequences with few calls each in response to leopards and few roaring sequences with many calls each in response to eagles (Schel et al., 2010). Furthermore, these context dependent sequences were recognized by receivers.

In sum, different types of signals can be used in predator communication: discrete call types, graded signals and/or call sequences/combinatorial rules. These signals may subsequently be classified as used in one of the three types of alarm call systems: referential, urgency-dependent, or mixed alarm call systems (table 1.1).

1.2.4 Multiple alarm call systems

Some non-primate species have been described to possess a system that combines referential information and also information on the level of urgency: black-capped chickadees (*Poecile atricapilla*) and meerkats (*Suricata suricatta*). Chickadees, for instance, produce a high-frequency low-amplitude “seet” call when detecting flying raptors, and a loud broad-band “chick-a-dee” when detecting perched raptors. Moreover, they vary the number of notes per call depending on of the perceived predation risk (e.g. predator size) (Templeton et al., 2005). Meerkats produce different

alarm calls in response to aerial and terrestrial predators, and also vary the acoustic structure depending on the distance of the predator (Manser, 2001).

These examples show that a variety of psychological processes appear to underlie animal alarm calls, ranging from categorical assessment of predator types to judgements of distance and movement vectors. However, none of these studies have yet tested whether the acoustic structure of alarm calls, or call series, varies simultaneously with predator type and location.

Table 1.1. Studies that investigated the alarm call systems of different mammal species, organized by the type of alarm call system used by these species. Signal type indicates the type of signal used in the alarm responses produced by these animal species. Updated from Schel (2009).

	Alarm Call system			Signal type		
PRIMATES	Functionally Referential	Urgency Response	Mixed	Discrete signals	Graded signals	Call sequences
Lemuridae						
<i>Propithecus verreauxi</i>			Fichtel & Kappeler (2002)	+		
<i>P. v. coquereli</i>			Fichtel & van Schaik (2006)	+		
<i>Lemur catta</i>	Macedonia (1990)			+		
<i>Eulemur f. rufus</i>			Fichtel & Kappeler (2002)	+	+	
<i>Varecia variegata</i>		Macedonia (1990)		+		
Cercopithecidae						
<i>Cercocebus atys</i>		Range & Fischer (2004)			+	
<i>Cercopithecus aethiops</i>	Struhsaker (1967) Seyfarth et al (1980)			+		
<i>C. campbelli</i>	Zuberbühler (2001)			+		+
<i>C. diana</i>	Zuberbühler et al (1999)			+		
<i>C. nictitans martini</i>		Arnold & Zuberbühler (2006)				+
<i>C. mitis</i>	Papworth et al (2008)			+		?
<i>Papio c. Ursinus</i>		Fischer et al (2001)			+	
<i>Colobus guereza</i>	Schel et al (2010)					+
Hylobatidae						
<i>Hylobates lar</i>	Clarke et al (2006)					+
Callithrichidae						
<i>Saguinus fuscicollis</i> <i>S. mystax</i>	Kirchhof & Hammerschmidt (2006)			+		
Cebidae						
<i>Cebus capucinus</i>			Fichtel et al (2005) Digweed et al (2005)		+	
<i>Cebus nigrinus</i>			Wheeler (2010)	+		
RODENTIA						

Sciuridae						
<i>Cynomys guunisoni</i>	Slobodchikoff et al (1991)			+		
<i>Marmota spp.</i>		Blumstein & Armitage (1997) Blumstein (1999)		+		
<i>Spermophilus beecheyi</i>		Owings & Virginia (1978)		+		
<i>Spermophilus beldingi</i>		Leger et al (1984)		+		
<i>Tamiasciuris hudsonicus</i>	Greene & Meagher (1998)			+		
Muridae					+	
<i>Parotomys brantsii</i>		Le Roux et al (2001)				
CARNIVORA						
Herpestidae						
<i>Suricatta suricatta</i>	Manser (2001)	Manser (2001)		+		

1.3. Comparative approach of animal communication and language

According to linguists and psycholinguists, one of the defining aspects of language (or ‘what it means to be human’) is the presence of syntax (Chomsky, 1957). **Syntax** is defined as “the rule-governed combination of small meaningful units (morphemes) into hierarchical structures (phrases and sentences), whose meanings are some complex function of those structures and morphemes” (Fitch, 2010, pg 104). “The combination of unlimited specificity of meaning, combined with a free flexibility to use language in novel ways (we easily understand sentences we have never heard, and express thoughts no one ever thought before) is the hallmark of language” (Fitch, 2010, pg 26).

Hauser et al (2002) proposed a comparative approach where mechanisms involved in language acquisition, such as memory, sequencing, vocal production and perception, are shared with other species and, therefore, open to a comparative approach. For example, several species have been demonstrated to possess the ability to communicate about specific objects or events in their environment (e.g. Seyfarth et al., 1980, Zuberbühler et al 1999, Manser, 2001, Templeton et al 2005). Likewise, although evidence is still limited, some species are also known to combine existing calls into meaningful sequences, which increases the variety of messages that can be generated (e.g. Arnold and Zuberbühler, 2006, Cleveland and Snowden, 1982, Zuberbühler 2002, Mitani and Marler, 1989, Robinson, 1979a, 1984, Marler et al. 1992).

1.3.1 Animal call combination

The existence of syntax-like patterns (or zoo-syntax) in animal communication systems has been demonstrated in some primate species, including: titi monkeys *Callicebus cupreus* (Robinson, 1979a), wedge-capped capuchins *Cebus olivaceus* (Robinson,

1984), Campbell's monkeys *Cercopithecus campbelli* (Zuberbühler 2002), putty-nosed monkeys (Arnold and Zuberbühler, 2006) gibbons (Mitani and Marler, 1989, Clarke et al 2006) and Guereza colobus monkeys, *Colobus guereza* (Schel et al 2010). These species appear to be able to create and understand specific combinatorial rules by employing a limited numbers of call types, which leads to a variable number of distinct sequences that differ in distinct contexts.

To understand these abilities in the animal communication system, Marler (1977) distinguished two types of syntax. 'Phonetic syntax' is equivalent to the formation of different words through rearrangement of phonemes. In this type of syntax meaningless call units are rearranged into new meaningful sequences. A second type of syntax is "lexical syntax", equivalent to the formation of phrases or sentences from different words. In this case, the resulting sequence maintains the meaning of the individual components.

An example of a phonetic syntax was described by Robinson (1979a) in a study with titi monkeys, *Callicebus cupreus*. In this species, unit loud calls, with apparently no individual meaning attached to them, were organized hierarchically into phrases that were then organized into more complex sequences that are produced in different circumstances. In a playback study designed to test titis' understanding of these sequences, the author constructed sequence stimuli of male calls sequenced into both normal and abnormal sequences types. Results suggested that monkeys perceived the structural arrangement (or syntax) of the sequences, based on the order of phrases. In response to abnormal sequences, subject groups showed high levels of "disturbance behaviour" (e.g. by producing more moans, which are normally produced in response to disturbing situations) in comparison to normal sequences.

Another example of specificity through call sequences, instead of individual calls comes from studies with free-ranging putty-nosed monkeys (*Cercopithecus nictitans*). Here, the males produce two alarm call types, 'hacks' and 'pyows', that are not individually

related to specific predator type (they are both produced to eagles and leopards). However, these monkeys concatenate the two calls into longer sequences, which can be highly predator-specific (Arnold & Zuberbühler, 2006b).

Robinson (1984) suggested that wedge-capped capuchins used lexical syntax. Some calls were combined to create compound calls that were given in intermediate situations between each individual call. Similarly, alarm and alert calls produced in combination by tamarins were given in contexts described as intermediate between the contexts in which each call type is produced alone (Cleveland & Snowdon, 1982). However, it has been argued that this relationship (i.e. combinations that are very closely related to the individual calls) could limit the range of things that can be communicated through syntax (Arnold et al, 2011), meaning that it is a very different system from the hierarchical complexity of grammar in human speech (Byrne, 1982). Nonetheless, even a simpler syntax can still be informative from the perspective of precursors to human speech and language.

1.3.2. Meaning of alarm calls

A key aspect to understanding any communication, including animal communication, is the study of **semantics**, or the study of meaning in language (Fitch, 2010). Evidence of ‘semantics’ in animal communication has come from several species in different contexts, including social (rhesus macaques’ recruitment screams: Gouzoules et al., 1984), feeding contexts (chimpanzees: Slocombe & Zuberbühler, 2005, tufted capuchin monkey: di Bitteti, 2003, and rhesus monkey: Hauser, 1998), but has been predominantly derived from calls in an alarm context (e.g. Seyfarth et al., 1980; Zuberbühler et al, 1997; Zuberbühler, 2001).

Two studies with Diana monkeys elegantly demonstrated the notion of semantics in animal communication. In the first one, monkeys were primed with a playback consisting of a series of conspecific predator alarm calls (the prime stimulus). After a

period of silence, a second series of identical predator alarm calls or corresponding/non-corresponding predator vocalisations were played from the same location (the probe stimulus). It was found that Diana monkeys primed with conspecific predator alarm calls no longer responded to the vocalizations of the corresponding predator. This suggested that the semantic component of the prime stimulus, not their acoustic feature alone, explained the response patterns of the listeners to the probe stimulus. Secondly, it suggested that the recipients had formed a mental representation of the corresponding predator; they had acted as **if** they already knew about its presence (Zuberbühler, 2000b). In the second study, listeners responded in the same way after listening to a playback with both conspecifics' eagle alarm calls and with shrieks of crowned eagles. The same was true to for their responses to conspecifics' leopard alarm calls and leopard growls (Zuberbühler 2000d).

As seen previously, these vocalizations are elicited by specific external events, the 'referents' (e.g. eagles, leopards, snakes), which are mediated by corresponding mental concepts, the references (e.g. Seyfarth and Cheney 1980, Macedonia and Evans, 1993, Evans and Marler, 1995). Thus, these calls can provide specific information for conspecifics to respond appropriately, even in the absence of contextual information (Seyfarth et al 1980).

1.4. Referential communication in New World Monkeys

The communication capacities of some species of primates, especially guenons, prosimians and some colobines, have been very well documented; this is much in contrast to the relatively unstudied New World primates (table 1.1), which is problematic for understanding the evolutionary origins of language-relevant capacities.

Recent studies on New World primates have shown that some species of callitrichids and cebids also produce at least two call variants that differ in their acoustic structure and that are accompanied by functionally distinct behavioural responses (Digweed et al., 2005; Fitchel et al., 2005; Kirchhof and Hammerchmidt, 2006). Conversely, one of these calls is produced to a range of terrestrial disturbances, including inter-group encounters (Fitchel et al., 2005), a pattern also found in some Old World monkeys (e.g. Arnold and Zuberbühler, 2006a, Arnold et al., 2008). These examples also raise the need for more empirical studies on naturally produced calls and their contexts, prior to conducting playback experiments.

Moreover, most studies of alarm calls in primates and rodents have presented results of only one of the two criteria of functionally referential calling (see Blumstein 2007). Among New World Monkeys, only capuchin monkeys have been systematically described as possessing both context and perception specificity of alarm calls (Wheeler, 2010). Examination of both call production and perception is important because situational variation in call production does not necessarily lead to distinct responses in call receivers (Blumstein 1995). Moreover, predator-specific responses to alarm calls can be elicited by calls that are not specific to predator encounters (e.g. Fichtel and Kappeler, 2002).

To begin filling this gap in information regarding referential alarm systems in New World monkeys I initiated a naturalistic field study followed by experimental studies of the anti-predator behaviour and alarm calling in one species of titi monkeys, *Callicebus nigrifrons*. Studies on New World Monkeys living in dense forest habitats with a range of natural predators are likely to produce a more complete understanding of the evolution of anti-predator behaviour and predator recognition, as well as the phylogenetic distribution and evolutionary origins of predator-specific signalling in primates.

Part II: Study genus and study species

1.5 General characterisation

Titi monkeys (*Callicebus sp*) are the second most diverse genus of New World Monkeys with currently 30 species (van Roosmalen et al., 2002, Wallace et al., 2006, Defler et al., 2010). They are found in South America from Colombia to Brazil, Peru and Paraguay. In the most recent taxonomic review, based on historical and geographical isolation and cranial measurements by Kobayashi (1995), van Roosmalen et al., (2002) placed 28 species of *Callicebus* into five different clades (*C. donacophilus*, *C. cupreus*, *C. torquatus*, *C. moloch*, *C. personatus*). According to this nomenclature, the black-fronted titi monkey, *Callicebus nigrifrons*, is part of the *C. personatus* group, which inhabits the coastal and inland forests of southeastern Brazil and is geographically separated from *C. donacophilus* to the west by at least 500 km and from *C. moloch* to the northwest by at least 1,000 km.

Callicebus monkeys are arboreal and diurnal monkeys, weighting between one and two kilos (Hershkovitz, 1990), that only rarely go to the ground (Kinzey, 1997b). They live in socially monogamous family groups, consisting of a pair of reproductive adults and up to four generations of offspring (Mason, 1966, Mason, 1974, Mendoza and Mason, 1986, Kinzey, 1981, Kinzey and Becker, 1983, Valeggia et al., 1999). Sub-adult individuals of both sexes disperse when they are approximately three years old (Bossuyt, 2002). However, under certain conditions, offspring can stay longer while already dispersed individuals sometimes temporarily return to their natal group, which can increase group size to seven individuals (table 2.1, chapter 2; also see (Bicca-Marques et al., 2002, for a different group composition).

Callicebus are highly territorial and reproductive pairs defend their territories by duetting and displaying with other aggressive behaviours to neighbouring pairs at their boundaries (Robinson, 1979b, 1981; Kinzey & Becker, 1983; Anzenberger et al., 1986).

However, some species do not appear to have the same degree of territory defence and, in these cases, the duets appear to be produced to signal group location and maintain distance between groups (Kinzey and Robinson, 1983; Price and Piedade, 2001).

Black-fronted titi monkeys, *Callicebus nigrifrons*, are endemic to the Atlantic forests of south-eastern Brazil. They are one of the largest species of titis, with no sexual dimorphism in the adults (max. weight: 1,650g; Rowe, 1996). Most aspects of their natural history and behavioural biology are unknown and have sometimes been inferred from other (Amazonian) species of their genus, which may not be appropriate. Dr Robert J. Young (PUC Minas, Brazil) and I coordinated a long-term study of this species in the Caraça Reserve in the state of Minas Gerais, beginning in 2003. This has allowed researchers to follow and monitor several now habituated groups from a relatively close distance. Some observation data from this population has shown that the monkeys have very flexible social behaviour: for example, an adoption event of an infant by another group, which already had its own infant (Cäsar & Young, 2008) and a case of infanticide of a three day old infant by an adult female of another group (Cäsar et al, 2008).

1.6. Communication

A detailed description of the communication in *Callicebus* monkeys was first given by Moynihan (1966) for the dusky titi, *C. cupreus*. His description, mainly based on captive individuals, with some additional observations of wild animals, illustrates various olfactory, tactile, visual and acoustic signals.

Olfactory signals were evidenced by “chest-rubbing” and “social sniffing”, which includes face to face sniffing and sniffing at the genital region of the mated pair (Moynihan 1966). Three different tactile signals appeared to mediate titis’ social interactions (Moynihan, 1966). These were “Allo-grooming” (grooming of one individual by another), “Tail-twining” (animals seated side by side usually intertwine

their tails, whether awake or asleep) and “Infantile” leaping on the back of another individual.

C. cupreus also showed some visual signals, which were usually produced in agonistic or hostile circumstances, and they conveyed an intention to escape and/or attack (Moynihan, 1966). The visual signal repertoire of these monkeys included "swaying," "looking-away," "head-down," "displacement-scratch," "eye-closing," "protruding-lips," "baring-the-teeth," "arch-posture," "tail-raising," "tail-lashing," "pilo-erection" and "general shakes" (Moynihan 1966). I observed some of these signals in wild *Callicebus nigrifrons* during encounters with predators and will discuss them later on.

1.6.1 Acoustic signals

A contextual, and spectrographic representation of the acoustic repertoire of *Callicebus cupreus* was first given by Moynihan (1966), who described 10 vocal signals in three different categories according to their frequency (high, medium and low pitch) and loudness (table 1.2). He also described two non-vocal signals: “sneezes” and “gnashing”. Following this study, Robinson (1979a) provided additional description of acoustic signals of the same species. By measuring the climax of some loud calls, Robinson put forward a finer differentiation of the *C. cupreus* repertoire with 13 acoustic signals, instead of 10 (see table 1.2). Apart from the “infant distress calls”, all vocalisations are produced by both juveniles and adults (Moynihan, 1966, Robinson, 1979a).

According to both authors, most vocalisations of *C. cupreus* were repeated to form phrases and combined into short or long sequences that were used in different contexts (Moynihan, 1966, Robinson, 1979a,b). By playing back artificially constructed male loud call sequences, Robinson (1979a) also showed that monkeys were sensitive to call order, as they produced more moans in reaction to the abnormal sequence (Robinson,

1979a). The most studied vocal behaviour of *Callicebus* monkeys is ‘duetting’, long and loud sequences of calls uttered by the mated pair in a coordinated way. Duets can be produced spontaneously or in response to the duets by other breeding pairs, a behaviour that seems to function in delineating or enforcing territorial boundaries (Moynihan, 1966, Kinzey et al., 1977, Kinzey, 1981, Kinzey and Robinson, 1983, Robinson, 1979b, Robinson, 1979a, 1981, Robinson et al., 1987, Müller, 1995a,b, Müller and Anzenberger, 2002).

Apart from the study of duets, very little work has been conducted on titi monkey vocal behaviour and little progress has been made concerning the function, meaning and context-specific use of *their* vocal utterances. Virtually nothing is known about their vocalisations in the predation context. This apparent lack of interest goes beyond the need for increasing the knowledge about titi monkeys’ vocal behaviour. Most primates vocalise when threatened by a predator and the study of these alarm signals have proved particularly valuable for examining the cognitive processes in non-human animals (Zuberbühler, 2006). Additionally, the study of alarm calls has attracted the attention of many different disciplines (including physics, linguistics, anthropology and sociology) particularly interested in the origins of language and semantic signalling (Fitch, 2010).

Table 1.2. Description of the vocal repertoire of *Callicebus cupreus*.

Call Type: Moynihan (1966)	Call type: Robinson (1979a)	Context/Situation of use
High pitched, quiet vocalizations		
Squeaks, Whistles and Trills	Squeaks, Whistles and Trills	During intra-specific disputes and fights; when other groups are calling; during movements towards the sound source; when seriously disturbed by the observer.
-	Chirps (low intense chirrups)	When foraging in the presence of an observer. No apparent response from others.
Screams	Screams ¹	Considered as similar pattern of squeaks, whistles and trill, although much louder than, and often intermediates, between whistles and trills. Robinson heard only twice from wild animals. One following fighting between two young non-resident males in the presence of a non-resident female. The other was when one female leapt back after apparently encountering something in a tree. The male approached rapidly and both animals gave Chirrup-panting simultaneously
Sneezes ²	Sneezes	Following chases between monkeys of different groups; During rapid avoidance of an observer. Some are autochthonous (attempts to clear the nasal passages).
-	Infant distress calls	Especially if disturbed by the observer's presence; if they are unable to negotiate a difficult crossing; the male often approaches and allows the infant to mount.
Medium pitched		
Chirrups	Chirrups ³	Chirrups are uttered in a wide variety of social circumstances; when locating and recognizing group members to foster group cohesion; common during boundary encounters and disturbance from the observer's presence.
Chuck	Chirrups ³	Chucks are more common in obviously hostile situations. Mainly in disputes among captive animals and as reactions to the sight or sound of humans, and in some territorial boundary disputes in the wild. It may function as alarm or warning calls when uttered as reactions to humans.
Low pitched, loud vocalizations		
Moans	Moans	During boundary interactions and after leaving the Sleeping tree. Moans usually introduce duets to ensure that the mates are in close proximity.

Resonating notes	Pants	Before moving towards the boundaries and following rest periods. Occur in phrases as part of longer sequences; Pants are sexually dimorphic, male can be heard 500m away and female can be heard 50m away; May be uttered by isolated individuals but are more common in compound songs during vigorous and prolonged disputes.
Resonating notes	Honks	Occur in phrases as part of longer sequences. Honks are given between phrases of pants during duetting.
Resonating notes	Bellows	Occur in phrases as part of longer sequences. The loudest in the repertoire; Occur in male and female solo sequences and duetting sequences.
Grunts	Grunts ⁴	Occasionally produced before and after duetting during intergroup interactions
Pumping notes	Pumps	Occur in all sequences with the exception of the short “chirrup-panting” sequence described by Robinson (1979a).

¹Screams were classified as loud low-pitched vocalisations by Robinson (1979a).

² Sneezes were described as a non-vocal signal by Moynihan (1966).

³Chirrupings were classified as loud, low-pitched vocalisations by Robinson (1979a).

⁴Gunts were classified as high-pitched vocalisations by Robinson (1979a).

1.6.2 A graded vocal system

The standard procedure for describing primate vocal signals continues to be that of defining a finite number of physically distinctive, relatively stereotyped acoustic units (i.e. the vocalisation or call), each with its own meaning or message (Peters, 1986). However, very often in the primate literature, one signal may grade into another, particularly under intermediate stimulus conditions (Collias 1987). This type of system was first described by Green (1975) with his detailed investigation into the coo vocalisations produced by Japanese macaques. Green (1975) identified seven acoustic variants within the coo call type and mapped these variants onto the circumstances of production; there were clear correlations between variants and the contexts in which they were produced. A similar system was also described by Cleveland and Snowdon (1982) with their detailed investigation into the vocal repertoire of cotton-top tamarins (*Saguinus oedipus oedipus*). Cleveland and Snowdon (1982) identified eight acoustic variants within the chirp call type which were also highly correlated with its circumstances of production. These examples illustrate that repertoires of highly graded calls can potentially encode large amounts of information, if the relationship between signal grading and circumstances of production is highly correlated (Marler, 1976).

When analysing *Callicebus* communication, Moynihan (1966) found that most of the acoustic signals frequently intergraded with one another, through many intermediate patterns. However, since he did not perceive “any of the patterns as being produced as a response to any (or every) sudden change in the external environment” (page 122), whether this aspect of the acoustic repertoire of *Callicebus cupreus* had functional significance remained obscure. Robinson’s (1979a) study with the same species found some evidence for specificity of production in the loud call sequences, defined by different transitional probabilities according to contexts, and playbacks of normal and abnormal sequences further illustrated that listeners were aware of these differences.

Although these studies suggested that order differences could affect response, no evidence was presented to support the existence of functionally referential calls and/or sequences in *Callicebus* monkeys. Moreover, since no systematic study has been carried out with black-fronted titi monkeys, it may be possible that different aspects of their environment have influenced their cognitive abilities to communicate in response to external events in a different manner from Amazonian species.

1.7. Main aims of study and thesis outline

As part of a general effort to investigate the origins of referential communication in primates, the main goal of my thesis work was to systematically investigate and describe the occurrence of alarm calls in a vocally complex species of New World primate. Studies on communication in the predation context have revealed the use of complex cognitive mechanisms by non-human primates, which have been traditionally used to draw parallels between animal communication and human language. Most studies in this field come from Old World monkeys and prosimians, and so far only a few species of New World monkeys have been investigated (table 1.1). These showed some similarities suggesting an early origin for this ability in the primate lineage, but aspects of the primate predator signalling remain unclear, either due to behavioural features or methodological limitations.

The *Callicebus* are an especially interesting group in this respect, because of the existence of both a diverse and complex vocal system; yet, so far, no evidence has been found to support claims that their calls encode information about predators. Working with a well-habituated population should enable systematic comparisons within and between call production contexts, and results from my study will I hope be used to gain a better understanding of the cognitive processes underlying the production and

perception of vocalisations in response to potential predator species. I describe their behaviour during natural and experimental predator encounters.

I begin by describing the field site, the predator species present in the area and the methods for the general data collection. In chapter three I give a gross description of all call types identified during natural and experimental predatory contexts. Although it is not exhaustive, this description will help the reader to better understand the variation and specificity of call types according to different predator types described in subsequent chapters. Chapter four describes the anti-predator behaviour of these monkeys during real encounters with live predators. In chapter five I present the results from a study designed to experimentally test monkeys' responses to different predator species and a non-predator animal.

Chapter six investigates the effect of playbacks of alarm calls previously produced in response to two types of predators (aerial and terrestrial) and establishes how the alarm calling system described for *nigrifrons* should be classified with regards to the wider theory (i.e. “functionally referential”, “urgency based” or a “mixed system”).

In chapter seven I report the results of a pioneering experimental design which tested both type and the location of a predator. The experiment compares monkeys' behavioural and vocal responses to two different predators presented in the canopy and on the ground. Chapter eight, finally summarises and discusses the main findings of this study, and draws a comprehensive conclusion about the form and function of *C. nigrifrons* alarm call responses. I will also present some future directions for this area of study.

CHAPTER 2: General Methodology

2.1 Study site

2.1.1. Characteristics and location

This research was conducted at the Reserva Particular do Patrimônio Natural (Private Natural Heritage reserve) Santuário da Serra do Caraça (or Caraça Reserve), an 11,000ha private reserve area located in the Minas Gerais state in the southeast of Brazil (20°05S; 43°29W), see Figure 2.1. The reserve is in the southern portion of the Espinhaço Mountain range, a mountainous complex that delimitates a transition zone between the "Cerrado" (savannas) and the Atlantic Forest, in the south, and a zone of transition from "Cerrado" to Atlantic Forest to "Caatinga" (xeric forest of small thorny trees and shrubs) in the north (Derby 1966, Giulietti & Pirani 1988, Giulietti *et al.* 1997). Vegetation in different stages of ecological succession is present in the region (figure 2.2), as a consequence of timber extraction and "slash-and-burn" practices employed in the past (Silva e Talamoni, 2003, Coelho et al., 2008).

The reserve belongs to the Província Brasileira da Congregação da Missão, a branch of the Catholic Church that receives a large number of tourists, around 68,000 per year. The main impact on monkeys' behaviour is the tourists, who talk loudly while walking through the main trails. This impact is increased in some periods, especially weekends and holidays. Apart from that, titi monkeys (and any other primate species) do not face any other human-related threat within the reserve and hunting does not appear to occur. However, the situation on the neighbouring lands, which are owned by mining companies, is not stable, and there is increasing pressure to amplify their activities at the border or even inside the reserve.



Figure 2.1. Map of Brazil, with the geographical location of the Serra do Caraça Natural Private Reserve encircled, and the Tanque Grande and Cascatinha field areas indicated. Map produced by Lilian Lacerda and Bruno Durão and used with permission.

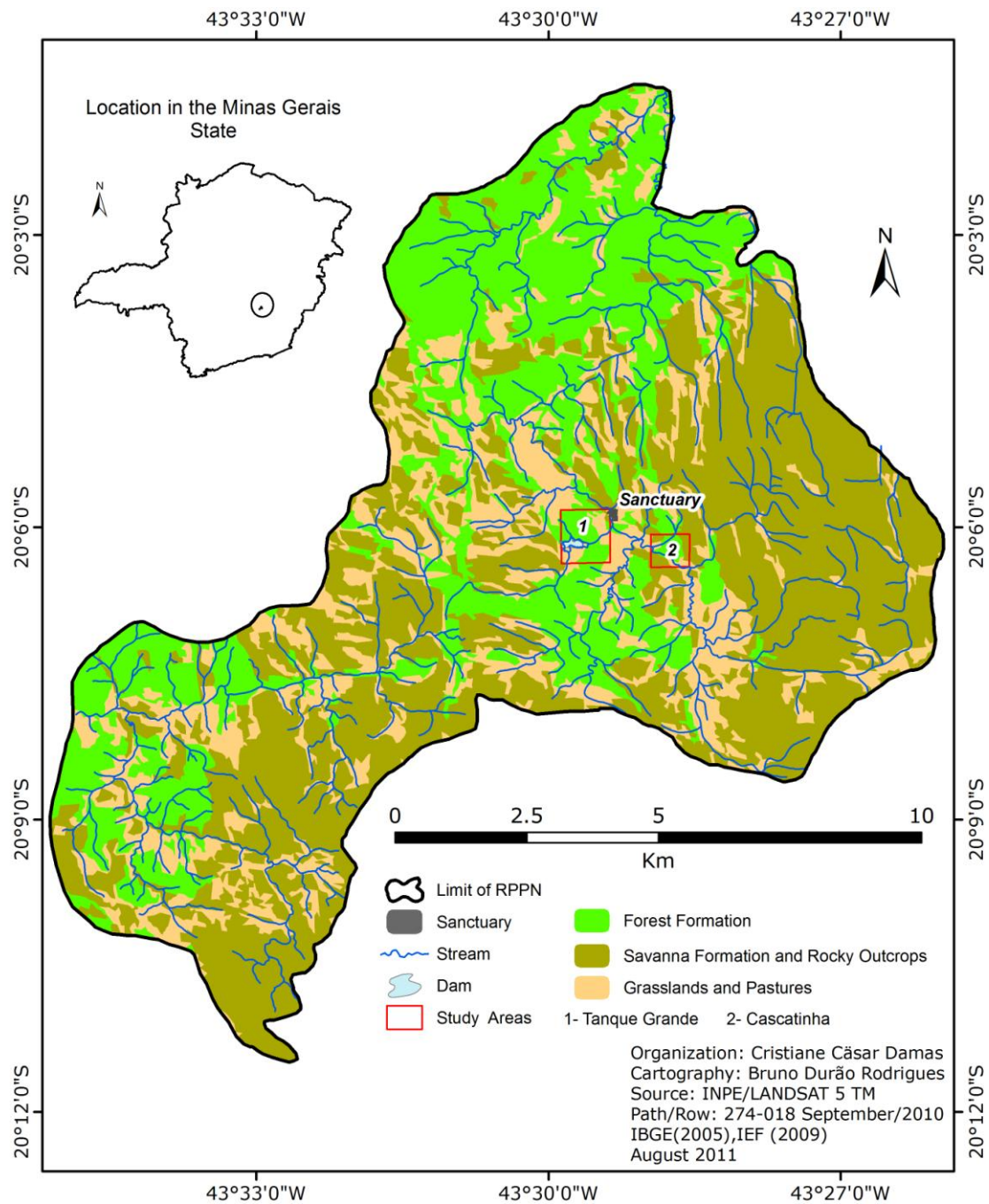


Figure 2.2. Main forest types within the Serra do Caraça Natural Private Reserve, in the state of Minas Gerais, Brazil.

Altitudes range from 850 to 2,072 m and the climate is marked by a rainy summer (October-March) and dry winter (April-September). The average annual rainfall is 1983.5 mm (1984-2007), of which approximately 88% concentrated on the rainy months (figure 2.3). Rainfall during the study period was within the average and it is illustrated in figure 2.4.

There is no systematic collection of temperature data in the reserve. Therefore, to describe the temperature during the study period I used data collected daily by a nearby mining company, Anglo Gold Ashanti. The weather station is open-air and collects hourly data on temperature, relative humidity, rainfall, and wind speed and direction. It is located at the “Mina Córrego do Sítio”/Anglo Gold Ashanti (longitude 656146.88, latitude 7785733.1 UTM – SAD 69), at an altitude of 1,015 metros, and some 9 km from the sanctuary, representing a similar pattern to Caraça. To correct for differences in altitude between the weather station (1,015m of altitude) and the field site (~1,300m of altitude) I used the Environmental Lapse Rate (ELR) of 6.49 K(°C)/1,000 m, resulting in a difference of 1.85 °C cooler in Caraça in relation to the station. I then plotted the data to illustrate the average temperature during the study months (Figure 2.5). According to this corrected database, the minimum temperature registered during the study period was 5.05°C on 13/06/2010 while the maximum was 33.65°C on 05/10/2008. I did not have access to data of July/2008 and July/2010, because the station only started functioning in August/2008, and it had some technical problems in the last month of my field period, respectively.

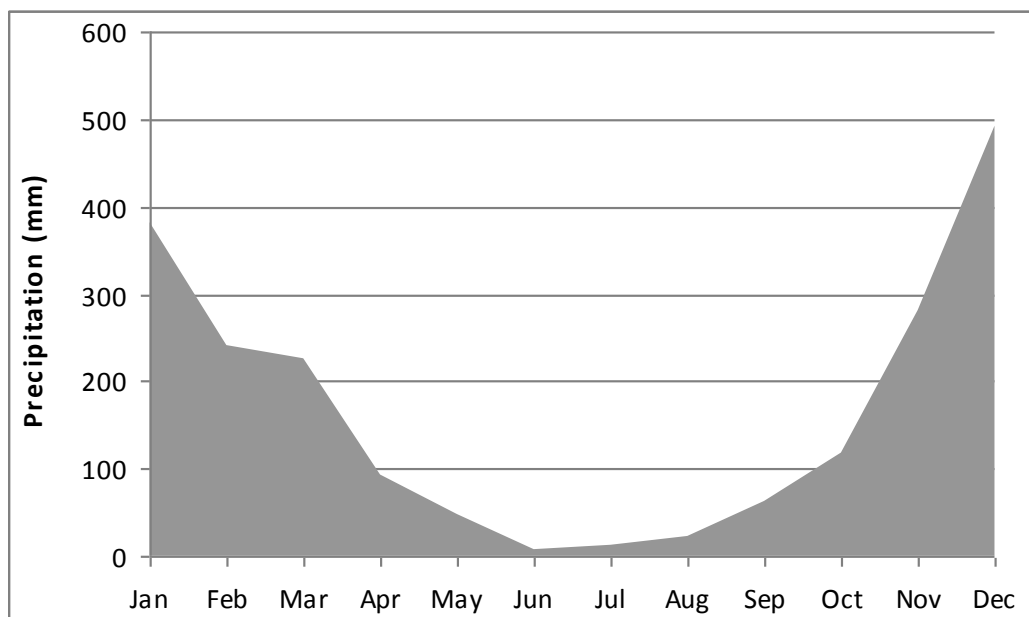


Figure 2.3. Average precipitation per month during the period 1984-2007. Graph built from the data collected in the field and available at the National Agency of Water website (ANA - Agência Nacional de Águas, www.hidroweb.ana.gov.br).

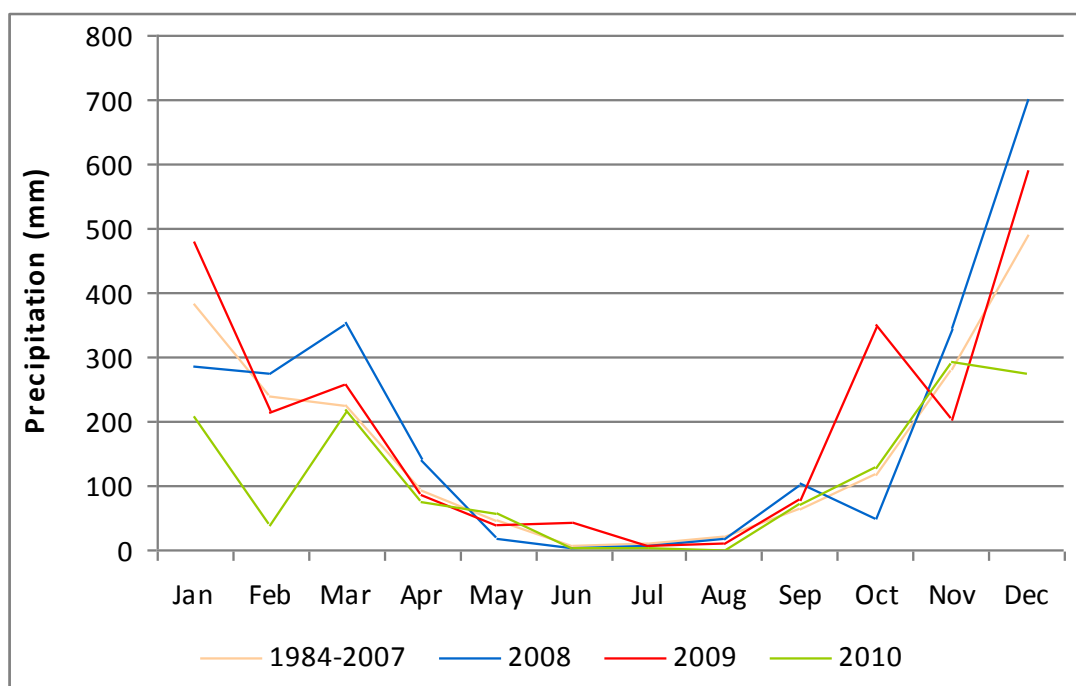


Figure 2.4. Total monthly rainfall during the study period (2008-2010) compared to average data from the period 1984-2007, in orange. Graph built from the data collected in the field and available at the National Agency of Water website (ANA - Agência Nacional de Águas, www.hidroweb.ana.gov.br).

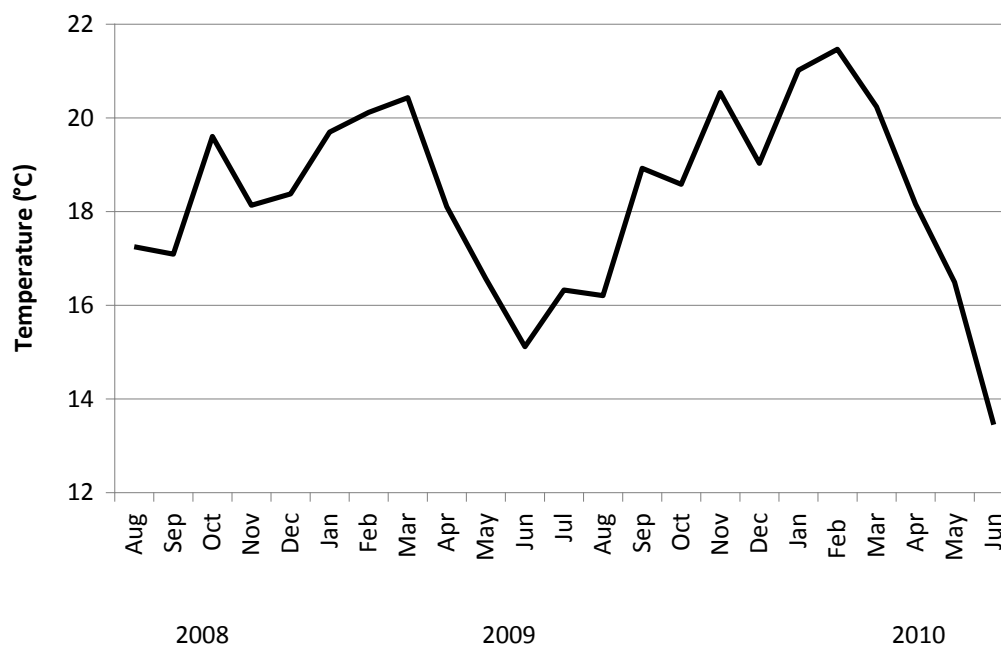


Figure 2.5. Average monthly temperatures of the study areas (Tanque Grande and Cascatinga, altitude around 1300m). Temperature was taken by Anglo Gold Ashanti in the period of August/2008 to June/2010 and corrected for the study areas in Caraça by reducing 1.85 °C in the mean values. Graph built using data provided by Juliana Carla Thomé/Anglo Gold Ashanti.

2.1.2. Fauna

According to recent studies, there is a rich fauna in the Caraça Reserve, including 286 published bird species (Vasconcelos et al., 2003, although the updated count is up to 340 species: Vasconcelos, personal communication), 43 amphibians (Canelas and Bertoluci, 2007), 37 reptiles (Abreu, personal communication) and 70 mammals (Talamoni, personal communication). Five species of diurnal primates occur in the forested areas of the Caraça Private Reserve: black-fronted titi monkeys (*Callicebus nigrifrons*), black-tufted-ear marmosets (*Callithrix penicillata*), white-fronted marmosets (*Callithrix geoffroyi*), black capuchin monkeys (*Cebus nigritus*) and Southern brown howler monkeys (*Alouatta clamitans*), although no group of the latter has been seen during the last 10 years (Hirsch, 2003; personal observation).

2.2. Study groups

In Caraça, black-fronted titi monkeys (*Callicebus nigrifrons*) appear to be present in most Atlantic Forest fragments (personal observation), however, my study was carried out mainly with five habituated groups of black-fronted titi monkeys that are part of a long-term study (“Projeto Guigó Minas”) coordinated by myself and Dr. R. J. Young.

Habituation of pairs and/or family groups to human observers started in “Tanque Grande” forest in August 2003. By August 2004, after an inconsistent effort, one group, GD, was very well habituated, permitting researchers (usually two at each time) to follow them in close proximity until they were settled on one sleeping tree. Other groups were habituated, including two that disappeared, in 2006 and 2007 respectively, and for this study I then habituated two other groups (GM and GP) in “Cascatinha” forest, to have a minimum of five groups.

Callicebus monkeys are considered to be adults around 2.5 years (30 months) old, an age at which they are potentially sexually reproductive (Valeggia et al 1999). For individuals present from the beginning of the habituation, I estimated the age based on size and apparent reproductive state. Infants and juveniles’ ages were based on size and date of birth, when known. Therefore, for this study, I consider: (a) adults to be fully grown individuals (>30months), (b) sub-adults as slightly smaller individuals than adults (between 18-30mo), (c) juveniles as approximately half grown individuals (6-18mo) and (d) infants as much less than half grown individuals (0-6mo) (modified from Moynihan 1966, and de Luna et al 2010). Group identification and composition during the study are presented in table 2.1.

Table 2.1. Age-sex composition of study groups during the study period (July/2008- July/2010).

Group	Size*	Observed since	AM	AF	S	J	I
A	5-7	July/2008‡	3	1	1	1	1
D	2-4	Aug/2004	2	1	0	0	1
M	4-5	July/2008†	1	2	1	0	1
P	3-5	July/2008†	1	2	0	1	1
R	2-4	Aug/2004	3	1	0	0	0

Legend: AM = adult male, AF= adult female, S = sub-adult, J = juvenile, I = infant.

*Group sizes varied due to births, migration and disappearances.

‡Group A in this study was different from previous studies (Cäsar and Young, 2008, Cäsar et al., 2008); however, at least one individual (adult female) was observed since August/2006.

†Groups M and P were observed from 2008 (and were fully habituated at the beginning of data collection) to guarantee a minimum of 5 different groups, as at least three previous groups that were habituated, or in the process of habituation, disappeared before the beginning of this study (Cäsar, unpublished data).

Groups A, D and R were neighbours and were living with at least four other unhabituated groups in “Tanque Grande” forest. Groups M and P were neighbours and shared the “Cascatinha” forest with at least two unhabituated groups. These forests were disconnected from one another, with about 2 km of distance between them. However, although they were physically isolated, loud calls produced by groups in Tanque Grande could be heard by adjacent groups living in Cascatinha forest (see figure 2.6 for illustration of the forests). Additional (opportunistic) data were collected from a semi-habituated group (group B), which were frequently involved in intergroup encounters with the three habituated groups in Tanque Grande area, especially group R. Changes in composition during the course of the study (2008-2010) occurred in all groups, but group M, and demographic information is available in table 2.2.



Figure 2.6. Photo of the field site showing the two forested areas where the study was conducted. Groups A, D, R and B live in Tanque Grande forest (right circle) and groups M and P on Cascatinha (left circle) forest.

2.2.1 Interspecies interactions

According to the literature, titis rarely associate with other primate species, except with *Saguinus* spp. in food trees in Amazon forests (Bicca-Marques et al 2006; Kinzey, 1981, Wright, 1996). In Caraça, black-fronted titi monkeys sometimes associate with marmosets (*Callithrix penicillata*), the most common species in the area; marmosets seem to follow the titis for a variable amount of time at a relatively close distance during foraging. This association is variable and, most of the time, titis seem to accept the marmosets' presence; however, when they happen to be in the same food tree, titis tend to chase marmosets away. Interestingly, on one occasion, however, a group of marmosets who had arrived first at a fruit tree then chased away two adult titis who approach them (Cäsar, personal observation).

When encountering capuchins, titis usually get very agitated and, usually after producing some quiet calls, either move away quickly or hide in the bushes or lower canopy until capuchins have left the area. Behavioural and vocal responses will be

described in more detail in the chapters dealing with anti-predator responses. Capuchins, on the other hand, seem to be particularly interested in titis, and they have been observed chasing some individuals, especially juveniles (Cäsar, personal observation). Accordingly, Sampaio and Ferrari (2005) reported a predation of an infant titi monkey (*Callicebus moloch*) by a tufted capuchin (*Cebus apella*), suggesting that the behaviour witnessed in black-fronted titi monkeys in response to *Cebus nigratus* might be anti-predator related. I will refer to this and other potential species that prey on *Callicebus* in chapter 4.

2.2.1 Rates of disappearance

Nine individuals from five different groups of *C. nigrifrons* disappeared between July/2008 and July/2010 (table 2.2). Disappearances of individuals older than 30 months were most likely due to dispersion. Disappearances of juveniles and infants were most likely due to predation, as individuals were either too young (less than 6 months) to survive by themselves or to have dispersed (13 months). One individual Ricota disappeared with 18 months of age and could have either been predated or dispersed, as she had just reached the sub-adulthood stage. Observations on the same population suggest that she was most likely predated, as all other individuals, in process of or, dispersing did so from an age of at least 30 months. For instance, one case of confirmed dispersion happened the following month after I left the field: Mel (>30 months) was last seen by myself with group M in July/2010 and in August/2010 was observed together with an unidentified adult male, apparently forming a new group (Cäsar et al., unpublished data). Other individuals would disappear for different amounts of time and return to their presumably natal group. For instance, Aguirre (≥ 30 months) disappeared from group A for two months, returned to his group in February/2009 and stayed until the end of this study. Diego and Rafael (both 36 months old) disappeared for one or more days, several times during the study period, but they

still spent some days with their presumably natal groups until the end of this study. Finally, an adult female, Diana, disappeared after her mate had an extra-pair copulation with a dispersing female, Denise. Diana had been paired with Desbotado for at least five years before Denise took over her place in group D (Căsar et al., unpublished data). These movements, along with other disappearances, influenced the number of individuals in some of the groups during different experiments.

Predations of at least two unidentified individuals were confirmed in both areas by me: I encountered titi's hair on the lower canopy and on the ground (figure 2.7). I also observed several predation attempts by different predator species (data will be presented later on).



Figure 2.7. Hair of an unidentified titi monkey found on the sub-canopy and ground (Photos taken by Cristiane Căsar).

Table 2.2. Identification of individuals studied during July/2008 and July/2010. Group status is described as P: paired couple, TO: theoretically offspring. Sex class as M: male, F: female and U: unknown. Age class is A: adult, SA: sub-adult, J: juvenile, I: Infant. Asterisks denote individuals that disappeared during the study.

Group	Members	Code	Group status	Sex	Age class	Presumed fate ¹
GA						
	Apolo	AP	P	M	A	
	Ana	ANA	P	F	A	
	Aquiles	AQ	TO	M	A	
	Aguirre	AG	TO	M	A	dispersion process
	Andre	AN	TO	M	J, SA	
	Infant 1*	A1	TO	U	I	suspected predation
	Infant 2	A2	TO	U	I, J	
GD						
	Desbotado	DE	P	M	A	
	Diana*	DI	P	F	A	suspected desertion
	Diego	DG	TO	M	A	dispersion process
	Daniel*	DA	TO	M	I, J	suspected predation
	Infant 1*	D1	TO	U	I	suspected predation
	Denise	DE	P	F	A	
GM						
	Michael	MJ	P	M	A	
	Marion	MA	P	F	A	
	Mel	ME	TO	F	A	
	Medico	MD	TO	U	I, J	
	Michelle	MI	TO	F	I, J	
GP						
	Picasso	PI	P	M	A	
	Paula	PAU	P‡	F	A	
	Paris	PA	P‡	F	A	
	Infant 1*	P1	TO	U	I	suspected predation
	Pedro	PE	TO	M	I, J	
	Infant 2*	P2	TO	U	I	suspected predation
	Infant 3*	P3	TO	U	I	suspected predation
GR						
	Roberto	RB	P	M	A	
	Rosa	RS	P	F	A	
	Renata*	RE	TO	F	A	dispersed
	Rafael	RF	TO	M	A	dispersion process
	Ricota*	RC	TO	F	J-SA	suspected predation or dispersed

¹See text for details. ‡ Paula and Paris both had infants, of about 3-4 months difference in age, when I started habituating the group. The existence of two reproductive females in one *Callicebus* group is unusual and represents the first evidence of polygyny in titi monkeys (Cäsar, unpublished data).

2.3. Potential predators

There are a number of potential predators of primates in the Reserve, including several species of raptors and mammalian carnivores. Potentially dangerous raptors include the crowned eagle (*Harpyhaliaetus coronatus*), the black-chested buzzard-eagle (*Geronoaetus melanoleucus*) and the black hawk-eagle (*Spizaetus tyrannus*), along with several species of hawks (e.g. *Accipiter sp.*) and owls (Vasconcelos and Melo Júnior, 2001; Vasconcelos, 2001). For several genera (*Harpia*, *Spizaetus*, *Accipiter*, *Morphnus*, *Leucopternis*, *Spizastur*) there is direct evidence of predation on Neotropical primates (Miller and Treves, 2011, Ferrari, 2009, Boinski and Chapman, 1995, Klein et al 1988), while the other species are suspected predators. The area is also inhabited by several mammalian carnivores, including tayras (*Eira barbara*) and at least four species of cats: ocelots (*Leopardus pardalis*), oncillas (*Leopardus tigrinus*), jaguarundis (*Herpailurus yagouaroundi*, pumas (*Puma concolor*) and possibly jaguars (*Panthera onca*). All, but oncilla and jaguarundis are confirmed primate predators (de Luna et al., 2010; Bezerra et al., 2009; Ferrari, 2009; Ludwig et al., 2007; Bianchi and Mendes, 2007; Miranda et al., 2005). Some species of poisonous snakes, such as jararacas and rattlesnake, also inhabit the reserve (personal observation) and, although there is no record of monkeys' fatality by these species, they may still represent a threat especially when monkeys go near to or on the ground. Finally, titi monkeys have been observed being preyed by capuchin monkeys (in Freese and Oppenheimer, 1981; Sampaio and Ferrari, 2005).

Raptors are likely to represent the greatest predatory threat to these monkeys because they can attack at all heights, whereas most mammalian carnivores are terrestrial and rely on ambush. Moreover, as in most other field studies, the presence of human observers is likely to have a bigger effect in deterring terrestrial, rather than aerial predators (de Luna, et al 2010).

2.3.1 Predator hunting techniques

As mentioned earlier in the general introduction, differences in the predators' hunting techniques have been suggested as an important factor in shaping different animals' anti-predator behaviours, including the use of alarm calls. Moreover, besides being exposed to a wide range of predators, living in three-dimensional environments, which requires a variety of potential escape options, is also considered an important factor that influenced the diversification of anti-predator vocalizations and responses (Macedonia & Evans, 1993). Thus, to be able to understand the anti-predator behaviour of titi monkeys, an understanding of their predators' hunting techniques is needed, and it is described below. There is a large range of potential predator species at Caraça but I only focus on the species I used as predator models in my experiments (see figure 5.1, chapter 5).

2.3.2 Predator models

Boa

I used two models of Boa constrictor in my experiment: one stuffed uncoiled 2.7m long (big snake) and one coiled 80cm long (small snake). The *Boa constrictor* is a heavy-bodied snake, and large specimens can weigh up to 27kg and measure up to 4 m in length (O'Shea, 2007, Cisneros-Heredia et al., 2005). Although considered semi-arboreal snakes, they become mostly terrestrial as they become older and heavier (Mehrtens, 1987). They feed on lizards, birds and small to medium sized mammals, including several monkeys: callitrichids (*Saguinus*) and cebids (*Saimiri*, *Cebus*, *Alouatta* and *Chiropotes*) (Chapman, 1986, Ferrari et al., 2004, Perry et al., 2003, Shahuano Tello et al., 2002, Bartecki & Heymann, 1987). Moreover, Cisneros-Heredia et al., (2005) reported the first boa predation on a titi monkey (*C. discolor*) in the Ecuadorian Amazon. On this occasion, the authors encountered a four meters length *Boa constrictor* constricting a titi monkey at some 5 meters off the ground. There is no

record for *Boa constrictor* in Caraça; however, I decided to use it as a snake model in my study mainly for two reasons. Firstly, most reported attacks by Neotropical snakes on monkeys are attributed to *Boa constrictor* (Ferrari, 2009), and secondly, since the area is home to several species of poisonous snakes (personal observation), which may represent a danger to monkeys (Correa and Coutinho, 1997, observed a death of an infant of *Callithrix aurita*), I assumed that monkeys might not differentiate between species of snakes, but rather consider them as a threat based on their shape and behaviour. An observation to support this assumption is that one student of the long-term project witnessed a female alarm calling to a rattlesnake on the ground (M. Queiróz, personal communication).

Caracara

I used a stuffed adult caracara. The Southern Caracara, *Caracara plancus*, is an opportunistic raptor that feeds mainly on carcasses of dead animals, but will also steal food from other raptors, and take live prey if the opportunity arises (mostly insects or other small animals, including birds and mammals). They are considered to have one of the most diversified diets and versatile foraging techniques among the Falconiformes (Sazima, 2007, Travaini et al., 2001), including foraging on swarming leafcutter ants (Sazima, 2007). When preying upon medium sized vertebrates, for instance, their techniques include to “search on wings”, “wait on perch” and “raids nests” (Sazima, 2007). There is no report of predation by Caracara on monkeys, however, since they are such an opportunistic predator, and have been seen triggering anti-predator responses from titi monkeys at the field site (results will be presented later on), I decided to include it as a potential predator species in my experiments.

Oncilla

I used a stuffed adult oncilla, an individual which was found dead within the reserve. The oncilla (*Leopardus tigrinus*), also known as little spotted cat, is a small wild cat of

South America, with a size similar to that of a domestic cat. Its fur has a yellow-gold pelage with dark rosettes arranged mainly on the dorsum and side of the body (Emmons 1990). Little is known about its behaviour and ecology, however, studies of scats and regurgitations has shown that oncillas mainly preyed upon on small mammals, as well as arboreal marsupials, birds, reptiles and invertebrates (Rocha-Mendes et al., 2010, Wang, 2002). Their hunting behaviour is unknown; however, one can draw some conclusions based on similarities with two other wild spotted cats: ocelots and margays. Ocelots, which are larger and more robust, hunt mainly on the ground (Emmons 1988), while margay, the smallest, show many adaptations for arboreal living, and therefore, forage mainly in trees (Guggisberg 1975, Konecny 1989). The smaller margays (and possibly oncillas), are able to walk further out on branches than the ocelot, and its longer tail enables it to more easily maintain balance (Emmons 1990). A recent report of oncillas preying on larger species, such as coatis (*Nasua nasua*), tapetis (*Sylvilagus brasiliensis*) and paca (*Cuniculus paca*), suggests a possible opportunistic/scavenging behavior (Rocha-Mendes et al., 2010). There is no evidence of titi predation by oncillas, however, vestige of titis found in faecal samples of ocelots (Bianchi, 2001, Bianchi and Mendes, 2007) and margays (Defler, 2004), suggest these monkeys may be preyed by other species of small cats as well.

Puma

I used a stuffed adult puma. The puma, *Puma (Herpailurus) yagouaroundi*, is a large felid described as an “ambush predator”, hunting during the daytime by means of stealth (Holmes and Laundré, 2006, Emmons, 1990). Its diet in the Neotropics is composed mainly of medium to large sized mammals, including: peccaries, deer, pacas, coatis and capybaras; but also small rodents, birds, reptiles and amphibians (Emmons 1987, Talamoni, personal communication). Predation of arboreal species (including neotropical primates) by pumas has been reported to occur (review in Calleia et al., 2009 and Miller and Treves, 2011). Although pumas may be able to climb trees, they

are too heavy to reach the outermost branches, and will normally be unable to move within the canopy (Ferrari, 2009) and are, therefore, most likely to take these prey on some rare encounter with a vulnerable individual (Emmons, 1987).

Tayra

I used a stuffed adult tayra. The tayra (*Eira barbara*) is a large sized mustelid carnivore, weighing up to 7kg, with a slender and muscular body, a long tail and long legs with strong claws (Presley 2000). It is a solitary generalist and opportunist omnivore that hunts during the day and at twilight. Tayras are expert climbers and can be seen foraging both in trees and on the ground (personal observation). They feed on a range of items, including fruits, reptiles, small birds and mammals (Presley, 2000). Mammal species in tayra's diet include tamarins (Moynihan, 1970), common marmoset and the pale-throated three-toed sloth (Bezerra et al., 2008) and attempts on titi monkeys (de Luna et al., 2010; this study).

2.4. Data collection

2.4.1 Study periods

The study was composed of 3 field seasons: two studies of six months each (July-December 2008 and May-October 2009), and a third season in May-July 2010. All observations were recorded during the activity period of the animals (approximately from 5:00 to 18:00 h in the wet season) ranging approximately 11-13 hours a day. I maintained contact with at least one study group for 564, 555 and 176 hours respectively, which corresponded to 85% of the total time (1,530 hours) in the field.

2.4.2 Behavioural data

The usual methods to locate groups were to walk along the trail system and follow vocal cues. Upon finding a group, I collected data continuously (Altmann, 1974) until the focal group was lost or settled in one sleeping tree (ST). When I stayed with the focal group until they were settled on a sleeping tree, I tried to arrive before they left on the next morning and follow the same group for a full day. I did that at least once a month with each group to record the movement pattern and intergroup encounters throughout the day (not presented in this thesis). After having a full day completed I would change to another group the next day, by either looking for it in its home-range or wait until the previous group had an encounter with a prominent group.

2.4.3 Recording and digitalisation of the vocal repertoire

Recordings were made with a SENNHEISER K6/M66 directional microphone and MARANTZ PMD660 solid-state recorder (44.1 kHz sampling rate; 16 bits accuracy). Any additional verbal comments were later transcribed. All recordings were transferred digitally onto a desktop computer. The auditory and visual categorization of the calls, together with the acoustic analysis were conducted through the PRAAT[®] acoustic analysis software (Boersma and Weenink, 2005, version 5.1; www.praat.org). In PRAAT, the following spectral settings were applied to measure fundamental frequency: pitch range 500-11,000 Hz, spectrogram view range 0-22 kHz (to determine the number of harmonics) and 0-5 kHz (window length 0.01 s, dynamic range 70 dB).

2.4.4 Behavioural responses during natural and experimental predatory events

General description

After a visual and auditory discrimination of the calls, I then coded and counted the large number of vocalisations produced by these monkeys during the whole time of their vocal responses, or up to the first five minutes after detection of a predator. For each vocal response, the following structural measures were determined:

- (a) The total length of the response (in minutes);
- (b) The types of calls present during a response to up to five minutes after detection.
- (c) The total number of calls during the first minute, and up to the first five minutes after detection of a potential predator. For this I used the tool 'create a text grid' on PRAAT, which enabled me to mark and name all the calls produced in a response (Fig. 2.8). Call rate per individual was calculated by dividing the total number of calls produced in a response to a potential predator, during the first minute after detection and during the first five minutes after detection, by the number of juveniles and adults in a group at the time of the response.
- (d) The proportion of each call type during the first minute and during the first five minutes after detection of a predator. The proportion of each call type was calculated by dividing the number of each call type by the total number of calls produced in a response.

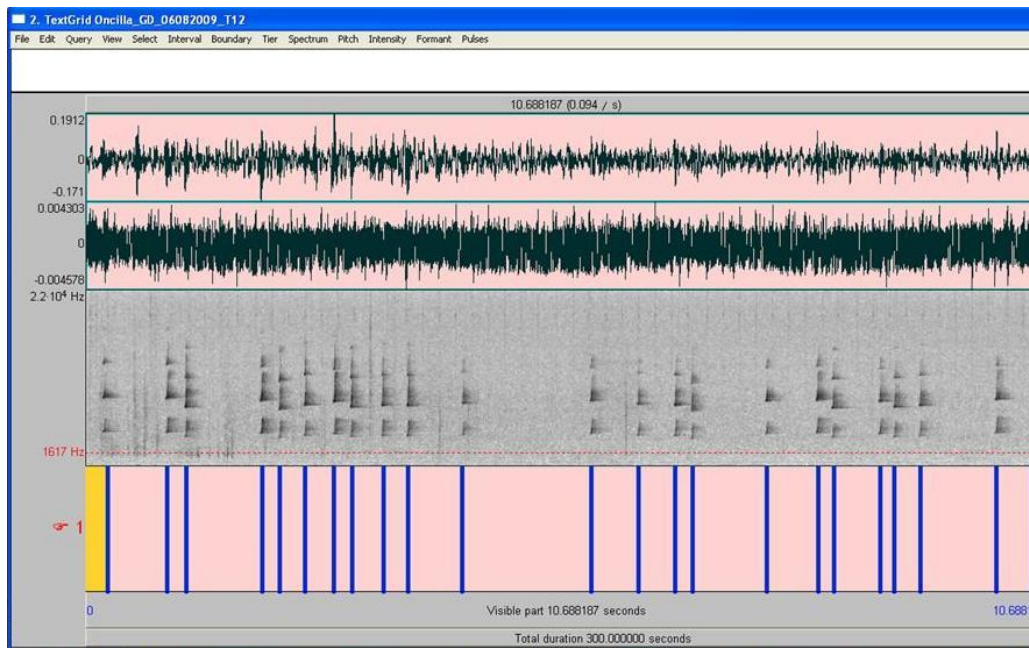


Figure 2.8. Illustration showing call coding and counting, blue bars, depicting 23 B calls in 10.6s.

2.4.5 Vocal data and definitions

To provide a conservative estimate of the repertoire size (during predatory contexts), I used a visual-discrimination method using frequency and time information from the spectrograms to classify calls. Studies on animal communication usually use different terms to refer to and to describe the vocalisations produced by a specific species. In this study I am using the following terms:

Call or vocalisation: the sound produced by the vibration of the vocal cords (Fitch, 2010). It was nominated as having a single or multiple syllables/units. A call was also determined as “tonal” when the fundamental and its harmonics could be seen clearly or “noisy” when the call was harsh.

Harmonics or bands: harmonics bands at integer multiples of the fundamental frequency (as in Rendell et al., 1999).

Syllable: a unit or note usually defined as a sound that at normal intensity makes a single continuous impression, with associated frequency bands (or harmonics), in time on the spectrogram (Eisenberger, 1976).

Simple call: A call of one syllable only. To classify a simple call, I used the criterion that the syllable must have been produced independently of other sounds within a call (not as composite, see below) and be produced by all groups (adapted from Davidson and Wilkinson 2002) (example figure 2.9).

Composite call: According to Robinson (1979a), titi monkeys' loud calls have a common pattern of inhalation and-exhalation to produce two or three syllables and a pause. Robinson (1979a) described these type of calls as having: (a) a “pre-introduction” high pitched, quiet, short syllable, followed immediately by (b) a loud, low-pitched “introduction”, which are both produced by inhalation, followed by (c) a “pause”, and (d) the “climax” produced by exhalation (figure 2.9). Not all multiple calls have all four components and variance will be found in almost all call types. Here, I am considering a composite call as all calls compound of at least two, usually one high- and one low-pitched, syllables (examples on figure 2.10). In most cases, the second syllable would be not produced independently of the first syllable, for instance the “suffix”/second syllable of call BS (chapter 3), would only happen after a call B and never by itself.

Series or phrases: a repetition or multiplication of at least two calls of the same type (figure 3.10 chapter 3).

Sequences: a combination of two or more calls of at least two different types in a series.

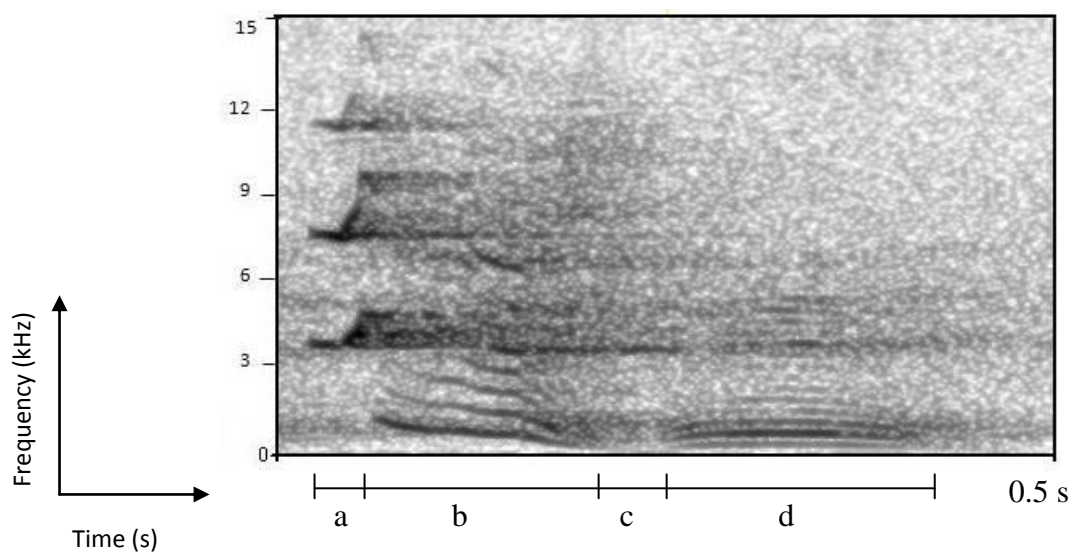


Figure 2.9. Components of a composite call with three syllables and a pause (a) “pre-introduction” (b) “introduction”, (c) a “pause”, and (d) “climax”. Classification according to Robinson (1979a).

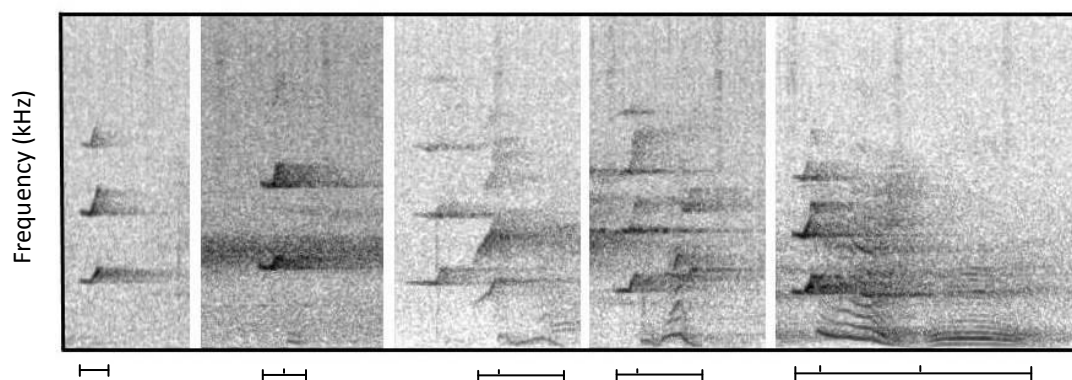


Figure 2.10. Example of calls of *Callicebus nigrifrons* showing one simple (one syllable) and four composite (with two or three different syllables) calls.

2.5 Data analysis

Statistical analysis were conducted with the statistical package PASW version 18.0 (SPSS Inc., Chicago, IL, U.S.A.), with significance levels set at $\alpha = 0.05$, unless stated otherwise. Data were examined to check if normally distributed (Shapiro-Wilk test) and had homogeneous variances (Levene’s test). When no appropriate transformations were

possible non-parametric alternatives were used. For small sample sizes, exact p-value were calculated (Mundry and Fisher 1998). Details of the various statistical tests and specific methodologies used in this study are provided in the relevant chapters.

CHAPTER 3: The vocal repertoire of *Callicebus nigrifrons* during encounters with predators

Abstract

In this chapter I present the vocal repertoire of black-fronted titi monkeys (*Callicebus nigrifrons*) during encounters with live and with stuffed predator species. Using visual and auditory discrimination I identified 11 calls types (5 simple and 6 composite), which differed strikingly in fundamental frequency (high, medium, low), modulation (e.g. upsweep, downsweep and flat) and amplitude (quiet, loud). Some calls can be produced singly or in sequences, while others are only produced in sequences of one or more call types that seem to function as communicative units. The vocal repertoire presented here is not exhaustive, and represents only the call types and variants given in predator contexts. Based on description and spectrograms, I could tentatively identify some of the vocal categories described in earlier studies on an Amazon species of titi monkey (*Callicebus cupreus*). More detailed analyses will be required to compare calls produced by these two disjunctive species. The main goal of this chapter was to present a first summary description of the main calls. More detailed descriptions of some of the quiet high-pitched calls produced when detecting predators will be presented in chapter 4.

3.1 Introduction

When describing *Callicebus* communication, Moynihan (1966) gave a detailed description of the olfactory, visual, tactile and acoustic signals of captive *Callicebus cupreus*, along with some observations of wild animals. He described 12 acoustic signals, including 10 vocal (squeaks, whistles, trills, screams, chucks and chirrups, moans, grunts, resonating notes and pumping notes) and two non-vocal (sneeze and “gnashing”) patterns. Most of which could be uttered in several different contexts, either alone or in different “phrases”, the term chosen by the author. Apart from some observations of calls produced by captive animals in reaction to human beings (chucks, whistles and trills), he did not find any evidence of vocalisations used in an alarm or warning function. Indeed, he mentioned a disadvantage of most of *Callicebus*’ acoustic patterns by making the caller conspicuous, exposing it to the predator. However, since he never witnessed a predator attack while in the field, and most of his description was based on captive animals, he may have overlooked the existence of alarm calls.

In the late 1970s, Robinson’s (1979) work with wild *Callicebus cupreus* provided a more detailed description of the vocal repertoire. Robinson presented a new description and, by measuring and comparing frequency and temporal measurements of loud calls, split the resonating notes of Moynihan’s original classification into three different vocalisations: “pants”, “honks” and “bellows”. Moreover, he added the term “chirps”, for low intensity chirrups, and grouped the chucks and chirrups in one unique class (chirrups). However, since his focus was on the loud sequences produced during intergroup communication, little mention was made of the possibility that some calls might be used as alarm calls. Specifically, he mentioned that grunts were sometimes given in response to his presence, while sneezes were produced by captive animals when approached by unfamiliar human beings. He also mentioned that chirrups were common in the wild during the confusion associated with the presence of different animals, including squirrels, howler and capuchin monkeys, and when cattle moved

through the area. Apart from that, no mention was made of the existence of alarm calls, and his description of the quiet high-pitched calls (rarely heard at his study site) were based on Moynihan's original work.

Later reports of predation on titi monkeys, with some sporadic observations of the species' anti-predator behaviour, mentioned the occurrence of some vocalisations that may be used in predatory contexts. For instance, when reporting predation on titi monkeys, some observers witnessed the animals producing some loud calls and mobbing the potential predator. However, no systematic description of the repertoire or the behavioural responses to these events was provided (de Luna et al, 2010, Cisneros-Heredia et al., 2005, Sampaio and Ferrari, 2005).

All these reports illustrate the lack of studies on anti-predator behaviour and associated vocalisations of *Callicebus* species, which is problematic to understand how they use an (apparently) extremely complex vocal system to communicate about predator detection to conspecifics, and maybe to other species. Additionally, systematic recordings of vocalisations (especially the quiet types) of wild animals can be very difficult in environments such as tropical forests, which are heavily influenced by extraneous background noises of other animals, especially birds. To minimise the influence of background noise and record inconspicuous calls it is crucial that subjects are habituated to human observers, allowing them to approach and record even soft calls from a relatively short distance without interfering with the monkeys' behaviour. Moreover, habituated animals allow observers to experimentally elicit predator-related calling (e.g. by presenting predator models) while systematic recordings of the monkeys' behavioural and vocal responses is performed in a relatively natural fashion.

In this chapter, I present an auditory and visual description of *Callicebus nigrifrons* vocalisations produced during encounters with natural and stuffed predators. I will illustrate each call type with an example spectrogram and a description of the specific circumstances which elicited it, from my own observations of the black-fronted titi

monkeys at the Caraça study site. A more detailed description of some of these alarm calls will be provided in following chapters.

3.2 Methods

3.2.1 Description of the repertoire

Each call was classified through an auditory and visual inspection of its spectrogram. By assessing the structure of the vocalisations, I classified them as simple (i.e. one syllable only) or composite (two or more syllables). In general, a syllable (note or unit) was defined as a sound that at normal intensity makes a single continuous impression, with associated frequency bands, in time on the spectrogram (Eisenberger, 1976, see general methods). I then gave them names and illustrated each call type with an example spectrogram and a description of the specific circumstances that elicited it, from my own observations of the black-fronted titi monkeys in Caraça. Since I was mostly interested in describing the first calls produced when detecting a predator, I will present a gross description of the loud calls to illustrate the types of calls produced later on in their sequences. I tentatively identified some of the vocal categories described by Moynihan (1966) and Robinson (1979a) on the basis of their descriptions and spectrograms and I include their terminology in parentheses when it appears to be similar to mine.

3.3 Results

I identified 11 different types of calls produced when encountering predator species. The different calls differed strikingly in pitch (low, medium, high), modulation (e.g. upsweep, downsweep, flat) and amplitude (quiet, loud). By assessing the structure of the vocalisations they were classified as simple (i.e. one syllable only), or composite (if compound of two or more syllables). The first category of simple calls included tonal calls with a fundamental frequency between 2 kHz and 9 kHz: a high-pitched “squeak”-

like, “chirp”-like and “cheep”-like call (fig. 3.1). The second category of simple calls included calls with a low pitched fundamental frequency: ‘grunts’ and ‘moans’ (fig. 3.2, 3.3). The third category contained mostly broadband composite calls of first, a high-pitched syllable immediately followed by a low-pitched syllable. These included calls AS, BS, BW (fig. 3.4, 3.5). The fourth category contained broadband composite calls of first a high-pitched syllable (non-compulsory) immediately followed by one or two low-pitched syllables: resonating notes, honks and pumps (figures 3.6, 3.7, 3.8).

3.3.1 Simple high-pitched quiet calls:

My preliminary observations suggested that titi monkeys produced three perceptually distinct high-pitched call types, characterised by different frequency contours, at the beginning of their vocal responses to potential predator species. They were usually very short and soft calls; the pitch of fundamental frequency ranged from 2 kHz of some variants of call B, to almost 9 kHz of extreme calls C. These calls were produced by all five groups in similar contexts.

- a) Call A (“chirp”-like call). A quiet high-pitched, with an ‘arch’-shaped down-sweep modulated call, with or without a stem upsweep (Figure 3.1a). Call A is a monosyllabic and tonal call with a frequency around 5 or 6 kHz and duration around 0.04 seconds. They were produced in response to several species of live raptors, a stuffed perched raptor, and some threats on the canopy, including capuchin monkeys and a stuffed oncilla (see chapter 6). Listeners tended to scan the sky and descend or look for protection under the canopy. This call was never observed during non-predatory contexts.
- b) Call B (“cheep”-like call). A relatively quiet high-pitched ‘S’-shaped, or upsweep, modulated call (Figure 3.1b). Call B is a monosyllabic and tonal call with a lot of variation on the pitch of the fundamental frequency (range from 2.5 to 8 kHz) and duration from 0.01 to 0.05 seconds. Call B was produced in

response to threats on the ground including two live animals: a deer and an unidentified spotted cat, and all stuffed predators (tayra, oncilla, puma, a coiled small snake, and a big uncoiled snake) and a stuffed baby deer. Call B was often produced in non-predatory contexts, especially when monkeys were descending or foraging close to the ground, when an observer was blocking their intended travel path, during some inter-group encounters and, for unhabituated groups, in response to humans.

- c) Call C (“squeak”-like calls). A high-pitched, mostly unmodulated call, but sometimes with a slight upsweep or downsweep towards the end (Figure 3.1c). Extreme calls C were very short and rather soft. The pitch of the fundamental frequency ranged from 4 to 8 kHz and duration from 0.01 to 0.09 seconds. Call C intergrade with other high-pitched calls, mainly whistles and trills, which are not described here due to their low occurrence in this study. It was produced in predatory contexts, although most frequently in response to capuchins and deer, both life and stuffed. During non-predatory contexts, it was usually produced when a neighbouring group was approaching and when monkeys apparently intend to move.

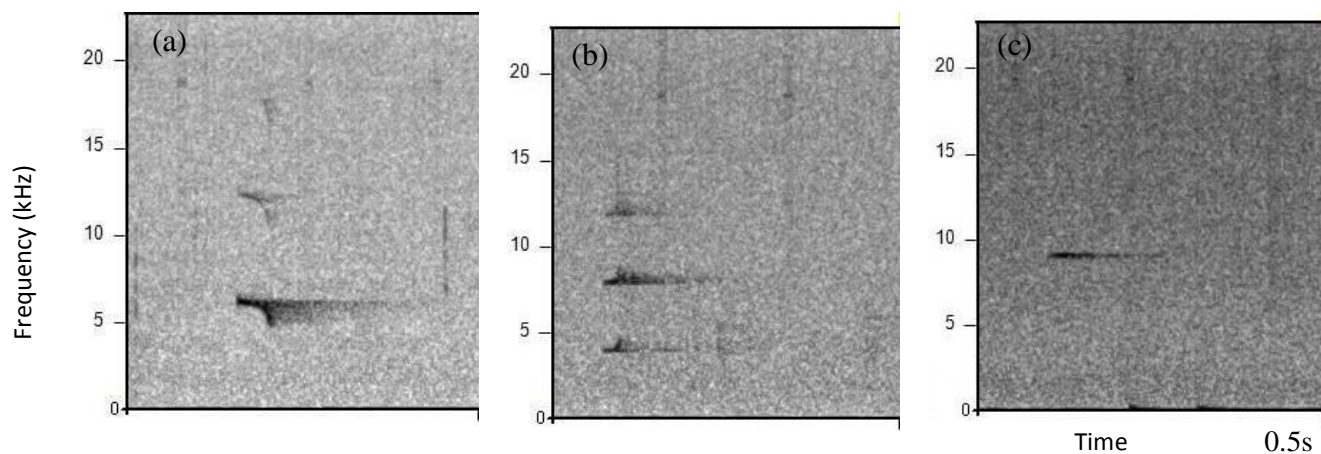


Figure 3.1. Examples of time–frequency spectrograms illustrating three different types of predator-associated calls, produced by group R when detecting potential predator species: (a) Call A, (b) Call B, (c) Call C. All call types were produced by all five groups in similar contexts.

3.3.2 Simple low-pitched calls:

I identified two perceptually distinct monosyllabic low-pitched call types: grunts and moans.

- a) Call G (“grunt”-like) (grunts: Moynihan 1966, Robinson 1979a). These were a noisier, typically unvoiced, low-pitched call with some variation in the number of harmonics. Grunts were monosyllabic and very rare in my sample (figure 3.2). They were only produced by two groups: one in response to a stuffed perched raptor and another in response to an uncoiled big snake. In the last event, however, part of the group was moving towards a neighbouring group and, therefore, this call may as well be related to the intergroup encounter.

- b) Call M (“moan”-like). These calls were low-pitched, usually long and monosyllabic. (Figure 3.3). They were only produced in response to stuffed oncillas and tayra and in one event in response to capuchins.

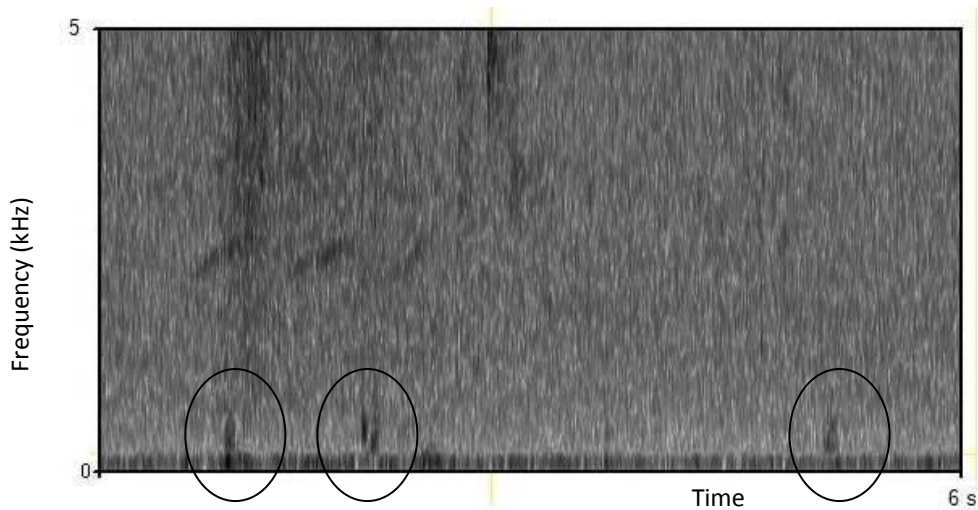


Figure 3.2. Examples of time–frequency spectrograms illustrating four grunts (circled) produced by an adult female of GR in a sequence in response to a raptor on the canopy on 19/09/2008.

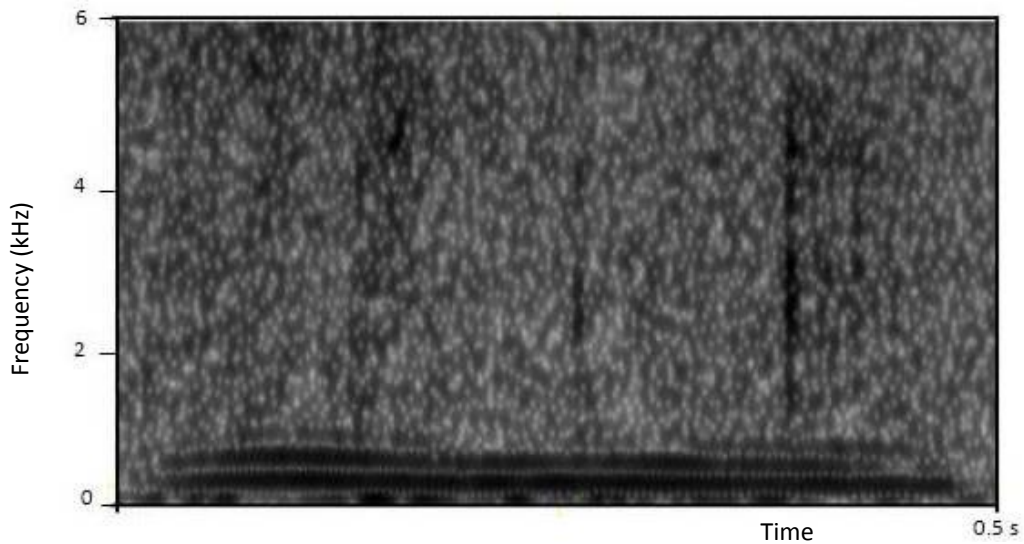


Figure 3.3. Example of time–frequency spectrogram illustrating one “moan” produced by group R in response to a group of capuchin monkeys foraging in the canopy on 02/06/2010.

3.3.3 Composite medium-pitched calls:

These calls were composed of at least two syllables, the first one being a high-pitched syllable immediately followed by a variable length and form low-pitched syllable.

I put them in a different class because: 1) the second syllable (often considered a suffix) is only produced after a high-pitched syllable and 2) they appear to be intermediate utterances between simple high-pitched calls and composite low-pitched calls. Most of these calls extend over a wide range of frequencies and the effect of medium pitch they produce, in human ears, may be the result of averaging. They may represent an increase in arousal as they tend to be produced in a continuum after calls B and before loud calls. Again, the number of calls described here is not exhaustive and, since no measurements were taken of these calls, further variation within and between subjects and contexts may well exist. The proportion of use in different predatory contexts will be presented in chapter 5.

- a) Call AS ('chirrup' and 'chuck': Moynihan 1966; 'chirrup': Robinson 1979a).

A compound call with two syllables, a high-pitched A immediately followed by a low-pitched suffix (Figure 3.4a), which makes it louder and more conspicuous than a pure A. It was mainly produced in response to two eagles flying and perching around group R.

- b) Call BS ('chirrup' and 'chuck': Moynihan 1966; 'chirrup': Robinson 1979a).

A compound call with two syllables, a high-pitched B immediately followed by a low-pitched suffix (Figure 3.4b), which makes it louder and more conspicuous than a pure B. It was produced in response to all stuffed models on the ground, with the exception of snakes.

- c) Call BW ('chirrup' and 'chuck': Moynihan 1966; 'chirrup': Robinson 1979a).

A compound call with two, and sometimes three, syllables, a high-pitched B

immediately followed by a multi-banded suffix or a long no-banded low-pitched suffix (Figure 3.5), which makes it even louder and more conspicuous than BS. The second syllable alone sounds like a ‘whip’ noise. They are usually produced in long sequences between series of, and appear to be intermediates between, BS and loud calls. It was only produced in the sequences in response to oncilla, tayra and puma.

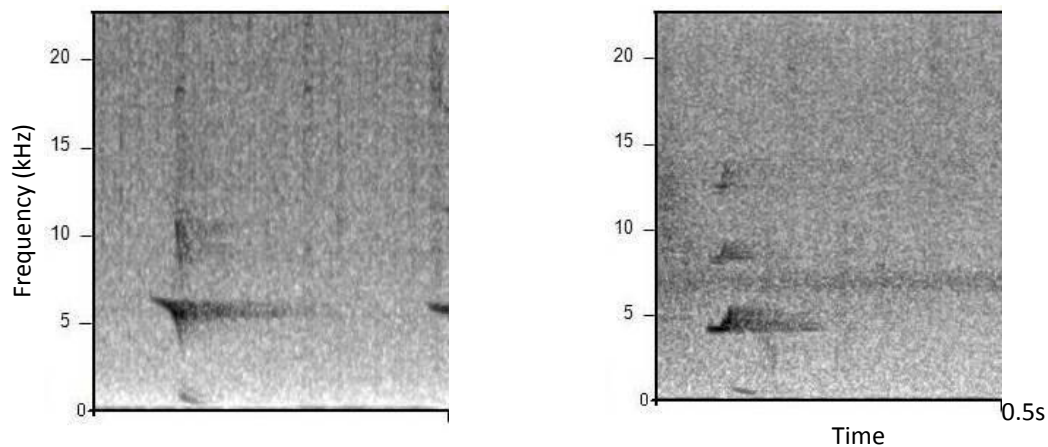


Figure 3.4. Examples of time–frequency spectrograms illustrating two different types of predator-associated calls, produced by group R when detecting potential predator species (a) Call AS (b) Call BS. Call AS was only observed in response to the two eagles flying and perching around the focal group (GR). Call BS was produced by all five groups in similar contexts.

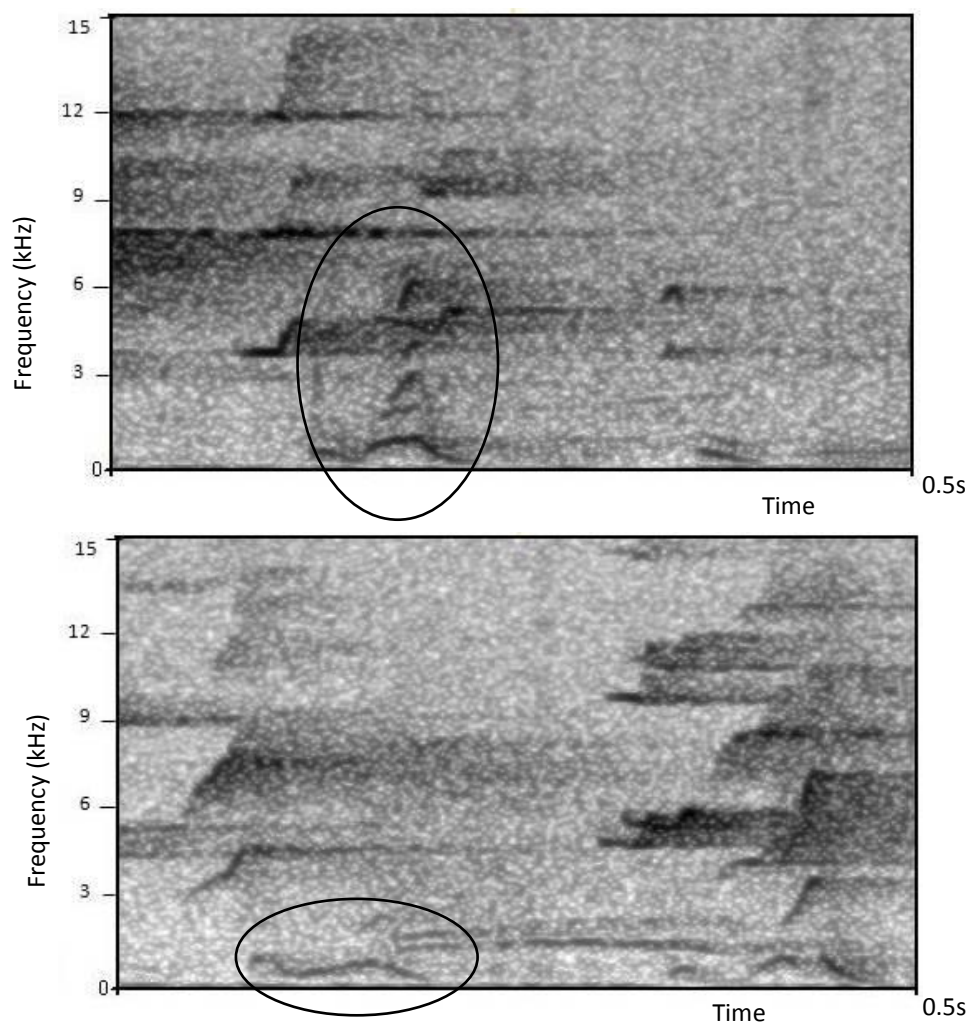


Figure 3.5. Examples of time–frequency spectrograms illustrating different variations of a medium pitch call (B+ whip) produced by GM in response to an unidentified spotted cat on 01/09/2009.

3.3.4 Composite low-pitched loud calls:

I identified three main types of low-pitched loud, calls, which were produced later in the monkeys' call sequences to predators. I did not perform acoustic measurements on them, both because they were not my main focus and also because they are usually produced simultaneously by two or more individuals, which makes it difficult to select a minimum sample of individual calls to analyse. At this point I assumed the loud calls identified here are similar to the calls of *C. cupreus*, as described by Moynihan (1966)

and Robinson (1979a). However, *C. nigrifrons* may not have the same repertoire as of *C. cupreus* and further analysis may indeed prove it otherwise. Thus, the description below is only relevant to account for auditory differences on the loud calls produced during encounters with predators. Nonetheless, I will compare the differences in occurrence and proportion (when they happen in more than one context) between contexts in chapter 5, and present spectrograms, to illustrate the variety and complexity of call types produced during predatory events. During non-predatory contexts, these calls are common in duets and solos.

- c) Honk ('resonating notes': Moynihan 1966; 'honks': Robinson 1979a). Honks were usually compound with two, low-pitched, syllables (Figure 3.6) and occurred in series and sequences, intergrading especially with other loud, low-pitched calls. They were only produced in response to oncilla on the ground.
- d) Resonating calls ('resonating notes': Moynihan 1966; 'pants' and 'bellows': Robinson 1979a). These are the loudest calls in their repertoire and they occurred only in sequences of the same, or different, call types. They were usually compound, and consisted of 3 syllables, which appear to correspond to the 4 'components' of loud calls described by Robinson (1979a): a) a high-pitched "introduction", immediately followed by a b) loud, low-pitched note, a c) "pause" and the d) "climax" (figure 3.7). They were only produced in response to oncilla (in the canopy and on the ground) and tayra.
- e) Pumps ('pumping notes': Moynihan 1966; 'pumps': Robinson 1979a). Figure 3.8. Pumps were usually compound with two similar, low-pitched, syllables and only occur in series and/or sequences, intergrading specially with other loud, low-pitched calls. They were produced in response to oncilla (in the ground and on the canopy) and tayra, and in one event when two eagles pursued them.

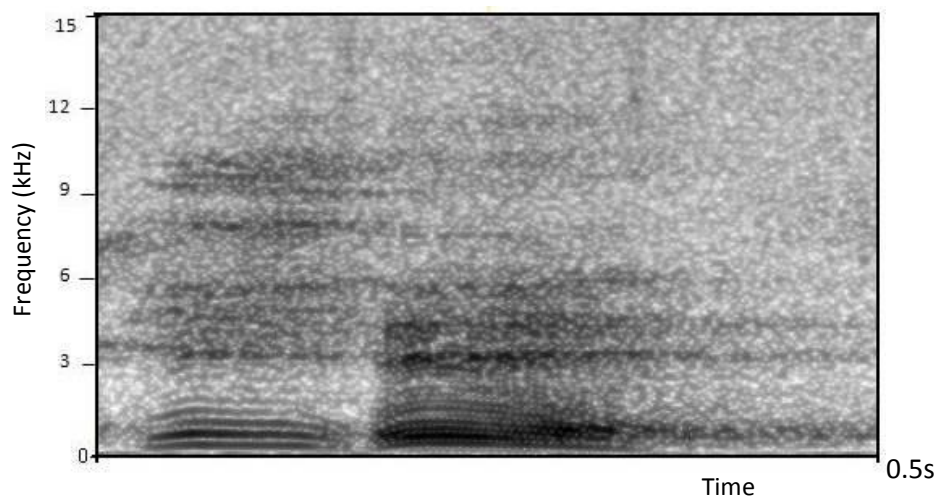


Figure 3.6. Examples of time–frequency spectrograms illustrating one composite “Honk” produced by group R in response to two eagles pursuing the group on 15/07/2009.

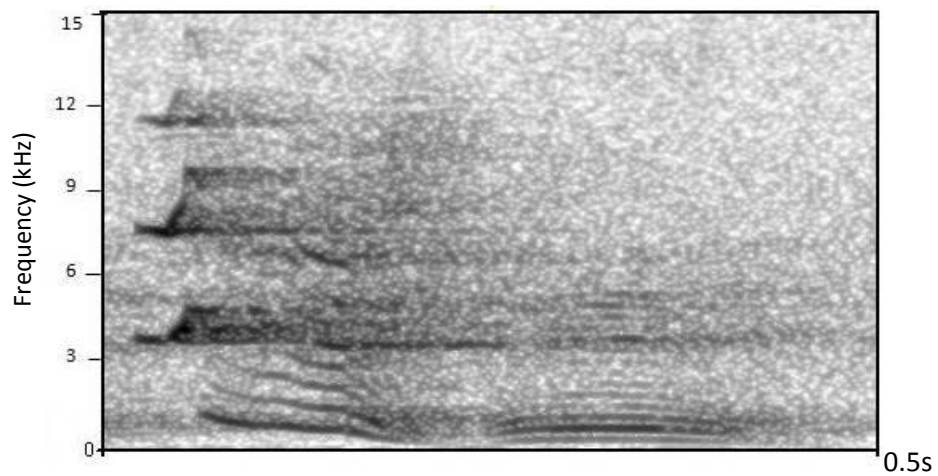


Figure 3.7. Examples of time–frequency spectrograms illustrating one composite “resonating” call produced by a group in response to a stuffed puma in 10/10/2008.

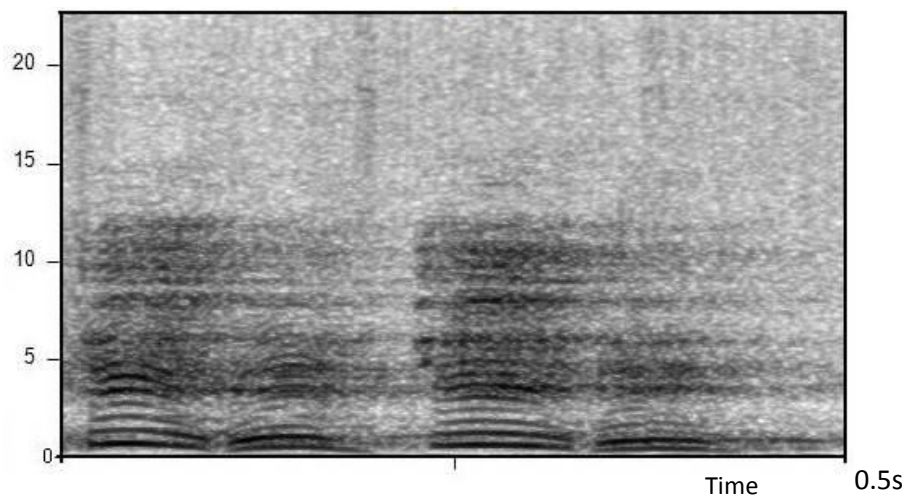


Figure 3.8. Example of time–frequency spectrograms illustrating two composite “Pumps” produced by group R in response to two eagles pursuing them on the 15/07/2009.

3.3.5 Sequences of vocalizations

Some calls, mainly high-pitched, could be produced singly or in repetitions (e.g. doubles, triplets; examples of series of calls A and B are illustrated in figure 3.9) while some, mostly composite low-pitched, were only produced repeatedly in series of the same call type (figure 3.8) or in sequences with different call types (example in figure 3.10).

Series and sequences of high-pitched calls produced in predatory context will be described in chapters 4 to 6.

3.3.6 Graded system

Calls that appeared to be intermediates between calls A/B/C and whistle/trill (not presented here, because of low occurrence) were also identified in my sample and mainly produced in response to an oncilla on the ground. A few intermediates were also produced in response to oncilla positioned in the canopy (see chapter 6) and to a tayra. The gradation will not be considered in this study, and calls classified as intermediate will be grouped as others in chapters 4 and 5.

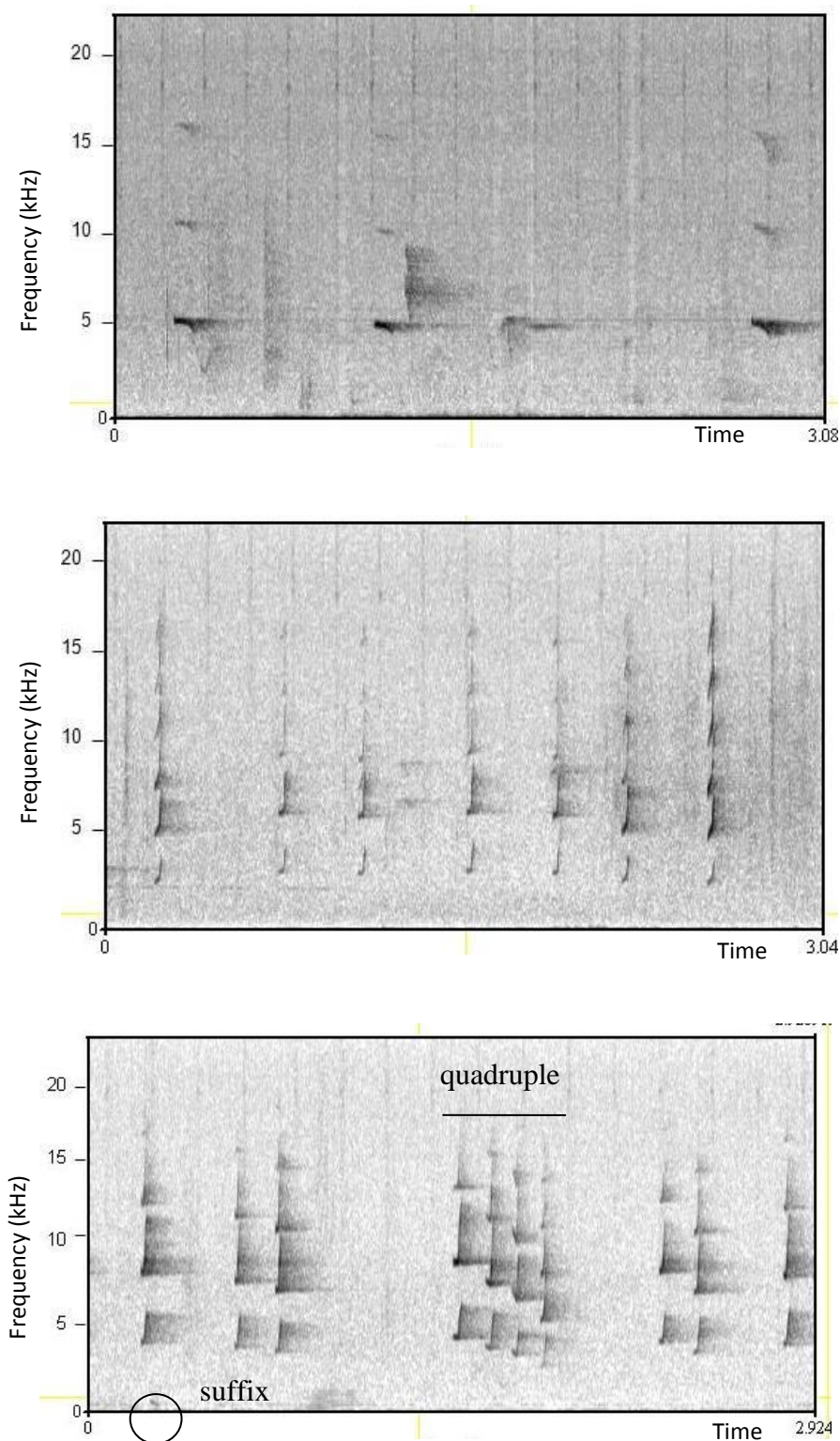


Figure 3.9. Examples of time–frequency spectrograms illustrating three different series of predator-associated calls, produced by different groups when detecting potential predator species: a) series of call A produced by GM in response to a perched eagle on 25/05/2010, b) series of call B produced by group A while descending to feed in the lower substrate at 24/06/2009; c) series of call B produce by GD in response to an oncilla on the ground, depicting a B+suffix, and a quadruple of Call B.

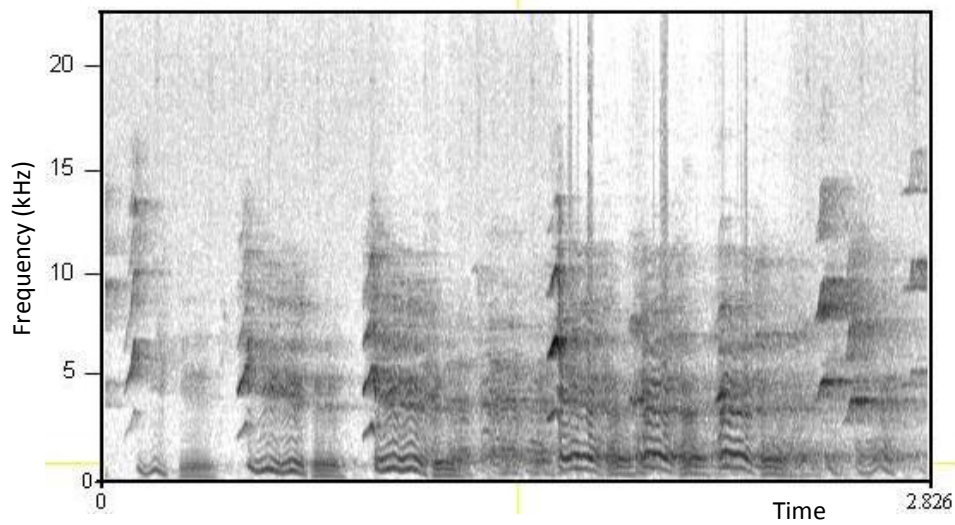


Figure 3.10. Example of time–frequency spectrograms illustrating part of a sequence with composite loud resonating calls produced in response to a tayra.

3.4 Discussion

Based on acoustic characteristics I identified 11 different calls types used by *Callicebus nigrifrons* when encountering predator species. The vocal repertoire described here appears to mirror the complexity of vocalisations produced by other species of *Callicebus*.

In terms of acoustic structure, calls A, B and C consisted of a high-pitched narrow frequency band (although some variants of call B are broadband and may have a different function), an acoustic structure often found in animal alarm calls (Marler, 1955). Such call features have the potential to alert conspecifics, without putting the caller at risk of detection (Campbell & Snowden, 2007). On the other hand, low-pitched broad band calls may function to communicate with both conspecifics and predators. Since low-pitched broadband calls are conspicuous and easier to localise (Marler, 1955) monkeys may be using these calls to communicate detection to a stealth predator.

Call B appears to show a lot of variation in terms of frequency modulation and number of bands (see figures 3.1 and 3.10b-c), which may be indicative of a motivational gradation throughout time. For instance, in my perception, monkeys appear to produce narrow band variants at the beginning of their responses, while broader band variants are more frequent later on. The same pattern appears to happen for the occurrence of the call BS, which will be demonstrated in chapter 5. Whether or not these variations are communicatively important or represent differences in arousal is unclear and will require further investigation.

By looking at spectrograms of the loud calls (figures 3.7, 3.8, 3.9) it appears that one syllable of one call sometimes resembles one of the syllables of a different call. For instance, the first syllable of a “honk” is structurally similar (i.e. has the same shape) to the second syllable of resonating and to the two syllables of pumps, and visually the main differences appear to be the duration and number of harmonics. However, they sound different, and Robinson (1979a) found significant differences in the acoustic structure of the last syllable (thereafter, “climax”) of each one of these calls. Because they are produced in several different contexts, for example during intergroup encounters and predator detection (see chapter 4), a multivariate analysis with measurements of both syllables would be most appropriate to describe these utterances in more detail and to check for differences according to the context. Furthermore, some composite loud calls are initiated by some high-pitched calls (see figure 3.8 for example) a pattern also found in *C. cupreus* loud calls (Robinson, 1979a).

Based on their descriptions and spectrograms I could tentatively identify some of the vocal categories described for *Callicebus cupreus* by Moynihan (1966) and Robinson (1979a), however these gross comparisons should be taken cautiously as one should have access to repertoires of both species to adequately compare their vocalisations and then be able to draw conclusions on similarities and differences.

A detailed description of the three simple high-pitched calls produced in a predatory context will be presented in chapter 4 and the use of composite loud calls illustrated in this chapter will be presented on chapter 5.

CHAPTER 4: The alarm call system of *Callicebus nigrifrons* – Natural Observations

The main results presented in this chapter have been published in the journal
Behavioural Ecology and Sociobiology (Cäsar et al, in press).

Abstract

In this chapter I present results of natural anti-predator responses from five different groups of black-fronted titi monkeys in their Atlantic forest habitat in South Eastern Brazil. When detecting predatory threats, adult group members responded with call sequences that initially consisted of two brief, high-pitched calls with distinct frequency contours. Call A was mainly given to raptors but also to predatory capuchin monkeys and other threats within the canopy, while call B was given to predatory or non-predatory disturbances on the ground. In later parts of the sequences I also recorded a high-pitched unmodulated call C and various low-pitched loud calls. Results therefore suggest that individual calls, especially A and B provide listeners with information about different classes of danger, and perhaps more specific information about specific threats within each class is further provided by adding other call types and different call combinations.

4.1 Introduction

Many birds and mammals produce specific vocalisations in response to predators, a behaviour that can function to alert conspecifics and to communicate detection to the predator (Caro 2005a). Some species produce several acoustically distinct alarm calls in response to different predator types (Seyfarth et al. 1980a, b; Manser et al. 2002; Templeton et al. 2005) but in others, the nature of the danger encountered can be encoded by the number of calls per sequence (Schel et al. 2009), the rate of call delivery (Lemasson et al. 2010), the intensity of calls (Blumstein 1999b) or by combinations of calls (Arnold & Zuberbühler 2006a, b).

If predator-induced calls evoke specific and adaptive responses in recipients researchers typically conclude that the utterance conveys something about the event experienced by the caller, although the nature of this experience has remained controversial (e.g. Seyfarth et al. 1980b; Zuberbühler et al. 1997; Zuberbühler 2001; Rendall et al. 2009). Related to this, it is not clear whether primates intend to produce calls that refer to specific external events, or whether they merely respond to ‘evolutionarily important’ events that place them into different motivations. One way to address this has been by investigating whether associated variables, such as the level of threat experienced by the caller, can explain the caller’s behaviour better than the predatory category (e.g. California ground squirrels: Owings and Virginia 1978). In some other species, it has been argued that alarm calls refer to both the level and type of threat (Manser et al. 2002; Templeton et al. 2005; Sieving et al. 2010). Chickadees (*Poecile atricapilla*), for instance, produce “seet” alarm calls in response to flying raptors and a “chick-a-dee” alarm call in response to a perched or stationary raptor, but their calls also provide information about the threat level (Templeton et al., 2005). Within the primate lineage, the predator type appears to have an overriding influence on alarm calling behaviour, with little evidence that variation in distance or direction has a major impact [vervet monkeys, Cheney and Seyfarth 1990a, and Diana monkeys, Zuberbühler 2000c).

Another line of research in animal alarm calling concerns the evolution of the acoustic morphology of alarm signals. Marler (1955) proposed that low-pitched, broadband calls were more conspicuous and easier to localise for predators than high-pitched, narrowband calls. One prediction from Marler's hypothesis was that the acoustic structure of alarm calls should reflect whether warning or signalling detection is the adaptive anti-predator strategy pursued by the caller. High-pitched alarm calls have usually been interpreted as the product of natural selection having favoured behaviour that alerts others without putting the caller at risk (Campbell and Snowdon 2007). For example, many birds produce high-pitched alarm calls that are difficult to locate. In contrast, many primate alarm calls are loud and conspicuous (e.g. Zuberbühler 2000b; Eckardt and Zuberbühler 2004; Schel et al. 2009), suggesting that callers are less concerned about being located. In some cases, there is direct evidence that these calls are also directed at the predator (Zuberbühler et al. 1997; Caro 2005a). Communicating to a predator can be adaptive if the signal indicates detection, and so interferes with an ambush and surprise-based hunting strategy (Zuberbühler et al. 1997; Zuberbühler et al. 1999; Clarke et al. 2006).

Callicebus monkeys are known for their complex vocal system with numerous high- and low-pitched calls, which can be uttered singly or combined in more complex structures (Moynihan 1966; Robinson 1979a, this study). Early experimental work has documented that the monkeys are sensitive to call order (Robinson 1979a), but since then little progress has been made concerning the function, meaning and context-specific use of their vocal utterances, and virtually nothing is known about their vocalisations in the predation context (Cisneros-Heredia et al. 2005; Sampaio and Ferrari 2005; Ferrari 2009; de Luna et al. 2010). Although predator-specific alarm calls are well described in Old World monkeys (see Zuberbühler 2009 for a review), this is not the case for most New World monkeys (but see Digweed et al. 2005; Fichtel et al. 2005; Kirchhof and Hammerschmidt 2006; Wheeler 2010); which besides having undergone an independent radiation within the primate lineage also differ in essential

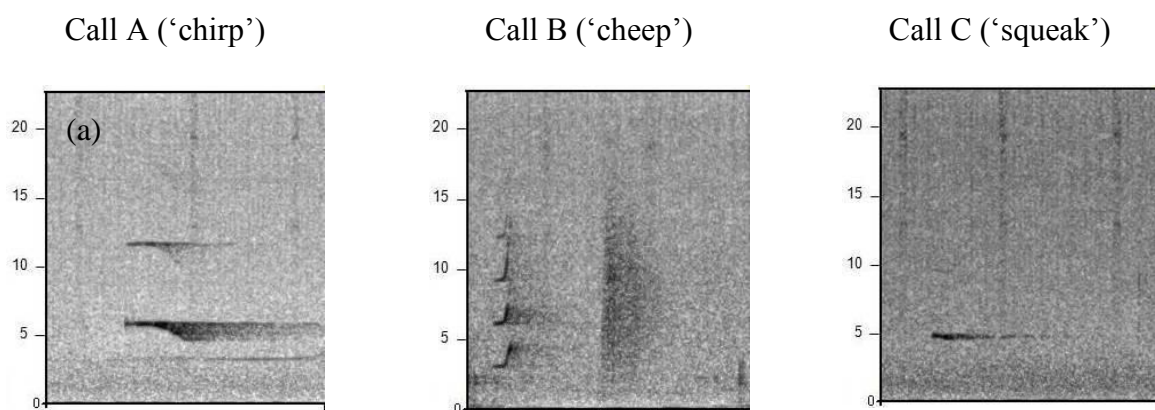
life-history and socio-ecological characteristics from cercopithecines and lemurs (Strier 2007). Therefore, discovering whether and how titi monkeys use specific vocal signals when interacting with predators has considerable theoretical implications for evolutionary theories of primate communication and cognitive process underlying call production. To this end, I conducted a detailed observational study on five groups of black-fronted titi monkeys (*Callicebus nigrifrons*) in their natural Atlantic forest habitat in South Eastern Brazil. My goal was to systematically describe the vocal and locomotor behaviour of free-ranging titi monkeys in response to natural disturbances.

Part I: Call discrimination

4.2 Methods

4.2.1 Acoustic Analyses

Based on previous reports and my pilot data, I was able to discriminate between three main types of soft, high-pitched calls based on frequency contours produced by all five groups during disturbance situations (fig. 4.1). A-calls were arch-shaped with a down-sweep modulation. B-calls were S-shaped with an upsweep modulation. C-calls were flat with a slight up or down modulation (fig 4.1).



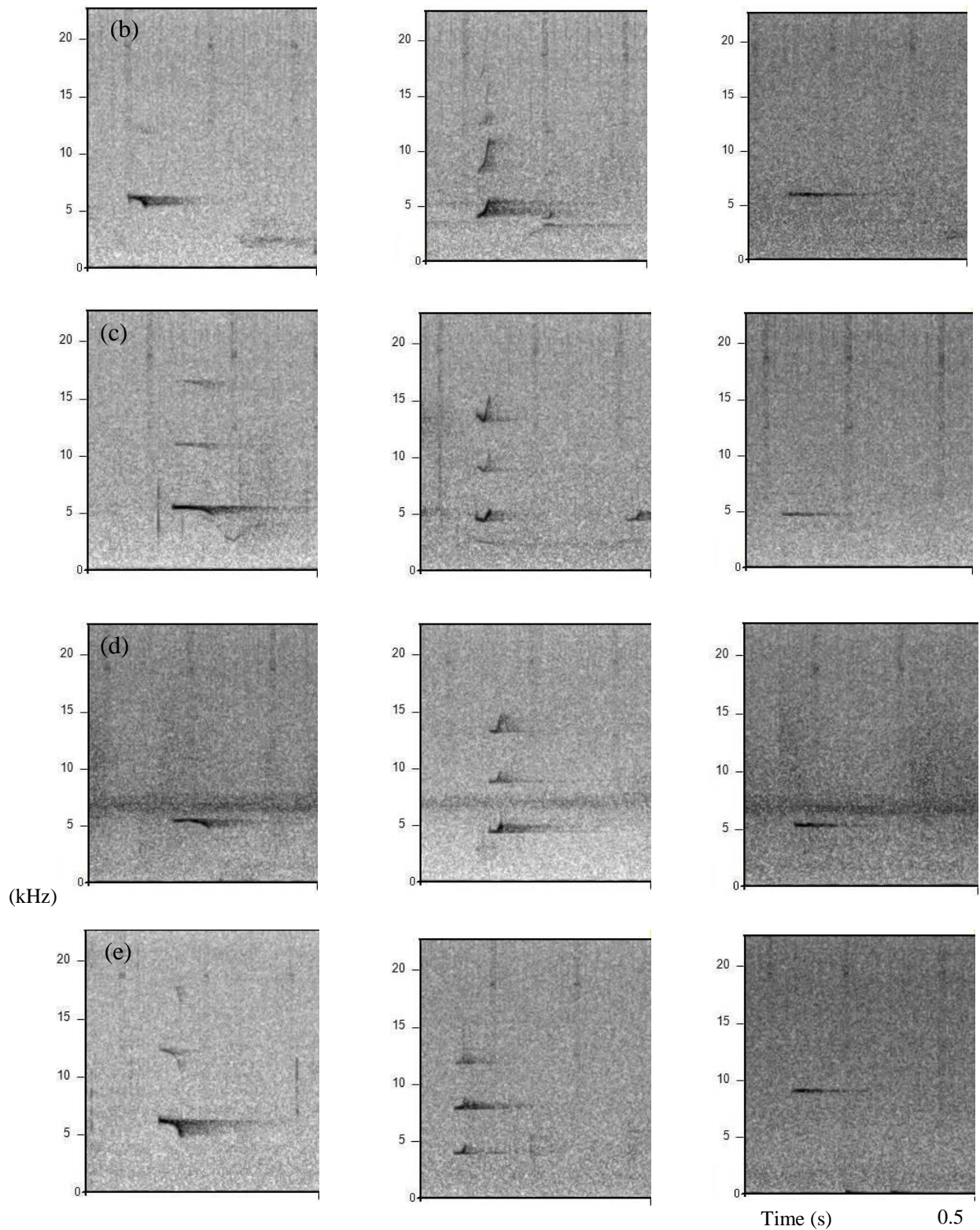


Figure 4.1. Spectrograms illustrating the three different types of predator-associated calls of black-fronted titi monkeys, recorded from (a) Group A, (b) Group D, (c) Group M, (d) Group P, (e) Group R.

To determine whether this qualitative categorisation was valid, I carried out an acoustic analysis. For each call, I measured its: duration and fundamental frequency F0 (‘pitch’) at the beginning, middle and end of the call, as well as the number of harmonics (number of bands at integer multiples of the fundamental frequency, Rendell et al. 1999). Because these calls were very similar in pitch frequency, I compare their modulation (or shape) by splitting the calls into two equal segments and calculating the transition onset, the transition offset and the overall transitions of F0. These variables were chosen both for representing the main features of the three calls and because they could be easily measured manually from a spectrogram. All measurements and spectrographic illustrations were conducted with PRAAT acoustic analysis software (version 5.1; www.praat.org). Figure 4.2 illustrates how the parameters were obtained.

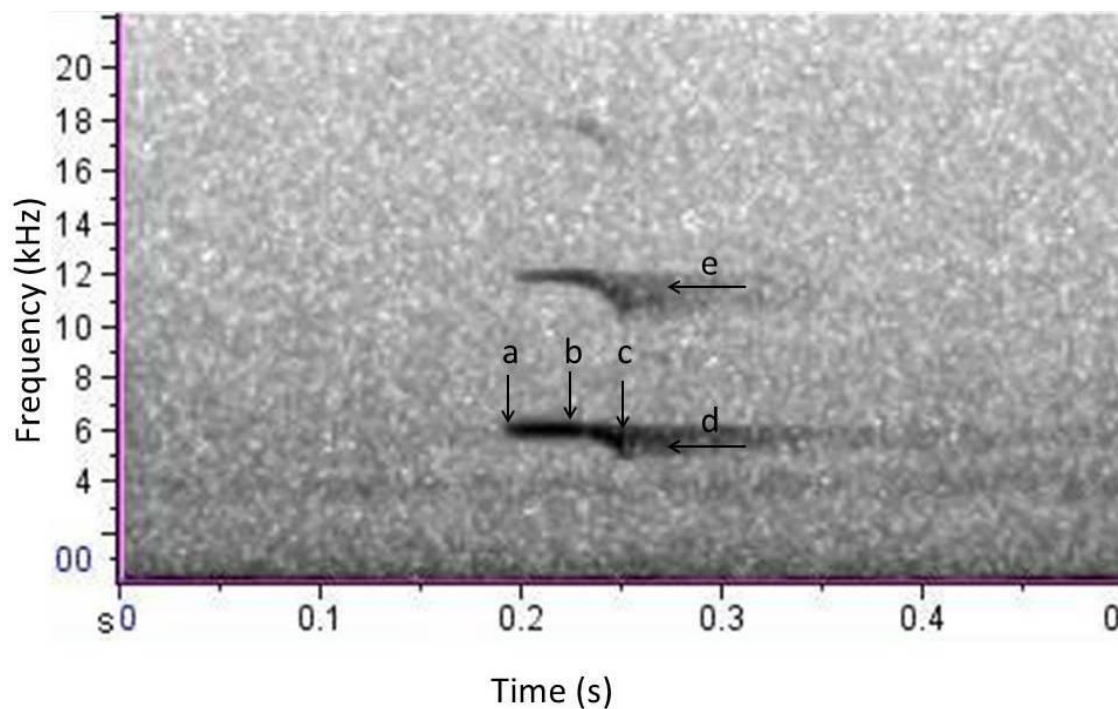


Figure 4.2. Temporal and frequency variables measured on predator-associated calls: call duration (s) = $c - a$; fundamental frequency, F0 (Hz) = d ; N harmonics (1 in this call) = e ; frequency of maximum energy at call onset = a ; frequency of maximum energy at call middle = b ; frequency of maximum energy at call end = c ; transition onset (Δ Hz) = $(a) - (b)$; transition offset (Δ Hz) = $(b) - (c)$; overall transition (Δ Hz) = $(c) - (a)$. Depicted is a time–frequency spectrogram of a “chirp” vocalization made by adult female “Paris”.

4.2.2 Statistical analyses

When carrying out statistical analyses of acoustic variables it is important to select measurements that are only moderately correlated with each other. A standard way of determining this set of variables is by regressing all parameters to check for co-linearity and removing parameters with a variance inflation factor greater than 4 (Glantz and Slinker 2001). Following this procedure, I looked for outliers by producing standardized Z scores for all values and rejecting all cases in which at least one parameter had a Z score of greater than 3.29 (Tabachnick and Fidell 2001). I then conducted a discriminant function analysis (DFA) to determine whether the set of acoustic variables, when combined in one model, could discriminate between the main three high-pitched call types given in response to predators.

I ran one-way related-samples analysis of variance tests to examine whether each of the acoustic parameters varied statistically with each call type. I conducted post hoc pairwise Sidak-corrected comparisons to examine whether any of the acoustic parameters could discriminate between the call types.

I also carried out an inter-observer reliability test between myself and a second rater, who was naïve to the hypotheses. After completing training on N=20 pre-classified calls (randomly selected, equivalent to 5% of the full call set), the second observer classified another 20 calls, again randomly selected. I calculated Cohen's Kappa coefficients to determine whether the levels of observer agreement reached the required reliability level (Cohen's $\kappa = 0.80$).

4.3 Results

4.3.1 Call structure

An inter-rater reliability test suggested that the type classification was reliable (93.3% agreement; Cohen's Kappa coefficient $\kappa = 0.865$). To further verify whether this classification was justified I selected the first five exemplars of A, B and C calls from each group for acoustic analyses. Following checks for multi-collinearity and singularity, I subjected five of the eight original acoustic parameters to a discriminant function analysis ($n = 75$ calls, five calls of each type per group): total duration, frequency at the end of the fundamental frequency, early transition, late transition and number of harmonics. I excluded two outliers (two C and one A call), resulting in a final sample of $n=72$.

Two functions explained a significant amount of the variation in the acoustic structure of the call types (fig. 4.3). The first function explained 92.5% of the variation (Wilks' lambda= 0.075, $\chi^2_{8}=174.785$, $P < 0.001$), while the second function, explained the remaining 7.5% of the variation (Wilks' lambda= 0.627, $\chi^2_{3}=31.490$, $P < 0.001$). In a cross-validated analysis, the functions successfully classified 94.4% (68/72) of the calls into the three categories. The success rate of classification was highest for C (100%), followed by B (92%) and A (91.7%). Disagreements were two calls A classified as call C and two calls B classified as call C. Acoustic measures of calls A, B and C from all 5 groups in natural contexts are presented in table 4.1.

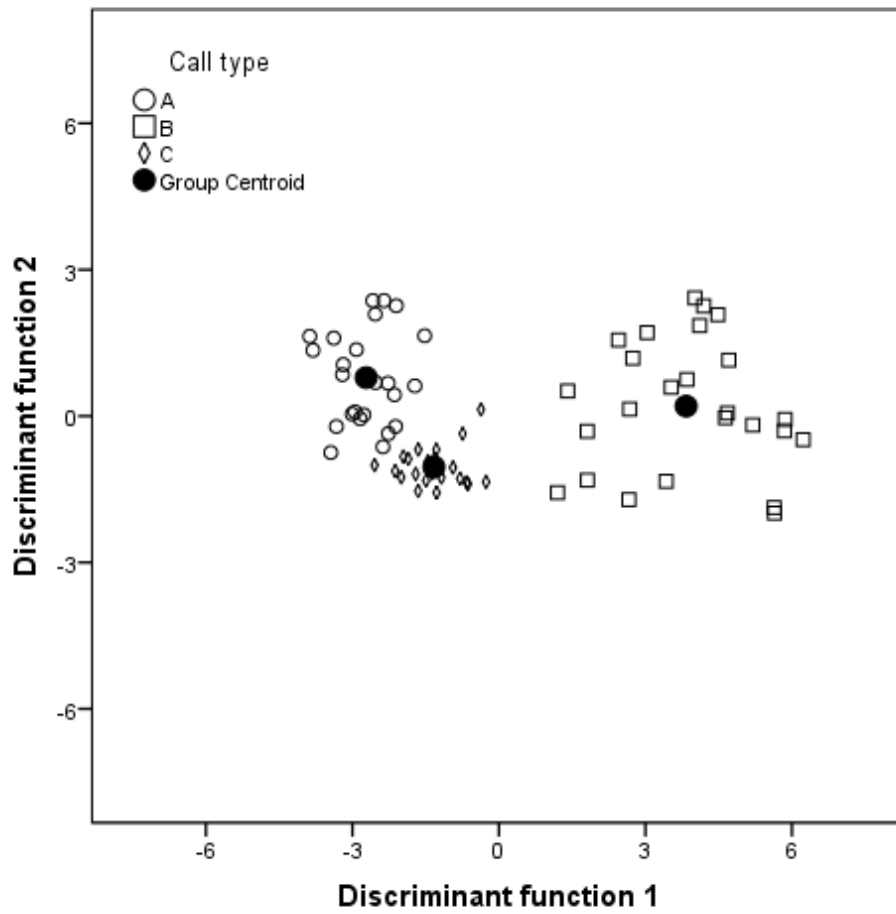


Figure 4.3 Distribution of discriminant scores along the two canonical discriminant functions to separate titi monkey predator-associated calls (Eigen values: Function 1 =8.485; Function 2 =0.594). Black circles represent group centroids.

Table 4.1. Acoustic measurements (mean \pm SD) of the three main call types given by adults in the five habituated groups of *C. nigrifrons* in response to various disturbances

Acoustic feature	Call A (N=25)	Call B (N=25)	Call C (N=25)
Duration (s)	0.054 \pm 0.017	0.033 \pm 0.006	0.053 \pm 0.026
F0 Onset (Hz)	5410.82 \pm 469.71	3852.68 \pm 686.07	5331.88 \pm 1120.08
F0 Middle (Hz)	5389.85 \pm 464.66	3831.07 \pm 663.89	5332.76 \pm 1124.75
F0 End (Hz)	4869.10 \pm 385.94	4812.75 \pm 548.53	5311.83 \pm 1143.70
Transition onset (Δ Hz)	-20.98 \pm 76.16	-21.61 \pm 59.58	0.87 \pm 56.80
Transition offset (Δ Hz)	-520.85 \pm 173.87	981.68 \pm 400.77	-20.93 \pm 62.25
Overall transition (Δ Hz)	-541.83 \pm 190.41	960.07 \pm 425.19	-20.06 \pm 89.83
# Harmonics	0.80 \pm 0.71	1.80 \pm 0.91	0.00 \pm 0.00

N=5 recordings per call type per group

To examine whether each of the uncorrelated acoustic parameters varied statistically between call types, I conducted one-way related-samples analysis of variance tests with call type as the fixed factor and group as the random factor. Two of the five acoustic features varied significantly between call types (transition offset: $F_{2,8} = 96.193$ $p < 0.001$ and number of harmonics: $F_{2,8} = 17.221$, $p < 0.001$; table 4.2., fig.4.4). Post hoc pairwise Sidak-corrected comparisons discriminated among all call types (fig 4.4). The other variables, duration, frequency in the end and transition onset, did not varied statistically between call types ($F_{2,8} = 2.575$, $p = 0.137$; $F_{2,8} = 0.400$, $p = 0.683$ and $F_{2,8} = 1.260$, $p = 0.334$, respectively). Nonetheless, post hoc Sidak-corrected comparisons revealed that the frequency at the end of calls A and B were significant lower that in call C (fig 4.4). Group identity did not affect any of the differences between call types (table 4.2).

Table 4.2 Results of between-subjects effect of Univariate Analysis of Variance.

Variables	Call type	Group	Call type x Group
Duration	$F_{2,8} = 2.575$, $p = 0.137$	$F_{4,8} = 0.570$, $p = 0.692$	$F_{8,57} = 6.288$, $p < 0.0001$
F0 End (Hz)	$F_{2,8} = 0.400$, $p = 0.638$	$F_{4,8} = 2.414$, $p = 0.134$	$F_{8,57} = 19.022$, $p < 0.0001$
Transition onset (Δ Hz)	$F_{2,8} = 1.260$, $p = 0.334$	$F_{4,8} = 1.071$, $p = 0.431$	$F_{8,57} = 1.357$, $p = 0.235$
Transition offset (Δ Hz)	$F_{2,8} = 96.193$, $p < 0.0001$	$F_{4,8} = 1.354$, $p = 0.330$	$F_{8,57} = 4.214$, $p < 0.001$
# Harmonics	$F_{2,8} = 17.221$, $p < 0.001$	$F_{4,8} = 0.807$, $p = 0.554$	$F_{8,57} = 4.188$, $p < 0.001$

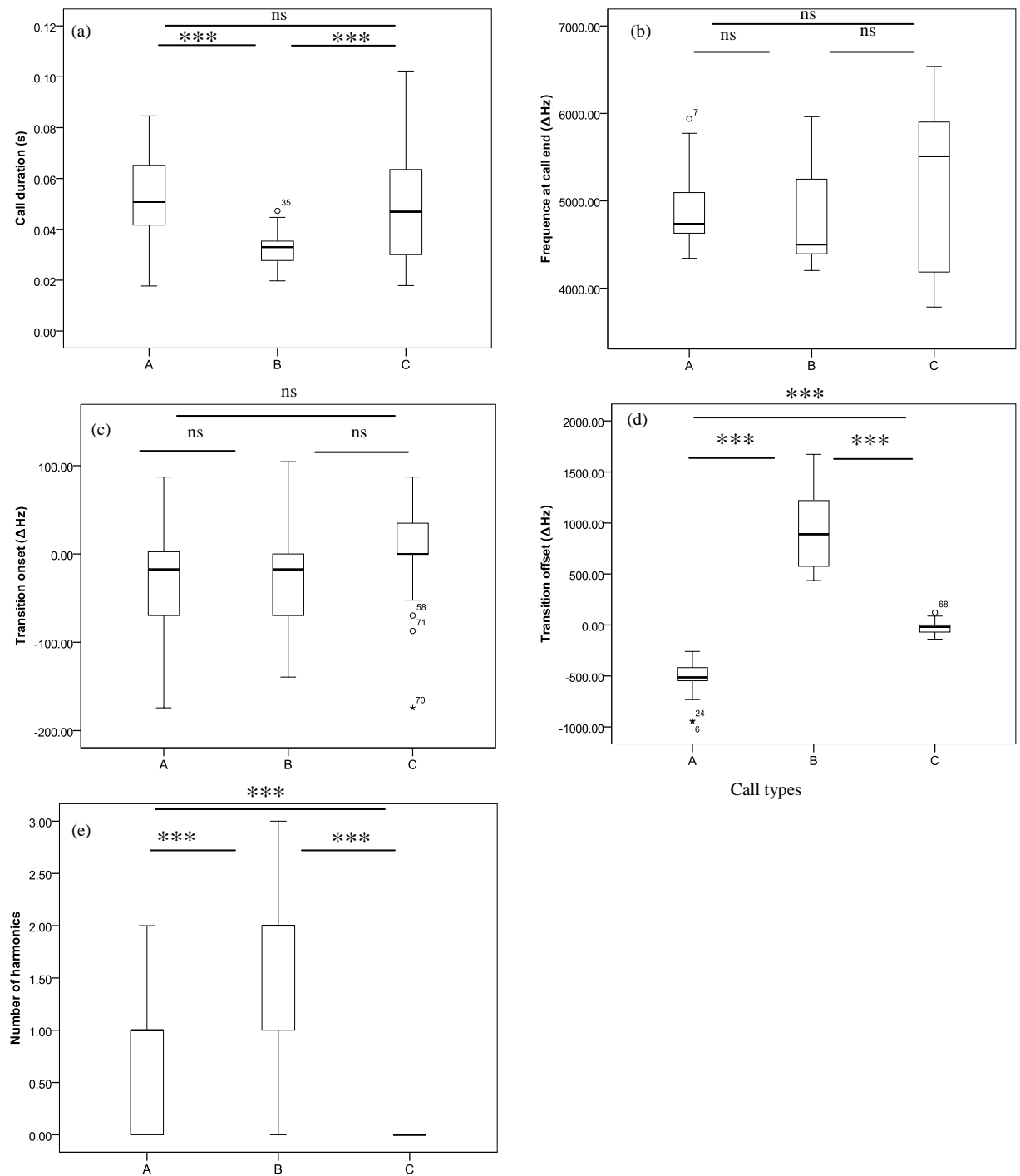


Figure 4.4 Box plots indicating the median, inter-quartiles, and range for each of five uncorrelated acoustic parameters describing black-fronted titi monkeys calls: (a) call duration, (b) frequency of maximum energy at call end, (c) transition onset (ΔHz), (d) transition offset (ΔHz) and (e) N harmonics. P values represent results of post hoc pairwise Sidak-corrected comparisons.

Part II: Behavioural and vocal responses to predator species

4.4. Methods

A second major analysis examined the call sequences given by the focal group. Ideally, this would have been carried out separately for each caller but, as this study was carried out in a natural forest habitat with difficult visual conditions, it was not possible to reliably observe individuals during calling. I therefore report the calling response as a combined effort by the group members. Although I could not identify the identity of the caller I could however, identify the number of individuals calling during the beginning of their responses in 85% of cases. This information confirmed that in most cases the sequence composition was based in one individual only, instead of multiple contributions from different individuals.

I coded all call types during the first minute, which allowed me to calculate the relative proportion and rate of each call type in the combined sequence. Some vocal responses were less than a minute in which case I used the actual duration to calculate call rates. Calls that could be not classified with confidence as either A, B, or C were coded as “other”. Rare types, such as grunts, trills and moans, were also coded as “other”.

Statistical analyses were conducted with the statistical package PASW version 18.0 (SPSS Inc., Chicago, IL, U.S.A.). All tests were two-tailed with a significance level set at 0.05, unless corrections were needed. When needed, I used non-parametric Kruskal-Wallis and Mann-Whitney tests with Bonferroni-corrected alpha values in case of multiple comparisons.

4.5. Results

4.5.1 General responses

During approximately 730 hours of continuous observations, I registered 287 vocal responses to potential predator species from five habituated groups (table 4.3). Most cases (n= 132, 46%) were responses to raptors (n=123 flying, n=4 perched, n= 5 calling; table 4.3). Only events with sufficient recording quality were further analysed (n=81).

Table 4.3 List of type and number of potential predatory events for which the focal groups called in Caraça Private Reserve during two field seasons (May-October 2009 and May-July 2010).

Predatory/disturbing event	Location	GA (181 h 1min)	GD (129 h 44 min)	GM (138 h 28 min)	GP (83 h 09 min)	GR (198 h 56 min)	Total (731 h 18 min)
<i>Raptors</i>							
Flying raptor	Canopy or sky	46	24	19	5	29	123
Calling raptor	Canopy or sky	1	0	2	1	1	5
Perched raptor	Canopy	0	1*	1	0	2	4
<i>Mammals</i>							
Capuchin †	Canopy	2	0	2 (1 NR)	2	3 (2 NR)	9
Spotted cat	Ground	0	0	1	0	0	1
Tayra ¥	Ground	0	0	0	0	2* NR	2
Deer	Ground	0	0	1	0	0	1
<i>Unidentified</i>							
Flying unidentified bird	Canopy or sky	16	5	10	10	8	49
Unknown 1 (long)	Canopy or sky	25 (+ 2)	12 (+ 1)	17	6 (+ 2)	16 (+ 2)	83
Unknown 2	Ground	3	2	2	3	0	10
Total		95	45	55	29	63	287

* Events observed by myself and collaborators on 2007 and 2008; NR (not recorded).

† Because monkeys were usually very agitated upon encountering capuchins, I was only able to record and code/analyse 6 of these events.

¥ We witnessed, but were unable to record, a few encounters of titi monkeys with Tayras, in which they called. In brackets below each focal group is the total amount of time spent with each group.

Upon encountering raptors and other threats from the canopy or sky, monkeys usually called for significantly shorter periods than when encountering a disturbance on the ground (Mann-Whitney U Test: $U = 49.0$, $n_1 = 69$, $n_2 = 12$, $p < 0.001$, figure 4.5). The exception was one encounter with two eagles trying to perch close to the group in which case the monkeys called continuously for almost 11 minutes.

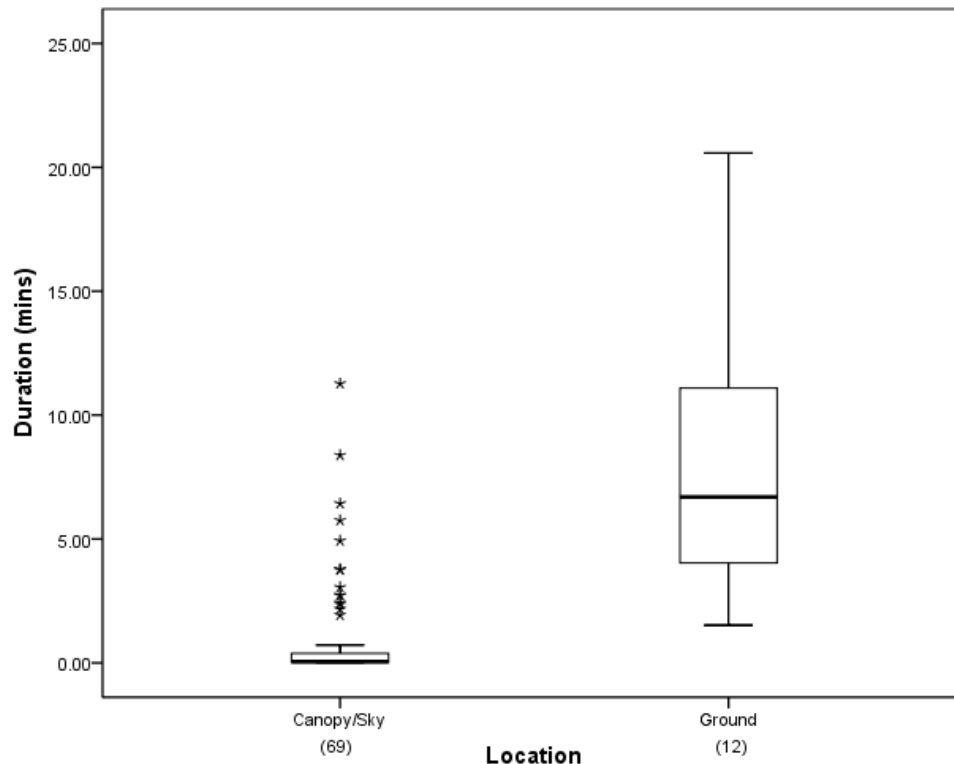
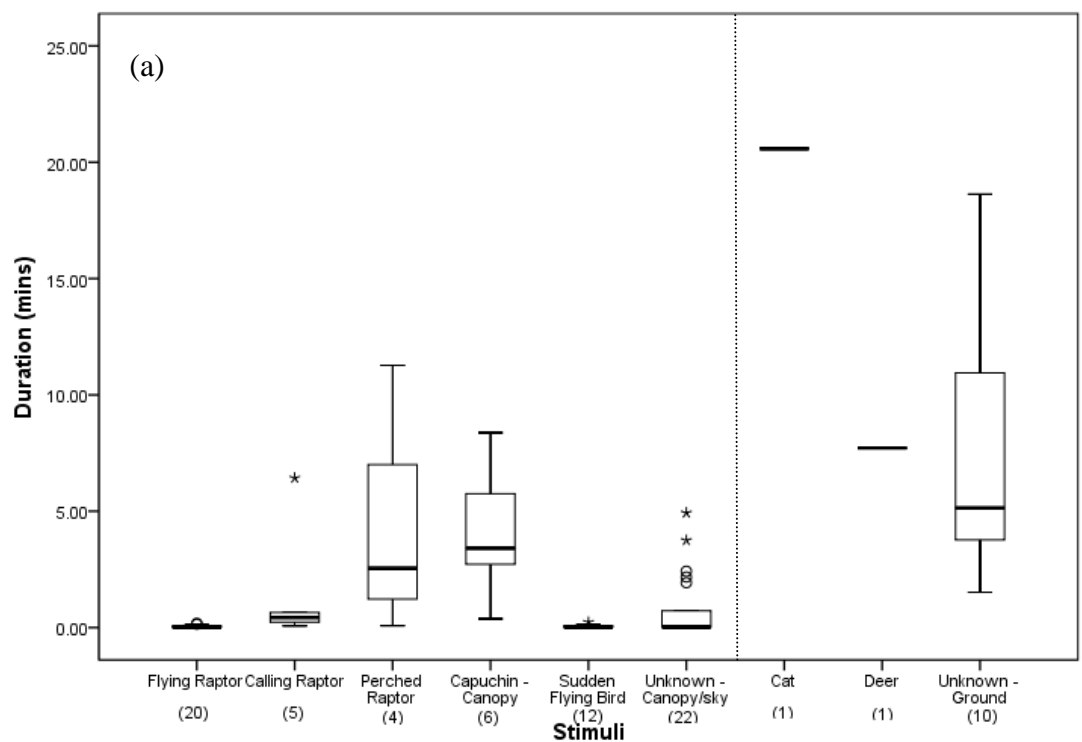


Figure 4.5. Box plots indicating the duration of calling behaviour when encountering predators or other threats in the canopy, in the sky or on the ground. Box plots represent medians and upper and lower quartiles. Outliers are marked with asterisk.

The duration of vocal responses was significantly related to stimulus type experienced (Kruskal-Wallis: $\chi^2 = 47.631$, $df = 6$, $p < 0.001$; fig. 4.6a; post hoc Mann-Whitney U tests, Bonferroni p-value adjusted for multiple comparisons, table 4.4).

Similarly, the call rate was significantly smaller to raptors and other threats from the canopy or sky in comparison to disturbances on the ground (Mann-Whitney U Test: $U =$

5.000, $n_1=69$, $n_2=12$, $p= <0.001$). Likewise, the call rate was also related to stimulus type (Kruskal-Wallis: $\chi^2=48.789$, $df=6$, $p<0.001$; fig. 4.6b; post hoc Mann-Whitney U tests, Bonferroni p-value adjusted for multiple comparisons, table 4.4).



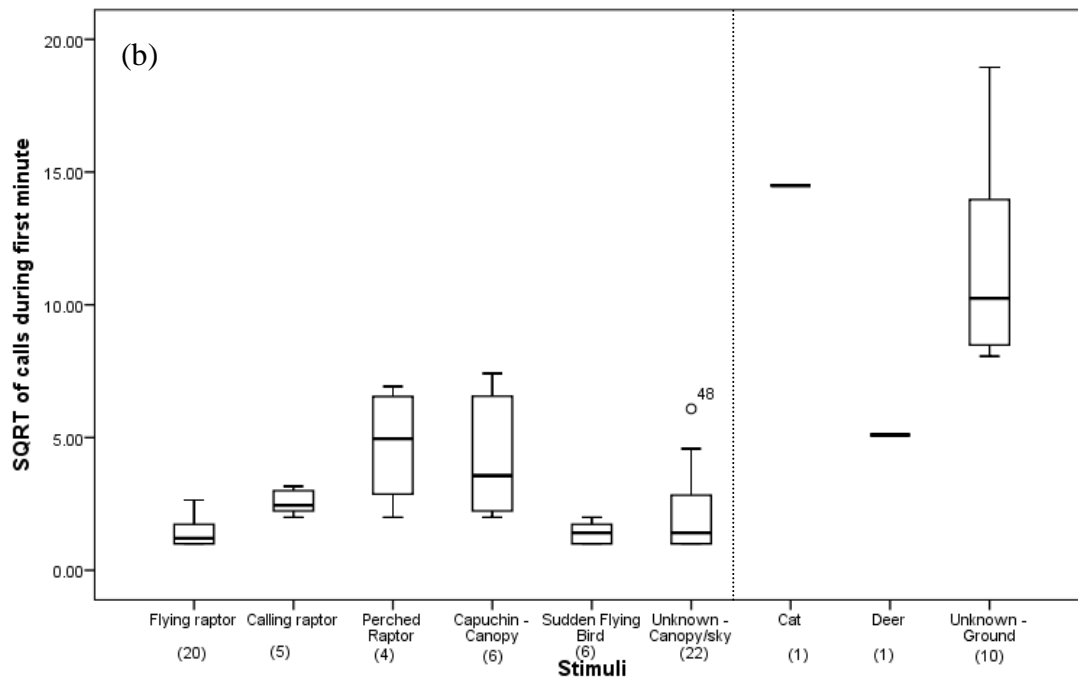


Figure 4.6 Box plots indicating a) the duration of calling behaviour and b) the call rate during the first minute upon encountering different types of predators or threats (medians, upper and lower quartiles, whiskers = adjacent values, asterisks = outliers). The two identified threats on the ground were responses from the same group (GM). Lines separate between predatory and other disturbances on the canopy/sky and on the ground. Call rate represents the square root of number of calls produced during the first minute, which was used to correct for differences in the number of individuals per group.

Table 4.4 Coefficient matrix of post hoc Mann-Whitney U tests corrected for multiple comparisons. (fr): flying raptor, (pr): perched raptor, (cr): calling raptor, (sfb): sudden flying bird, (cc): capuchins in the canopy, (dc): disturbance on the canopy, and (dg): disturbance on the ground.

Stimuli	pr	cr	sfb	cc	dc	dg (12)
fr (20)	*/*	**/*	ns/ns	***/**	ns/ns	***/**
prR (4)		ns/ns	*/*	ns/ns	ns/ns	ns/ns
cr (5)			ns/*	ns/ns	ns/ns	ns/**
sfb (12)				**/**	ns/ns	***/**
cc (6)					**/ns	ns/*
dc (22)						***/**

* $P < 0.002$; ** $P < 0.0004$; *** $P < 0.00004$ (two-tailed). Significant P-values adjusted for multiple comparisons. ns= Not significant. Disturbance on ground included one large cat and one deer encounter. Number of events is given in brackets. Figures refer to comparisons between the duration of vocal responses and call rate during first minute.

The typical response pattern to raptors was for the detecting individual to call while observing the predator and freezing or rapidly descending or moving to a protected location. Nearby group members typically remained silent, while scanning the canopy or sky and freezing or rapidly descending or moving towards a protected place as well. Distant group members, who could probably not hear the caller and detected the predator independently, produced the same call type as the initial caller.

To terrestrial disturbances, the first animal to call usually attracted other group members to the site, who then also called. This was accompanied by alert, approach, or mobbing behaviour. In one case a spotted cat was mobbed for over 20min (see fig. 4.6a). The caller's behaviour included gazing at the cat and producing visual displays, such as arch postures, pilo-erection, tail lashing (swinging tail sideways), head swaying, and rapid erratic movements towards and away from the disturbance, while maintaining visual fixation. Other's behaviour included calling, looking towards or approaching the caller, scanning the forest ground or lower canopy, producing visual displays and mobbing the predator. Mobbing was also observed to tayras, but not to a non-predatory disturbance (deer), although they were agitated in all situations.

4.5.2 Context-specificity

To raptors, the first call in each sequence was always an A-call, regardless of the raptor behaviour (fig 4.7). A-calls were also the only or main calls during the first 30 calls produced ($\chi^2=36.105$, $n=19$, $df=2$, $p<0.001$, fig 4.7). This was observed to crowned eagles, black-chested buzzard-eagles, black hawk-eagles, caracaras, vultures and several species of hawks. Monkeys did not give A calls to other bird species, except when surprised by medium sized flying birds. On one occasion, an adult male (Desbotado) gave A calls to a big bird flying by before perching in a nearby tree. The monkey kept on giving A calls while trying to locate the bird in the vegetation but then stopped immediately after identifying it as a dusky-legged guan (*Penelope obscura*), a common non-predatory bird. Additionally, A calls were given in response to the presence of

capuchin monkeys, and other (unidentified) threats within the canopy, but never to disturbances on the ground (fig 4.7). In contrast, to raptor responses, call sequences to Capuchin monkeys contained a large number of B calls following an initial sequence of A calls.

To disturbances on the ground, the first call per sequence was always a B-call. This was observed to a spotted cat, tayra, deer, and several unidentified disturbances. Subsequent calls were also always B calls sometimes mixed with C calls later on in the sequence, but never A calls ($\chi^2=19.436$, $n=12$, $df=2$, $p<0.001$, fig 4.7). Although the proportion of use of call B was higher in response to terrestrial threats than capuchins, the p-value was not significant after a Bonferroni correction ($z=-2.207$, $p= 0.031$). Importantly, B calls were also often produced in non-predatory contexts and sometimes in the absence of external events, especially when monkeys were descending or foraging close to the ground, when an observer was blocking their intended path, during inter-group encounters and, for unhabituated groups, in response to humans.

Call type C was the least common and produced in almost all contexts, but especially to capuchin monkeys and deer (fig 4.7, number of calls coded to describe the first 30 calls are presented in table 4.5). In non-predatory contexts, it was given during intra-specific disputes, in response to other groups calling and during movements towards or away from significant events, such inter-group encounters.

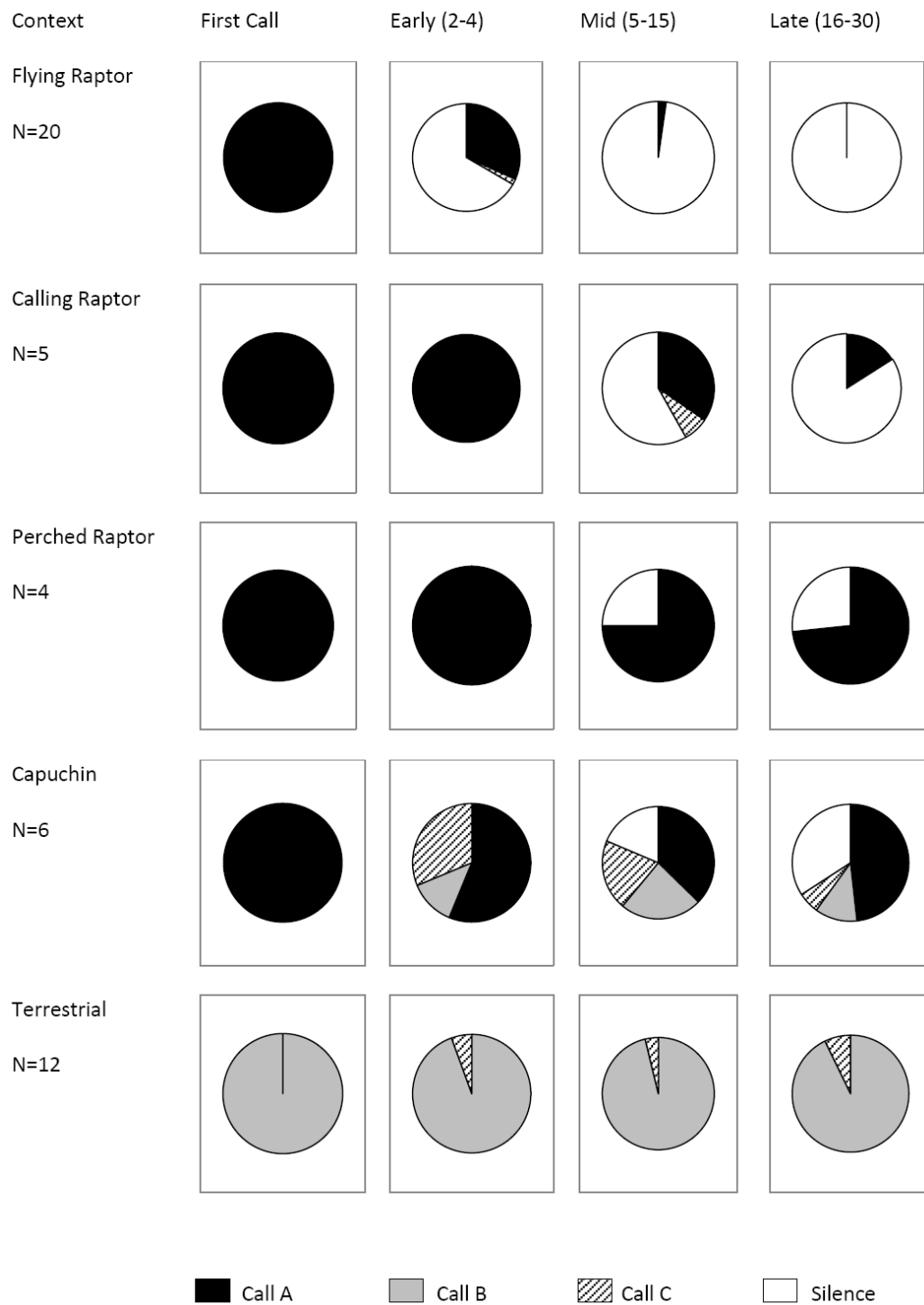


Figure 4.7. Sequential analyses of the first 30 calls produced in predatory contexts (see figure 4.1 for spectrograms of the calls). Terrestrial context includes one response to an unidentified spotted cat and one adult deer from the same group (GM).

Table 4.5 Number of calls coded to describe the first 30 calls produced in response to potential predators/threats (Raptors: Flying, F; Perched, P; Calling, C).

Stimuli	N	Groups	First call	Early (2-4)	Mid (5-15)	Late (16-30)
F raptor	20	A,D,P,R	20/20	60/60	220/220	300/300
P raptor	4	D,M,R	4/4	12/12	44/44	60/60
C raptor	5	A,M,P,R	4/4	15/14	55/55	75/75
Capuchin	6	A,M,P,R	6/4	18/16	66/59	90/85
Terrestrial	12	A,D,M,P	12/12	36/36	132/132	180/180

N: number of events per predator stimuli recorded and analysed. Group letters represent the individual groups (total of 5) contributing to each type of predator stimuli. Values on First, Early, Mid and Late calls, represent firstly the total number of calls produced (which are the result of multiplying the number of events by the number of calls in each category), and secondly the total number of calls codeable and used to illustrate the differences on Figure 4.7.

4.5.3 Sequence composition during the first minute

The proportion of A, B and C calls within the first minute were all significantly dependent on the type of stimuli (A: $\chi^2 = 53.061$, $df=6$, $p<0.001$; B: $\chi^2 = 59.845$, $df= 6$, $p=0.000$; C: $\chi^2 = 24.632$, $df= 6$, $p<0.001$, fig 4.8). The proportion of A calls was significantly higher for raptors (median= 1.0) than capuchins (median= 0.378, Mann-Whitney U= 4.0, $n_1=29$, $n_2=6$, $p<0.001$) or terrestrial threats (Median= 0, U= 0.0, $n_1=29$, $n_2=12$, $p<0.001$). The proportion of B calls was significantly higher for terrestrial threats (median= 0.9058) than capuchins (median=0, U=0.0, $n_1=12$, $n_2=6$, $p<0.001$) or raptors (median=0, U=0.0, $n_1=12$, $n_2=29$, $p<0.001$). The proportion of call C was significantly higher for capuchins (median= 0.3875) than terrestrial threats (median=0.0, U=6.0, $n_1=6$, $n_2=12$, $p=0.002$) or raptors (median= 0.0, U=124.0, $n_1=6$, $n_2=29$, $p=0.032$, fig. 4.8).

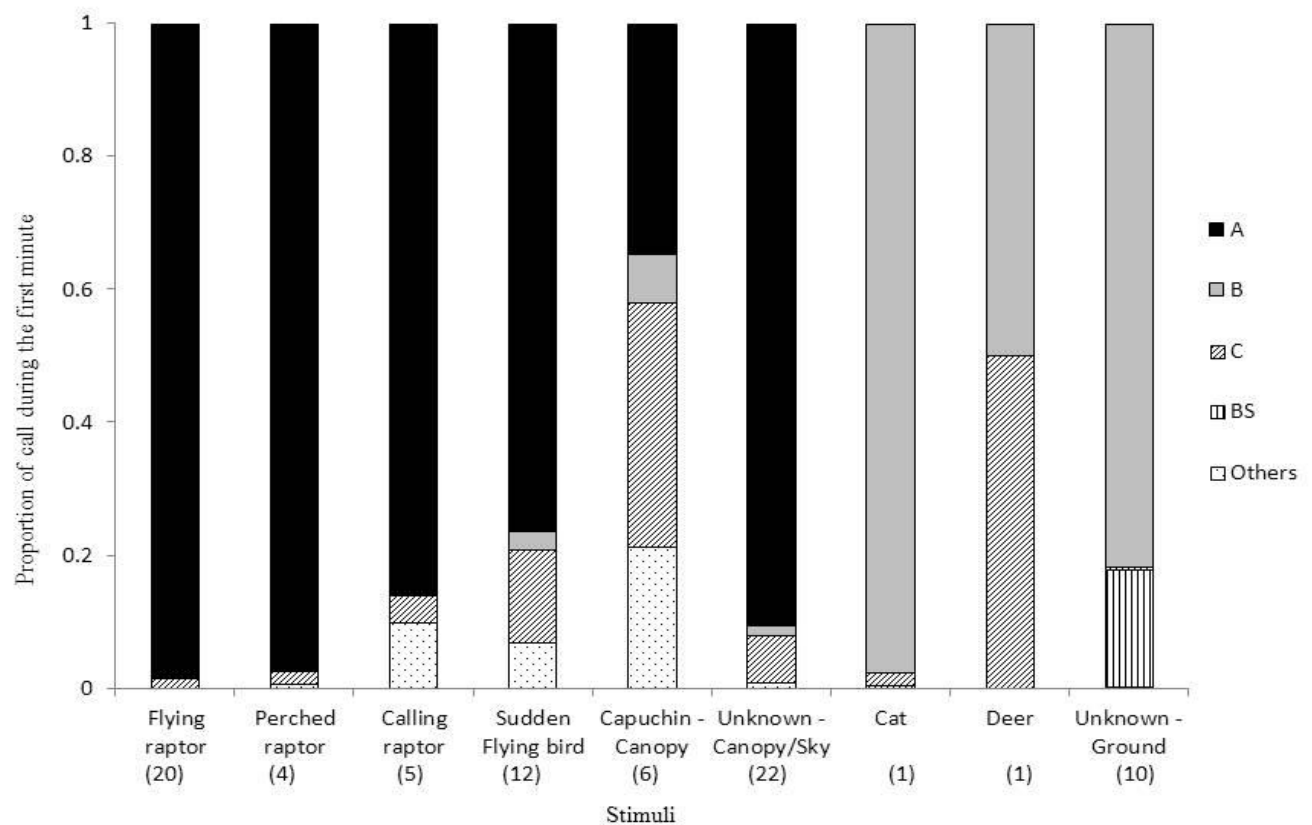


Figure 4.8. Proportion of each call type during the first minute. When vocal responses were less than a minute, I considered the true call rate, and when longer than a minute I considered the call rate during the first minute. “BS” is another call compound by two units; a call B immediately followed by a low-pitched vocal unit or syllable, which changes the amplitude and acoustic appearance of the combined utterance, named as ‘chirrup’ and ‘chuck’ by Moynihan (1966) and ‘chirrup’ by Robinson (1979a). Moreover, call BS seems to be produced later on in their responses, and not at the beginning, suggesting a different/gradual motivation and/or function. However, due to small sample size (only in response to a cat) I did not perform any measurements or comparisons.

4.5.4 Calls during the first five minutes after detection – Preliminary comparisons between a predator and non-predator animals on the ground

In the first five minutes after detection of an adult deer and an unidentified spotted cat, call A was never produced by group M (figure 4.9). The most common call during the first five minutes was call B for both disturbances. Other call types were dependent on the stimulus. BW and loud calls (moans, honks, resonating calls and pumps) were only produced in response to the cat, while call C was more common in response to the deer (Figure 4.9). Call C was more common during the first minute and decreased over time in response to the deer (figure 4.10a). Loud calls were produced from the second minute after detection and their proportion were increasing over time (figure 4.10b).

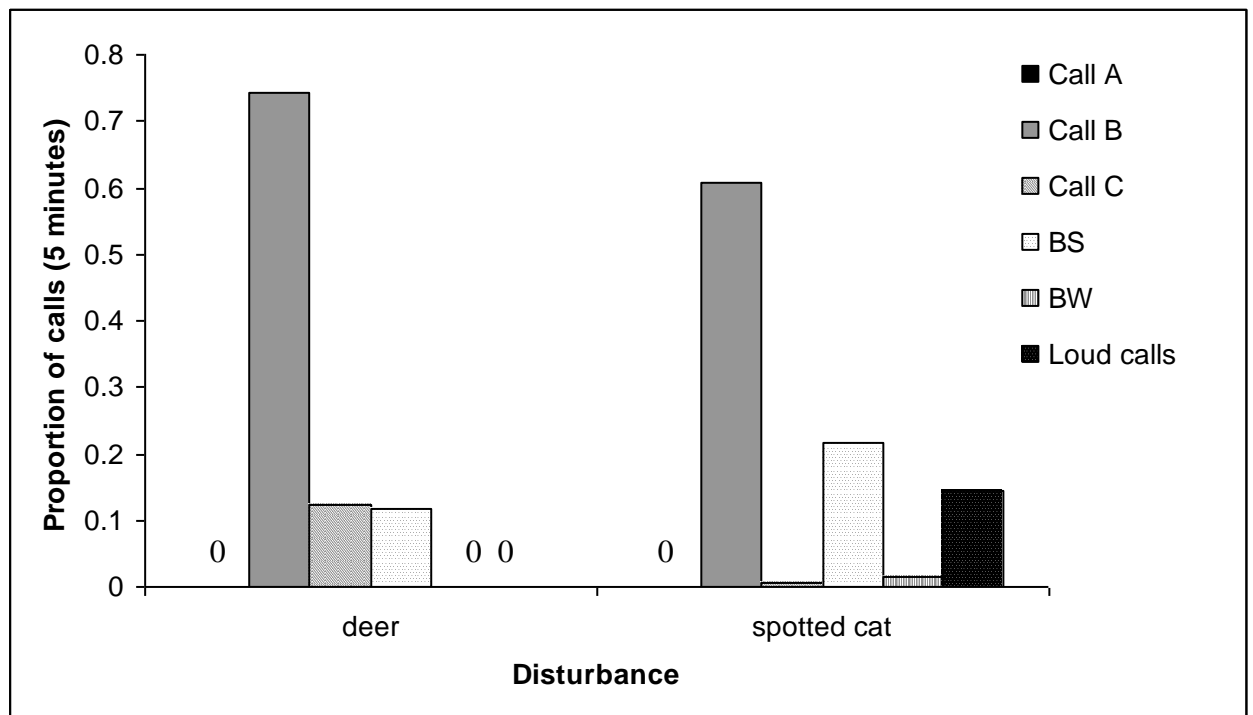


Figure 4.9 Proportion of calls produced within the first five minutes by group M after detecting an adult deer and an unidentified spotted cat.

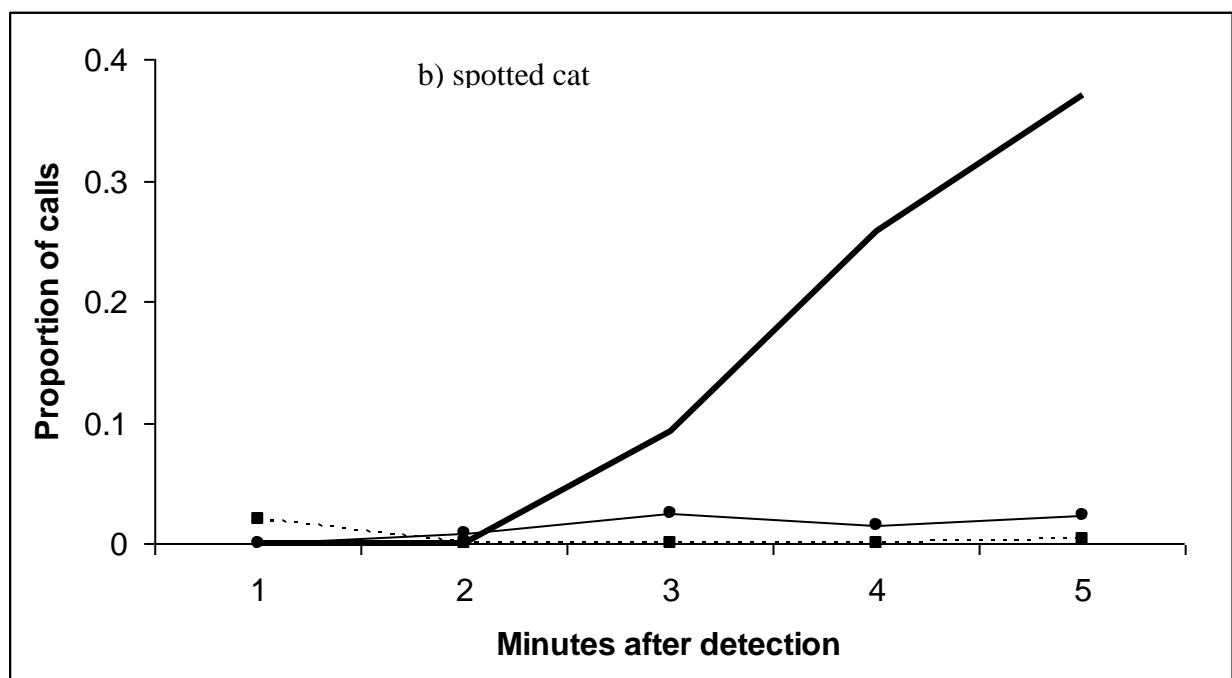
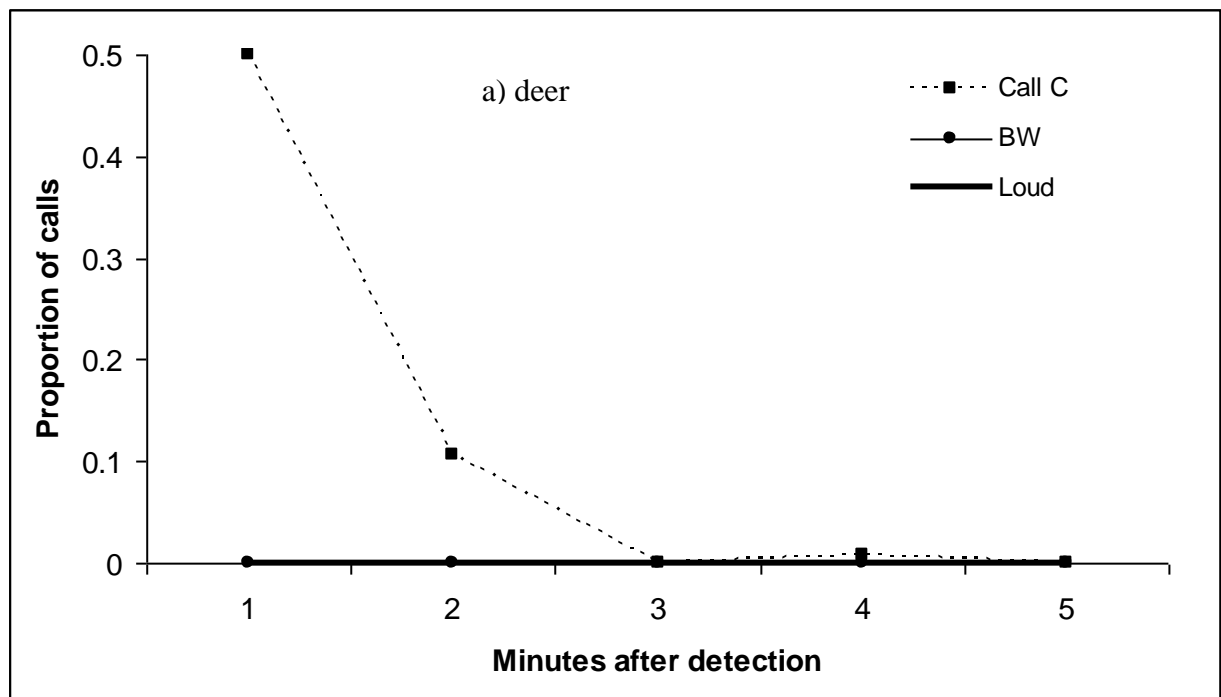


Figure 4.10 Proportion of the less common call types (C, BW and loud calls) produced within the first 5 minutes after detection of a non-predator animal (deer) and a predator animal (spotted cat). Loud calls include: moans, honks, resonating calls and pumps. Spectrographic representations of each call are presented in chapter 3.

4.6 Discussion

Black-fronted titi monkeys produce different call types in response to a variety of disturbances, including predators. Groups reliably uttered A calls in response to raptors, with the number of calls varying from one to many, depending on the birds' behaviour. One or few A calls were given in response to flying raptors, several calls in response to perched or calling raptors, with calling often only stopping after the predator flew away (figs. 4.6a and 4.7). However, A calls do not qualify as 'eagle alarms', or even aerial predator alarms since the monkeys produced the same call type also when encountering capuchin monkeys or other threats within the canopy. Instead A calls appear to indicate that the caller detected a threat within the canopy, while later parts of the sequence reveal something about the nature of this disturbance. While raptors elicited series of A calls, depending on their behaviour, capuchin monkeys triggered B and C calls, despite the fact that they were encountered in the canopy.

Similarly, B calls do not qualify as terrestrial predator alarm because they are also given in a variety of situations where the caller has not detected a typical ground predator but is about to engage in risky behaviour, such as descending towards the ground or when foraging close to the ground. The fact that arboreal Capuchin monkeys also trigger B calls in later parts of the sequence further illustrate this point (although this call here may function to gather the group together and maybe to descend, a pattern that should be systematically tested). Context-specific differences are apparent in later parts of the sequence, however. For instance, in response to cats, deer, tayras (not recorded), and other terrestrial threats the monkeys consistently produced sequences of B calls, sometimes followed by low-pitched 'other' calls later in the sequence, but never A calls (figure 4.9).

A third call, type C, was given less specifically, although regularly to capuchins, deer, and when neighbouring groups were in proximity, suggesting that it functions as a general alert call or that it is related to the caller's intention to move.

Calling responses sometimes lasted for several minutes, particularly to terrestrial predators. In the later parts of such sequences, I identified loud calls that were structurally very different from the first calls, and similar to what has been described by Moynihan (1966) and Robinson (1979a) for Amazonian species. Due to their low occurrence, I did not describe them any further here. Nonetheless, I found that most low-pitched loud calls were produced in response to a terrestrial predator (cat) but not a non-predatory disturbance (deer) (figures 4.9 and 4.10). These responses suggest that titi monkeys differentiate between different types of terrestrial threats, despite the fact that all call sequences begin with long series of B calls.

A somewhat special case was the monkeys' responses to capuchin monkeys. Here, the monkeys' first calls were always A calls, but callers then switched to B calls, sometimes interspersed by C calls and other calls. Interactions with capuchin monkeys were usually very disruptive and monkeys were usually very agitated. After a few calls, they often moved downwards, stayed quiet, or ran away, sometimes pursued by Capuchin monkeys. Here again, the production of calls B and C may be also related to the caller's intention to move.

These findings are consistent with the current theory of primate alarm calls, which states that aerial and terrestrial predators elicit acoustically distinct vocal behaviour (e.g. Seyfarth and Cheney 1980; Macedonia and Evans 1993; Zuberbühler 2000c; Digweed et al. 2005; Fichtel et al. 2005; Kirchhof and Hammerschmidt 2006; Schel et al. 2009; Wheeler 2010). However, my findings are also at odds with this theory in a number of ways. First, titi monkeys regularly produce B calls not only to terrestrial predators but also in non-predatory contexts, something that has also been observed in other New World primates, particularly during inter-group encounters (Digweed et al. 2005;

Fichtel et al. 2005; Kirchhof and Hammerschmidt 2006; Wheeler 2010). In putty nosed monkeys (*Cercopithecus nictitans martini*), males regularly produce loud and conspicuous calls to predators (Arnold and Zuberbühler 2006a, b) but the same calls are also produced during non-predator events, such as during inter-group encounters, to falling branches, or to initiate group travel (Arnold and Zuberbühler 2006a, 2008). If B call sequences produced in predatory and non-predatory situations are acoustically identical then listeners will have to consider the external context and the behaviour of others in deciding how to respond. Another possibility is that there are acoustic variants within the B calls or that differences in call delivery that are context-related. For instance, monkeys seem to begin B call sequences with quiet and high-pitched variants and then progressively increase amplitude and add suffices (see Ouatarra et al., 2009b, for similar observations in Campbell's monkeys). Whether or not these differences are communicatively relevant will have to be addressed by future research.

As discussed earlier I found extensive and contextual use of vocalisations during predator encounters, a pattern not yet described for other species of *Callicebus*. Although there were some observations of loud calls during predatory events, some studies had suggested that the titi monkeys' main anti-predatory strategy has to be cryptic behaviour by hiding from potential predators (Terborgh 1983; Ferrari 2009; de Luna et al. 2010). However, in this study I witnessed such behaviour only on few occasions. In one case, a semi-habituated group, consisting of three individuals, did not call after detecting a tayra foraging some 20m from their tree, although this may have been caused by the presence of human observers.

Another interesting aspect in predator animal signalling is that flexible alarm call usage and comprehension is often influenced by the predator types present in a particular habitat (e.g. Fichtel & van Schaik, 2006) and that high predator pressure leads to increased complexity in primates' vocal and cognitive capacities (Zuberbühler 2000b, 2000d; Zuberbühler and Jenny 2002). If that is the case with titi monkeys facing a wide

array of potential predators, these monkeys may be able to use different calls and call combinations to communicate about different types of predators within and between classes of predators. Indeed, it would be interesting to test how an increased predator pressure had influenced monkeys' anti-predator responses.

4.6.1 Summary

Overall, these patterns suggest that titi monkey alarm call sequences refer to the location of danger, real or anticipated, but that listeners may also obtain information about the predator class detected by the caller. Such type of alarm signals with (different) multiple strands of information has been described in other non-primate species. In meerkats, for instance, callers produce acoustically different alarms to different predator types, but call structure is also influenced by the level of urgency (Manser 2001; Manser et al. 2002). Another well studied example is the graded alarm call system of chickadees with evidence for a functionally referential system encoding both predator type and urgency (Templeton et al. 2005). The results presented here are thus novel in that they provide evidence that primate (and animal) alarm calls can refer to the location of threat in addition to predator category. Systematic experiments to test this hypothesis will be presented in chapters 5 and 6.

CHAPTER 5: The anti-predator behaviour of *Callicebus nigrifrons* in response to visual predator models

Abstract

In chapter four I found that titi monkeys produced at least three main types of acoustically distinct high-pitched calls to external disturbances, including predators. Call A ('chirp') was given to raptors and some other threats located within the canopy; whilst call B ('cheep') was given to both predators and non-predator animals on the ground. A third call C ('squeak') was most common, given in different contexts, which suggested that it did not relate to any specific external event. Because most naturalistic observations were in response to raptors and because the cause of most responses to terrestrial disturbances could not be identified it was not clear whether these monkeys differentiated between different types of predators. Here, I present the results of an experiment designed to systematically investigate the natural responses of black-fronted titi monkeys to predators and to systematically test their anti-predator behaviour in response to seven different stimuli: one species of raptor, five species of mostly terrestrial predators and one non-predatory animal that served as a control. Results were consistent with natural observations. Call A was only given in response to the raptor model presented in the canopy whereas call B was given in response to all terrestrial predators but also to the control. In addition, I found that the monkeys' behavioural and vocal responses to terrestrial disturbances were dependent on the type of model. Subjects mobbed and produced loud low-pitched calls only in response to the oncilla, puma and tayra models but not to the deer model (control) or to the snake models (two species of *Boa*). Although the monkeys' first response to all disturbances on the ground was the production of at least one call B, later parts of their vocal responses varied in predator-specific ways, which suggests that they discriminate different types of threats or risks.

5.1. Introduction

Being exposed to a wide range of predators and living in a three-dimensional environment that requires a variety of escape responses are considered important factors, which have influenced the diversification of anti-predator vocalizations and responses (Macedonia & Evans, 1993). One possible evolutionary outcome of this complexity can be seen in the alarm call behaviour of non-human primates. A consistent finding is that some primate alarm calls are closely related to the context in which they are produced. Vervet monkeys (*Chlorocebus aethiops*), for instance, produce acoustically different alarm calls to their main predators (pythons, eagles and leopards) (Struhsaker, 1967, Seyfarth et al, 1980). However, not all alarm call systems are based on differences in acoustic structure and some use the sequential structure to refer to different contexts. For example, Guereza colobus monkeys (*Colobus guereza*) produce one call type in response to several disturbances but vary the number of calls per sequence according to context (Schel et al., 2009). In some species, the nature of danger can be encoded in the rate of call delivery (Lemasson et al. 2010), the intensity of calls (Blumstein 1999b) or by a specific combination of calls (Arnold and Zuberbühler, 2006).

In some cases, primates produce alarm calls that are directed to the predator in addition to conspecifics (Zuberbühler et al., 1997). These calls usually indicate to the predator that it has been detected - especially if the predator relies on a surprise-hunting strategy (Zuberbühler et al., 1997, Zuberbühler, 1999a, Clarke et al., 2006). Other studies have shown that alarm calls can elicit predator mobbing behaviour by other group members (Fichtel et al., 2005; Digweed et al., 2005, Campbell & Snowdon, 2007; Clara et al, 2008), an anti-predator strategy that may be more common amongst the smaller primates (Miller and Treves, 2011, but see Bshary & Noe (1995) and Boesch & Boesch-Achermann (2000) for examples in Red colobus and chimpanzees).

In chapter four I found that in natural situations titi monkeys produced at least three main acoustically distinct types of high-pitched calls to external disturbances, including predators. A first call type (call A) was produced mostly in response to raptors, regardless of whether they were flying, perched or calling, but this call was not usually given when encountering other non-predatory bird species. Furthermore, monkeys produced another call (call B) in response to disturbances on the ground, including detection of a predator (spotted cat) and a large non-predatory animal (deer). As seen previously (chapter 4, figs. 4.6, 4.8-4.10), responses of group M to these two terrestrial events were very different in terms of number of calls and type of calls produced later on their responses. This pattern suggested that although monkeys started their responses to terrestrial threats with call B, they then switched to other call types. This may enable them to: a) convey information regarding the type of threat through different call rates and/or b) change their behaviour according to the type of predator and/or risk of predation later on. For instance, loud calls were only recorded in response to the spotted cat during the first five minutes, suggesting that monkeys confirmed to others the type of threat or communicated to the predator its detection. However, since these were single observations, it was unclear whether or not the responses represented a pattern consistent across groups or just some individual variation.

As predator attacks are difficult to see in natural conditions (Ferrari, 2010, Miller and Treves, 2011, chapter 4), I used stuffed animals as predator models. To be able to confirm if monkeys can differentiate between type of predator and/or risk of predation I tested all five groups with the same models. Specifically, I was interested to know whether there was any difference in call delivery (number of calls) or combination of calls in response to different disturbances on the ground. Based on my natural observations of group M, I expected that groups would produce call B when first detecting all predator models and the control on the ground. However, if their calls conveyed information about predator category, I expected their vocal responses to vary between models in the following ways: (a) **call rate**: monkeys were expected to

produce more calls in response to predator species than to the control during the first minute after detection; (b) **proportion and combination of calls**: monkeys were expected to produce different proportions and combinations of calls as a function of model type, especially early on (first sequence, first minute after detection). To investigate more long-term effects, I compared their responses to terrestrial predators and the control during the first 5 minutes after detection. Following natural observations, I expected monkeys to mob and produce **loud calls** only in response to predator species and not to the control.

5.2 Methods

5.2.1 Visual experimental stimuli

I tested titi monkeys' anti-predator behaviour systematically by presenting taxidermised animals as 'model predators' with different hunting techniques, i.e. raptor: caracara (*Caracara plancus*); mammalian terrestrial carnivores: tayra (*Eira barbara*), oncilla (*Leopardus tigrinus*), puma (*Puma concolor*); snakes: small coiled snake (*Boa constrictor*); big uncoiled snake (*Boa constrictor*); non-predatory control: deer (*Mazama sp.*) (Figure 5.1, table 5.1).

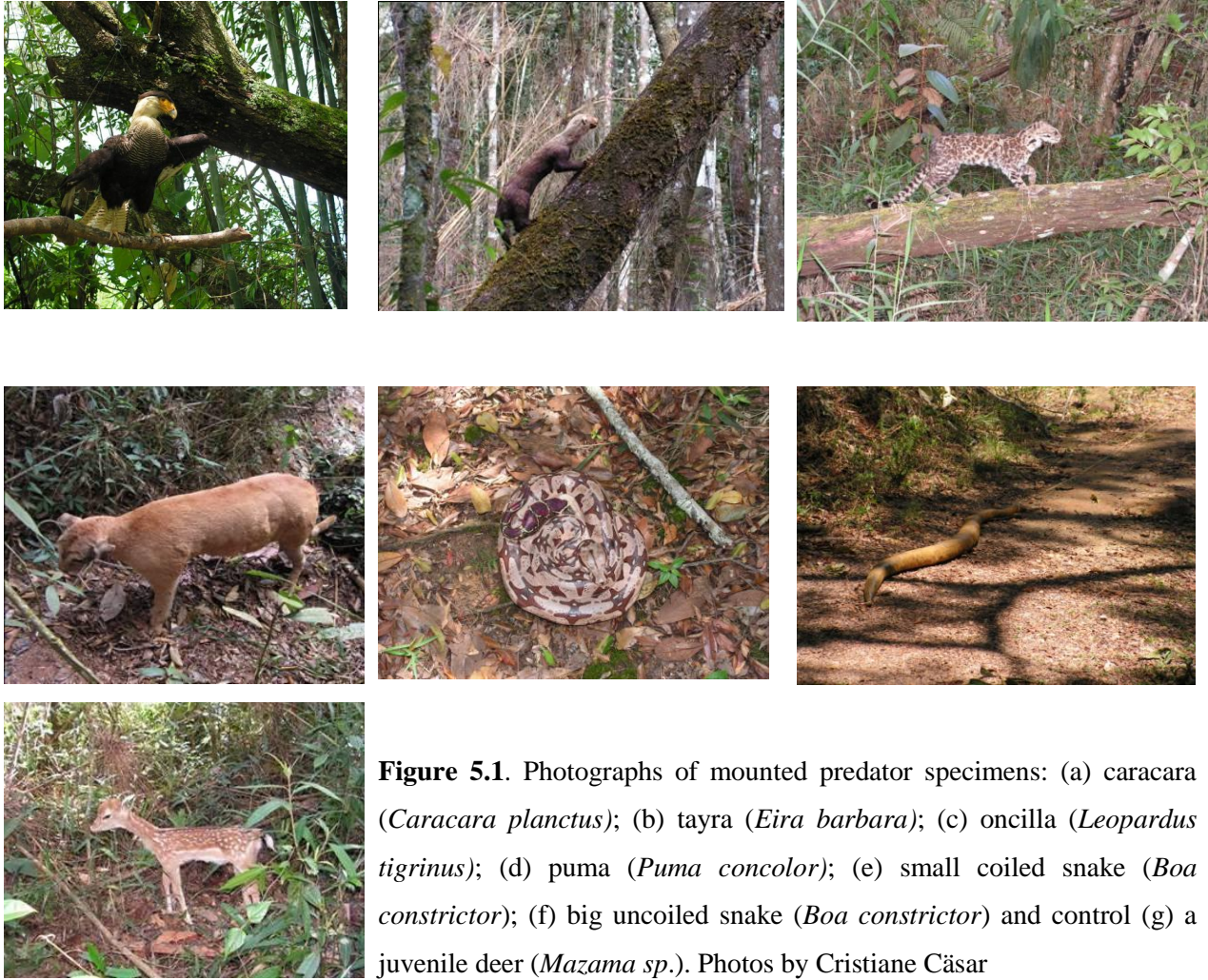


Figure 5.1. Photographs of mounted predator specimens: (a) caracara (*Caracara planctus*); (b) tayra (*Eira barbara*); (c) oncilla (*Leopardus tigrinus*); (d) puma (*Puma concolor*); (e) small coiled snake (*Boa constrictor*); (f) big uncoiled snake (*Boa constrictor*) and control (g) a juvenile deer (*Mazama sp.*). Photos by Cristiane Cäsar

Table 5.1. Predator models presented to five different family groups of black-fronted titi monkeys in Caraça Reserve, Minas Gerais, Brazil.

Predator species	Primary diet	Main hunting technique	Main direction of attack	Expected behaviour of the group
Caracara	carcasses, birds and small animals	Opportunistic	Aerial	Detection signalling and avoidance; warning mates and kin
Boa	mammals, birds	Ambush	Semi-arboreal	Detection signalling and approach to mob; warning mates and kin
Oncilla	Small mammals, lizards, birds	Stalking, ambush, stealth	Terrestrial	Detection signalling and approach to mob; warning mates and kin
Puma	Small to medium size mammals	stalk-and-ambush	Terrestrial	Detection signalling and approach to mob; warning mates and kin
Tayra	mammals, birds fruit	Stalking, ambush, stealth	Terrestrial	Detection signalling and approach to mob; warning mates and kin

5.2.2 Experimental protocol

The five habituated groups were located by actively searching for them and listening for their vocalisations. After finding a group, I recorded its identity and mapped its exact geographical location, using a GPS Garmin Map 60CSX. A field-assistant (VF) and I monitored the behaviour of the group for at least 30 minutes prior to any experiment to make sure that the group was aware of the observers' presence and not disturbed by it. I then estimated the most likely direction of the group's progression and circumnavigated the group at a distance far enough to avoid detection in order to position the predator model along their anticipated path. During the set up and experiment, VF continued following the group to note any change in direction and to ensure that group's reaction was only to the stimulus.

5.2.3 Presentation of visual stimuli

The models were positioned either on the ground (puma, snakes and deer), close to the ground at an elevation of 20-180 cm (tayra and oncilla) or in the canopy at an elevation of 5-10m (caracara), thereby simulating natural situations. The height of the models was largely determined by the local canopy structure. Models presented within the canopy were suspended from tree branches with the help of a transparent fishing line. To increase the chance of the monkeys spotting the models, I positioned them in relatively open locations. After positioning the predator model, I moved away and, while hiding under a camouflage cover (figure 5.2), started recording the approaching monkeys' vocal behaviour for at least 5 minutes (but often longer) before the first monkey detected the model.



Figure 5.2. Photographs demonstrating the procedure to record monkeys vocalisations in response to visual models of predators and a non-predator animal. Photos by Vandilso Farias

The order of presentation was randomized for each group, and each group was tested only once with each stimulus. Within-group trials were separated by at least 10 days. The exceptions were GM and GP. For GM, I presented the oncilla 8 days after the caracara and the snake 3 days after the puma presentation. For GP, I presented the puma 7 days after the caracara. Some trials ($n = 7$) had to be repeated either because of equipment failure, background noise (especially tourists), or intergroup encounters just before detection of the stimulus by the focal group. Repetitions with the same model were performed on average 8.5 months after the first trial (median: 8 months, range: 4.5-12mo). Structural measures (see chapter two) were taken from the first trial, unless not possible.

I usually carried out experimental trials in the afternoons when the frequency of naturally produced loud calls was low (Melo and Mendes, 2000, Cäsar, unpublished data). Most experiments (61%) were performed in the afternoon when intergroup calls are less frequent. Valid trials were all trials in which the focal group was not vocalizing and/or involved in an inter-group encounter for at least 5 minutes before the first monkey detected the model. A trial was terminated when the group moved away or

started to engage in another activity. After the end of each trial the group was normally followed until they were settled in the sleeping tree, or until we lost the group.

5.2.4 Vocalization sample

All five groups were tested with seven stimuli, at least once, between August 2008 and May 2010. Most measurements, unless not possible, were taken from the first trial. Total duration of all vocal responses was based on the first trial. Almost all sequence compositions (30 first calls) were based on first trials, with the exception of GP/oncilla. Most call measurements were taken from first trials, with the exception of GA/big snake, GD/deer, GP oncilla down, GA/tayra, GP/tayra, GR/tayra, where the bad quality of the recordings prevented me from measuring the calls. Two puma trials were only valid for part of the measurements (see below). A group of tourists interfered on the trial with GA, which after a couple of minutes were responding to the tourists instead of the predator model. Therefore, I only considered the first minute of the group response. During the trial with GM, the background noise (cicadas) prevented me from coding the group's vocal response. Thus, in this trial I only considered the duration of the vocal response.

All models were presented motionless, except for two trials with the caracara where the model was moved for about 1 metre from its original position. This movement did not change the vocal response, but stimulated the caller to run away from the model by moving down or to a safer location, a similar response they give to flying raptors. A summary of experiments conducted and analysed is presented in table 5.2.

Table 5.2. Description of experimental trials conducted with 5 different black-fronted titi monkeys in Caraça Private Reserve, Minas Gerais, Brazil.

Model	Date	Experiment time	Group	N of Individuals*	First caller	Duration (min)	Valid
Caracara	25/09/2008	12:25	GA	5 (+1)	AF	1.00	DSM
	19/09/2008	15:00	GD	3	AM	6.65	DSM
	14/09/2009	13:20	GM	4 (+1)	J or AM/I	18.48	DSM
	11/11/2008	09:05	GP	4 (+1)	AF2	2.50	DSM
	19/09/2008	08:50	GR	5	AF	3.40	DSM
Big snake	14/10/2009	11:49	GA	5 (+1)	?	2.83	DS
	26/05/2010†	09:40	GA	6	AM	1.78	M
	25/06/2009	10:17	GD	3	AM2	2.87	DSM
	23/10/2009	07:10	GM	4 (+1)	AF	1.27	DSM
	17/10/2009	05:30	GP	4	AF?	4.08	DSM
	10/09/2009	11:41	GR	3	AM	4.15	DS
Small snake	14/05/2010	10:30	GA	6	AM	4.82	DSM
	20/10/2009	15:10	GD	2	AF	3.87	DSM
	19/10/2009	11:46	GM	4 (+1)	AF2	0.65	DSM
	15/10/2009	10:00	GP	4	AF2	0.60	DSM
	28/05/2009	11:10	GR	3	AF	0.03	DSM
Oncilla	14/08/2009	12:29	GA	5	AM	48.05	DSM
	06/08/2009	13:11	GD	2	AM	26.37	DSM
	22/09/2009	14:51	GM	4 (+1)	AF2	33.85	DSM
	23/07/2009	13:21	GP	4 (+1)	AM?	68.90	D
	25/05/2010†	13:00	GP	3	AM?	35.45	SM
	07/08/2009	13:29	GR	4	AF	59.35	DSM
Puma	05/11/2008	14:07	GA	4 (+1)	? or AF	18.53	SM‡
	14/10/2008	-	GD/R	9	?	-	-
	02/06/2009†	14:12	GD	4	?	39.08	DSM
	16/10/2009	08:22	GM	4 (+1)	AF	23.45	DS
	18/11/2008	14:20	GP	4 (+1)	AM	19.07	DSM
	10/10/2008	14:29	GR	4	?	26.80	DSM
Tayra	12/10/2008	15:26	GA	5 (+1)	?	15.43	DS
	03/06/2009†	14:10	GA	5	?	21.00	M
	22/08/2008	15:00	GD	4	AM/I	16.88	DSM
	20/08/2009	12:28	GM	4	?	42.52	DSM
	22/10/2008	13:23	GP	4 (+1)	AF2	35.48	DS
	21/10/2009†	09:00	GP	4	AF	34.18	M
	30/07/2008	15:45	GR	5	?	20.97	DS
	17/06/2009†	13:20	GR	3	AM2	39.52	M
Deer (control)	24/06/2009	12:33	GA	5	?	30.48	DSM
	20/05/2009	14:30	GD	4	?	24.43	DS
	01/10/2009†	13:20	GD	3	AM2	23.03	M
	13/05/2010	14:38	GM	4 (+1)	AM or AF	11.98	DSM
	16/09/2009	10:46	GP	4	?	16.33	DSM
	25/08/2009	11:58	GR	2	?	21.28	DSM

AM = paired adult male, AM/I = adult male carrying infant, AM2 = unpaired Adult male, AF= paired adult female, AF2= unpaired adult female, J = juvenile, I = infant; * group sizes varied due to births, migration and disappearances; number in brackets represent the presence of dependent infant being carried mainly by the father (paired adult male). Valid trials for analyses (D: duration of vocal response; S: first sequence composition; M: acoustic measurements of calls). † Repetitions; ‡ call types were coded only for the first minute.

5.2.5 Data analysis

To describe titi monkeys' behavioural responses I scored: 1) the distance of the caller from the model at detection, 2) the behaviour of the first caller, 3) the number of individuals in the group during the experiment, 4) the behaviour of other group members and 5) the length of the vocal response (duration of calling from visualisation until they left the area or were engaged in another activity). Whenever possible, I scored the identity of the first caller; due to low visibility, it was frequently not possible to identify the first individual that detected the stimulus. All responses are thus represented as group reactions, a common procedure in research on arboreal forest monkeys living in visually dense habitat (e.g. Zuberbühler et al., 1997).

Furthermore, for each recording I measured: 1) the call rate during the first five minutes after detection and 2) the type of calls produced during the first five minutes after detection. Call rate was calculated by dividing the total number of calls per number of individuals (juveniles and adults) in each group over the duration of the experiment (number of individuals per group varied due to dispersions and disappearances, see chapter two).

To examine the differences in the occurrence of each call type during the first five minutes after detection, I analysed only the responses to the terrestrial predator stimulus (oncilla and tayra) and the control (deer), which all lasted for at least 5 minutes. Responses to puma were excluded due to small sample size of complete and codeable trials ($N=3$). Responses to caracara and to the two snake models were not considered for this analysis because most trials lasted less than five minutes.

I carried out quantitative analyses of the acoustic structure of calls produced in all terrestrial contexts (see methods for description of calls in chapter 4). To get a balanced sample size, I selected 40-50 calls from different contexts. I screened the data for outliers by producing standardized Z scores and rejected calls with a Z score greater

than 3.29 in one or more parameters (Tabachnick and Fidell 2001). I then regressed all parameters with a variance inflation factor greater than 4 (Glantz and Slinker 2001). I then conducted a discriminant function analysis (DFA) to assess whether each of the uncorrelated acoustic variables, when combined in one model, could discriminate between the six terrestrial models. In order to have independent data and to avoid individual differences in call structure across contexts, I used alarm calls of at least four of the five different groups.

I ran one-way related-samples analysis of variance tests to examine whether each of the acoustic parameters varied statistically with each stimulus type. At least four of the five groups contributed a mean value per stimulus per parameter, which was derived from several calls per stimulus category (= 249 raw calls). I conducted post hoc pairwise Sidak-corrected comparisons to examine whether any of the acoustic parameters could discriminate between the stimulus types.

Part I: Anti-predator responses of *Callicebus nigrifrons* to visual predator models – comparisons with natural observations

5.3 Results

5.3.1 Behavioural responses

All groups called upon encountering the models in all experimental trials. I was able to identify the first caller in 58% (24/41) of trials. In these cases, the paired male and female called first in response to the model at equal rates (8 times each, on different trials). Including offspring, the females were the first to see and call in 54% (13/24), while males did in 46% (11/24) of valid trials (table 5.2).

The duration of groups' vocal responses was significantly related to the model presented ($F_{6,19} = 8.815$, $p < 0.0001$, figure 5.3), *post hoc* pairwise Sidak-corrected comparisons are presented in table 5.3. Group identity and number of individuals did not affect the duration of vocal responses ($F_{4,19} = 0.259$, $p = 0.90$; $F_{4,19} = 0.633$, $p = 0.645$), respectively.

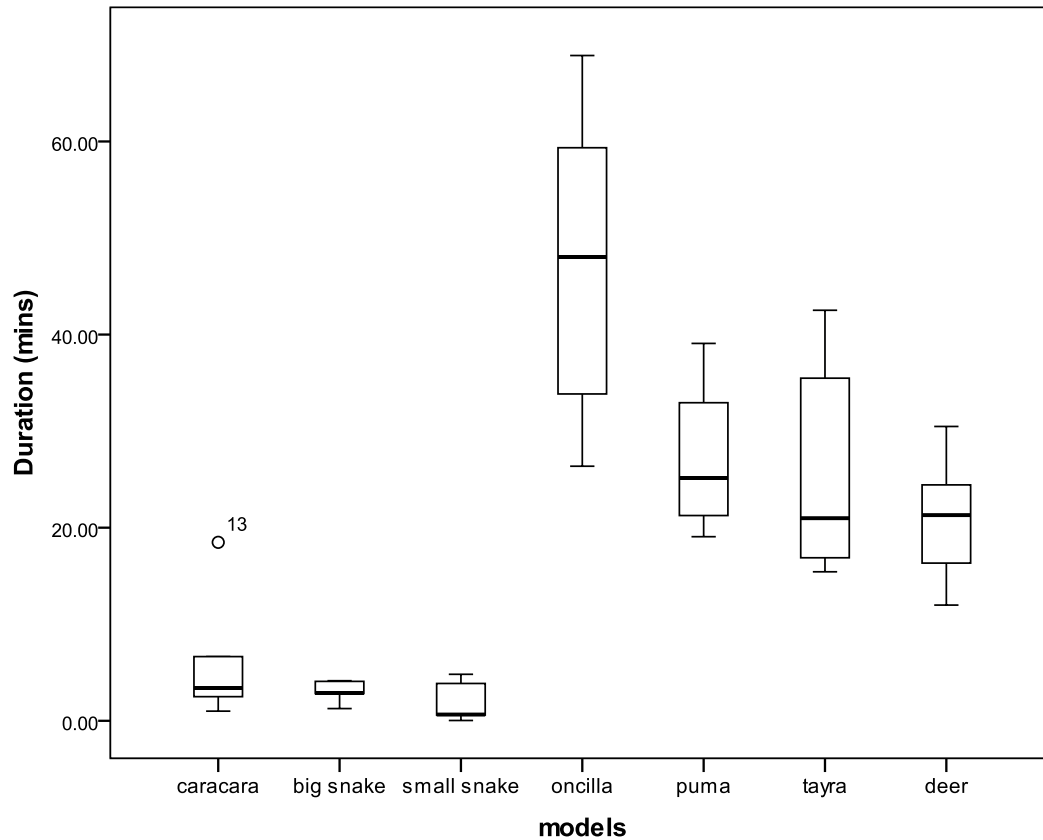


Figure 5.3. Box plots indicating the duration of calling behaviour after detecting different types of predators and a non-predator animal (medians, upper and lower quartiles, circles= outliers).

Table 5.3. Coefficient matrix of univariate results of *post hoc* Sidak-corrected comparisons. (ca): caracara, (bs): big snake, (ss): small snake, (on): oncilla, (pu): puma, (ta): tayra and (de): deer.

Model	bs	ss	on	pu	ta	de
ca	ns	ns	***	ns	ns	ns
Bs	-	ns	***	ns	ns	ns
ss		-	***	*	*	ns
on			-	ns	ns	*
pu				-	ns	ns
ta					-	ns

* $P < 0.05$; ** $P < 0.01$, *** $P < 0.001$ (two-tailed). ns= Not significant.

In response to the caracara perched in the canopy usually only the first individual to detect the stimulus called, while observing, freezing or showing rapid flight, and usually descending or moving to a protected location. Responses from other group members depended on their distance to the model and to the caller. If other members were close by and presumably able to hear the first caller, they remained silent and immediately looked up, and descended or hid if they were in an exposed place. If they were not close enough to hear the first individual calling, other group members were able to detect the stimulus later on and also produced the same call-type to the stimulus as the first caller. In two trials (GD and GP), the first individual to see the model and call (adult paired male and adult female 2, respectively) approached the model after some time and, after a closer inspection, moved away. Their approaches did not stimulate other members to approach.

Behavioural responses to terrestrial disturbances depended on the stimuli (table 5.4). In response to oncilla, tayra and puma, the first animal to call usually attracted other group members who then also called. First caller's behaviour included looking to the stimulus and producing visual displays, such as arch postures, pilo-erection, tail lashing (swinging tail sideways) and head swaying, and rapid erratic movements towards and away from the threat, while maintaining visual fixation. Listeners' (i.e. group members who had not yet seen the model) behaviour included looking towards the caller, scanning the forest ground or lower canopy, approaching the caller, calling, visual displays and harassing (mobbing) the predator cooperatively.

In response to snakes (two specimens of *Boa constrictor*), usually only the first individual to detect the stimulus called, while observing the models. The behaviour of listeners included looking towards the caller, scanning the forest ground or lower canopy. Listeners did not approach the snakes after the detection was signalled by the first caller. Other group members that were not close enough to hear the first individual calling also produced the same call-type to the stimulus if they detected it.

Table 5.4. Behaviour of group members, or at least one other member, after hearing the first caller. (ca): caracara, (bs): big snake, (ss): small snake, (on): oncilla, (pu): puma, (ta): tayra and (de): deer.

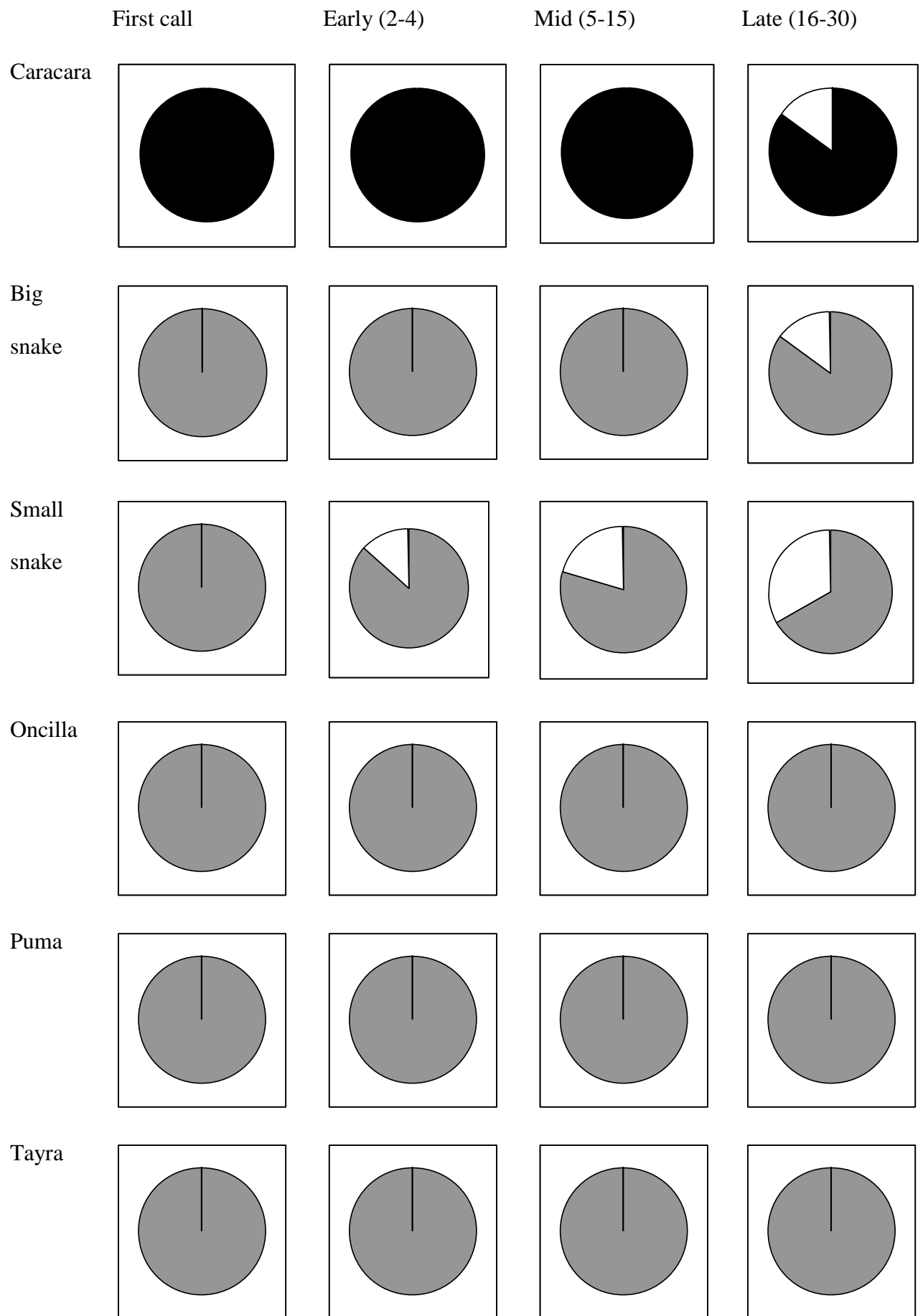
Behaviour	ca	bs	ss	on	pu	ta	de
Call	0	2	2	5	5	5	5
Scan sky/canopy	5	0	0	0	0	0	0
Scan lower canopy	2	5	5	5	5	5	5
Hide	5	0	0	0	0	0	0
Approach	0*	0	0	5	5	5	3
mob	0	0	0	5	5	5	5

Values represent the number of groups (n=5) that perform each behaviour. * Two individuals (first callers) approached the model but moved away after closer inspection (see text for details)

5.3.2 Context-specificity

First calls

As expected, call A was the first and only call given in response to the raptor (caracara) and was not present in vocal response sequences given to terrestrial predators (small snake, big snake, oncilla, puma and tayra) nor to the non-predator model (deer) on the ground (Figure 5.4, table 5.5). In response to all terrestrial predators and the control (deer), the focal groups' first call was always call B (figure 5.4, table 5.5), with the exception of one group (GD) that gave call C upon detecting the deer.



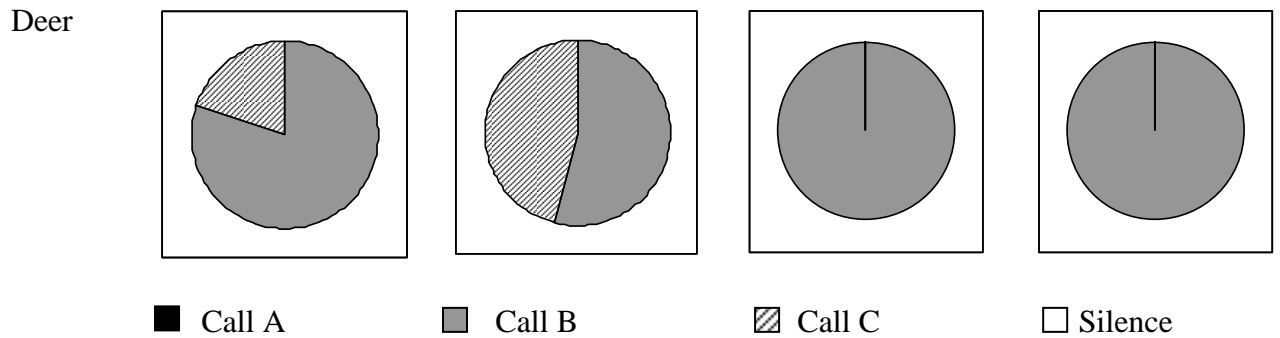


Figure 5.4. Sequential analyses of the first 30 calls produced in predatory and control contexts.

Table 5.5. Number of calls coded to describe the first 30 calls produced in response to predator models and a non-predator model.

Stimuli	N	Groups	First call	Early (2-4)	Mid (5-15)	Late (16-30)
Caracara	5	A,D,M,P,R	5/5	15/15	55/52	75/74
Big snake	5	A,D,M,P,R	5/5	15/15	55/48	75/75
Small snake	5	A,D,M,P,R	5/5	15/15	55/54	75/75
Oncilla	5	A,D,M,P,R	5/5	15/15	55/55	75/75
Puma	4	A,D,P,R	4/3	12/10	44/44	60/60
Tayra	5	A,D,M,P,R	5/5	15/15	55/55	75/75
Deer	5	A,D,M,P,R	5/5	12/10	55/55	75/75

N: number of events per predator stimulus recorded and analysed. Group letters represent the individual groups (total of 5) contributing to each type of predator stimulus. Values on First, Early, Mid and Late calls, represent firstly the total number of calls produced (which are the result of multiplying the number of events by the number of calls in each category), and secondly the total number of calls codeable and used to illustrate the differences on Figure 5.4.

5.3.2.2 Calls during the first minute after detection

There were no significant differences in the number of calls given in response to each stimulus during the first minute ($F_{6,23} = 1.689$, $p = 0.169$, figure 5.5).

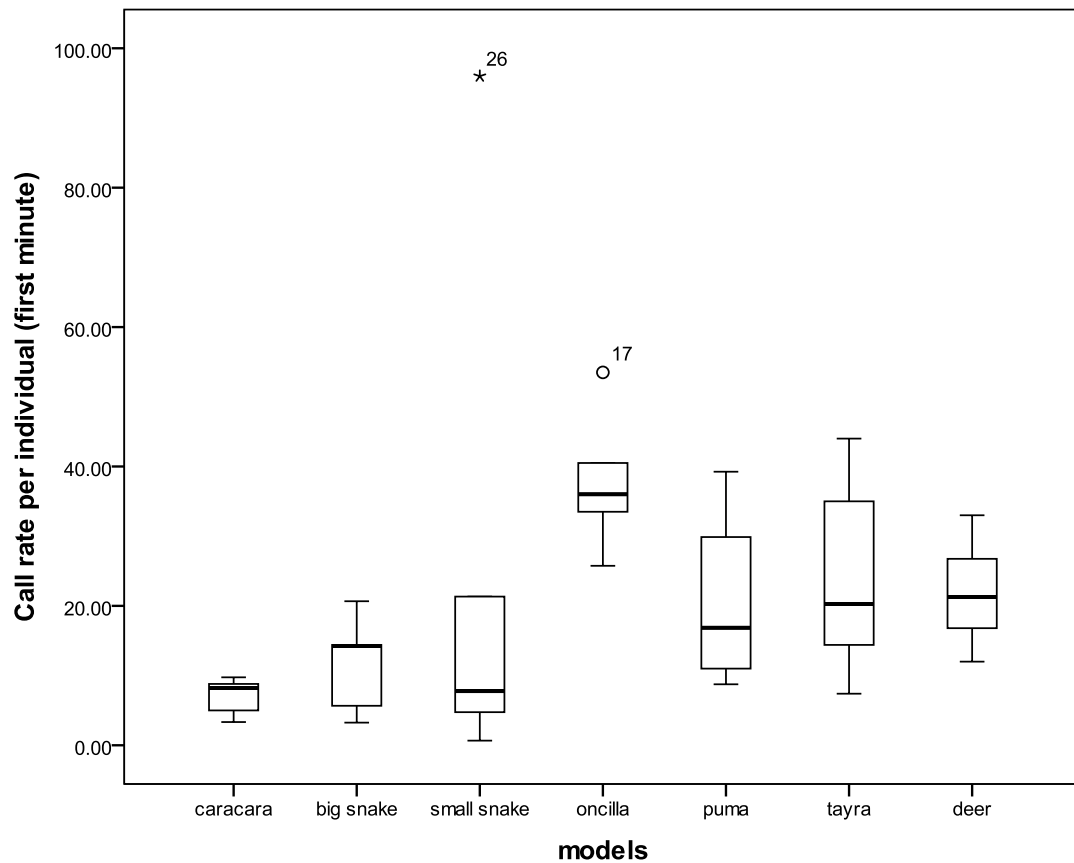


Figure 5.5. Box plots indicating the call rate per individual during the first minute after detecting different types of predators and a non-predator animal (medians, upper and lower quartiles, circles= outliers). Call rate per individual was calculated by dividing the number of total calls produced during the first minute by the number of individuals (adults, sub-adults and juveniles) in the group during the experiment.

5.3.3 Sequence composition during the first minute

The proportion of A, B and C calls within the first minute were all significantly dependent on the type of stimuli (A: $\chi^2 = 32.734$, $df=6$, $p<0.0001$; B: $\chi^2 = 21.687$, $df= 6$, $p=0.001$; C: $\chi^2 = 16.600$, $df= 6$, $p=0.011$, fig 5.6).

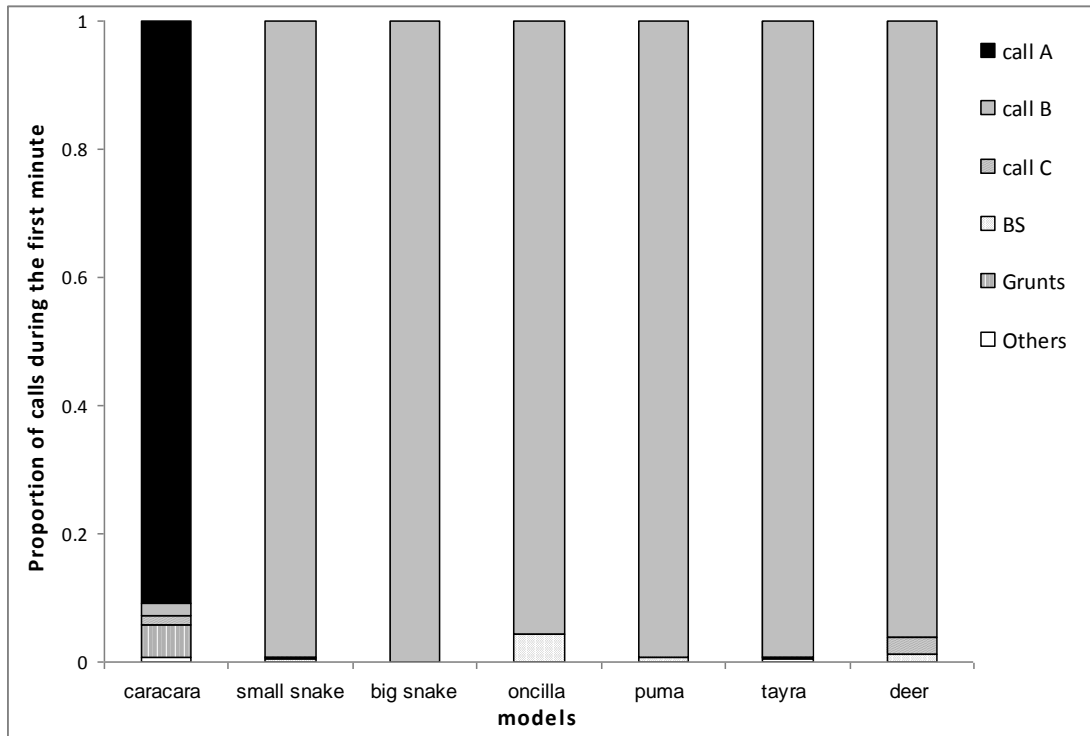


Figure 5.6. Proportion of each call type during the first minute. Spectrographic representations of each call and variants are presented in chapter 3.

Part II: Comparisons between predatory and non-predatory stimuli on the ground

5.4 Results

5.4.1 Calls during the first five minutes after detection

In the first five minutes after detection of two species of predator (oncilla and tayra) and the control (deer) presented on the ground, call A continued to be absent from the groups' vocal responses (figure 5.7). The most common calls during the first five minutes were call B and BS for all these stimuli. However, the former was decreasing and the latter was increasing over time (figure 5.8), especially in response to the predators. Loud calls were only produced in response to oncilla and tayra, while call C

was mostly produced in response to the deer (figure 5.9). BW and loud calls (moans, honks, resonating calls and pumps) were produced in the second or third minute after detection of oncilla and tayra, respectively, and were not present in response to the deer (figure 5.10).

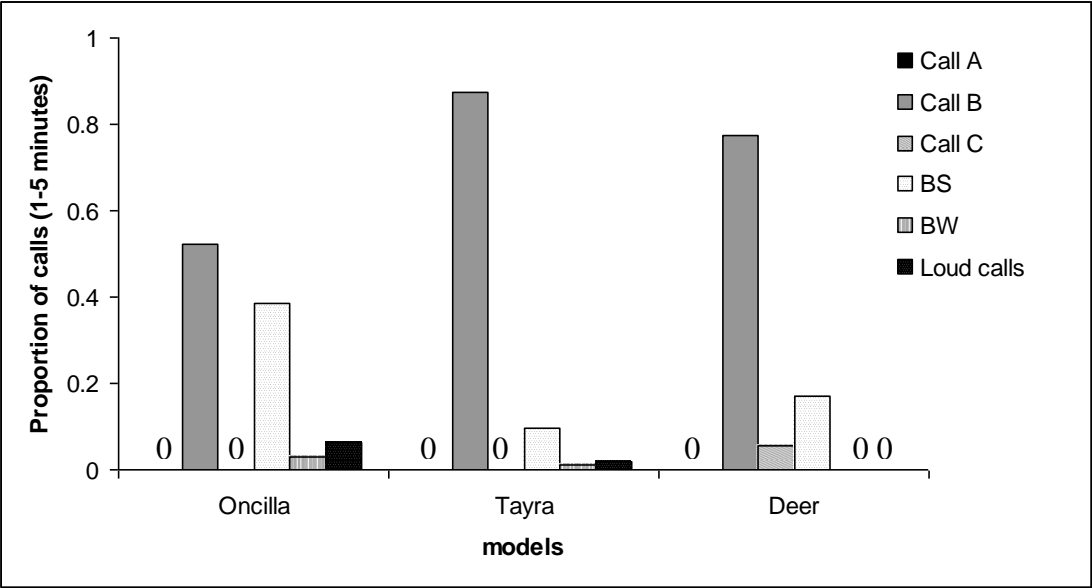
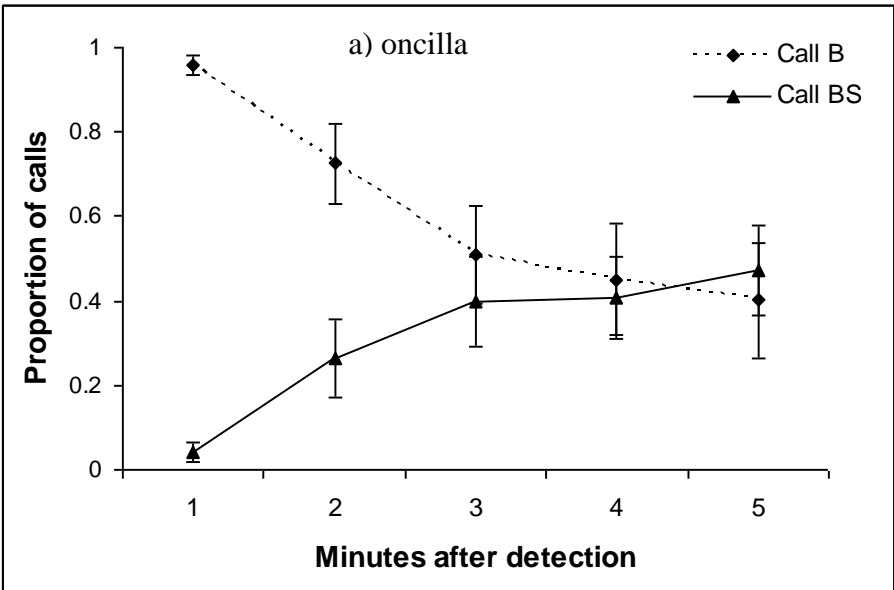


Figure 5.7. Proportion of calls produced within the first five minutes after detecting two species of predators (oncilla, tayra) and a control non-predator model (deer).



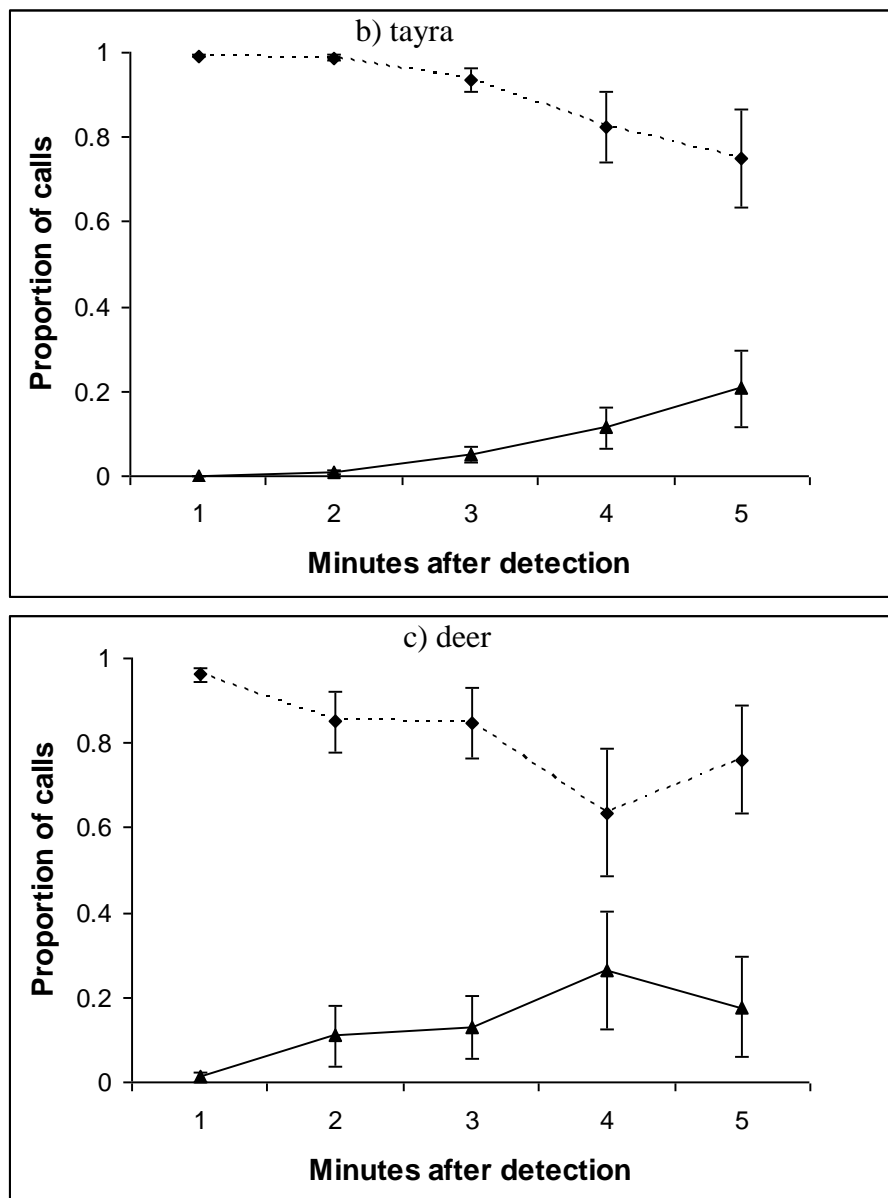


Figure 5.8 Proportion of most frequent call types (B, BS) produced within the first 5 minutes after detection of two predator species (oncilla and tayra) and a control non-predator model (deer).

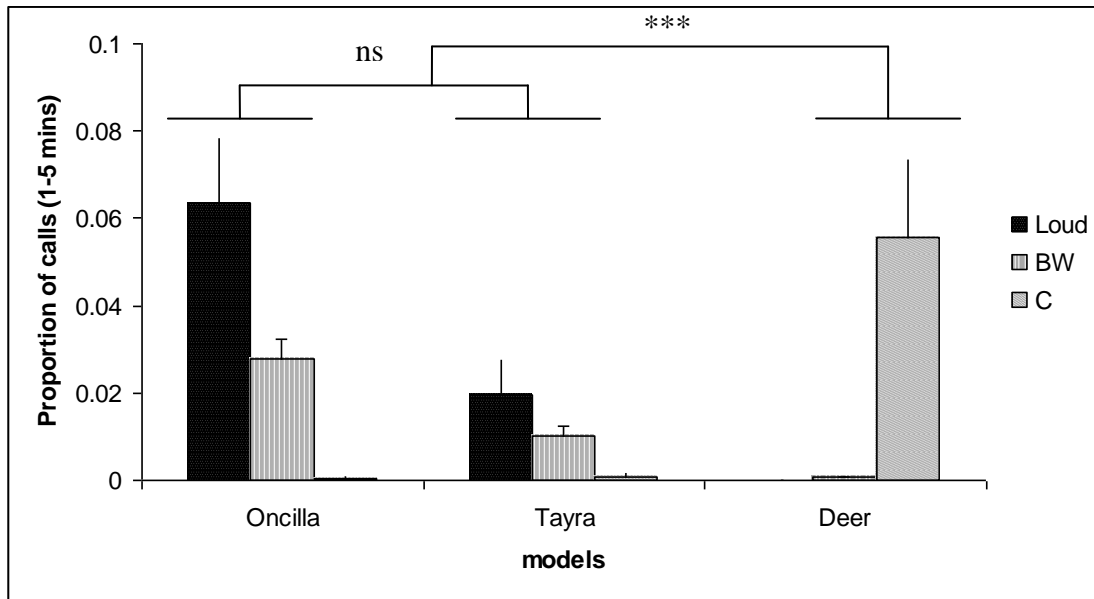
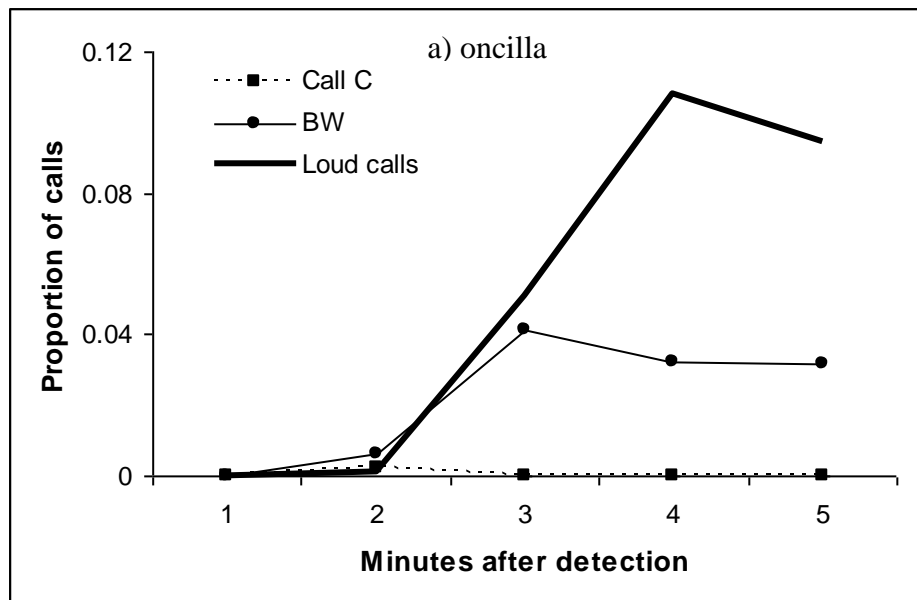


Figure 5.9. Proportion of less common calls produced within the first five minutes after detecting two species of predators (oncilla, tayra) and a control non-predator model (deer). Means \pm SEs are shown. *** $P < 0.001$; ns = not significant; Fisher's exact test.



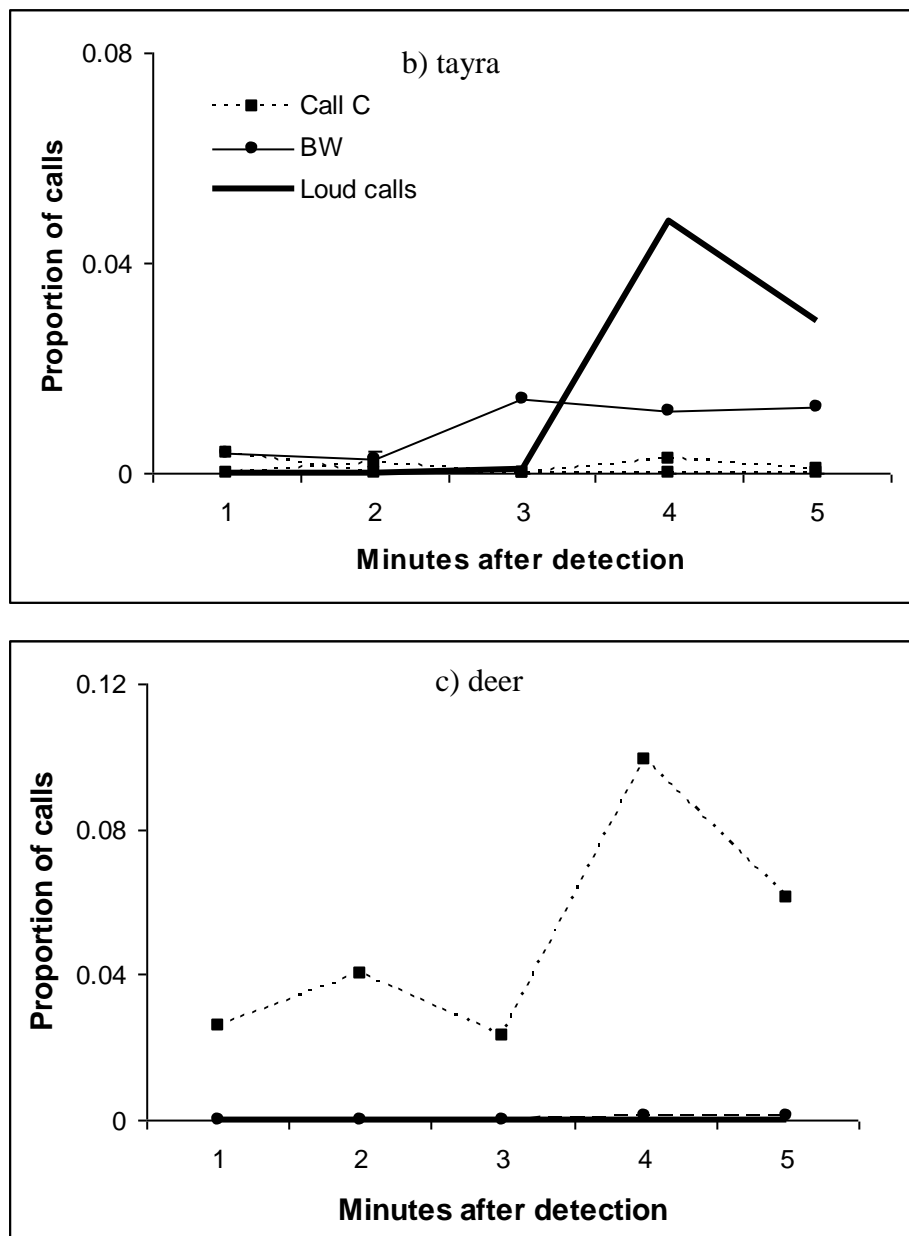


Figure 5.10 Proportion of the less common call types (C, BW and loud calls) produced within the first 5 minutes after detection of two predator species (oncilla and tayra) and a control non-predator model (deer). Loud calls include: moans, honks, resonating calls and pumps. Spectrographic representations of each call are presented in chapter 3.

5.4.2 Acoustic differences between call B ('cheep') produced to terrestrial predators and control

Following checks for multi-collinearity and singularity, I subjected five of the eight original acoustic parameters to a discriminant function analysis: total duration, frequency at the end of the fundamental frequency, transition onset, overall transition and number of harmonics. In total, I analysed 249 calls given by at least four of the five focal groups (number of calls per stimulus ranged from 37 to 48 calls). The first two functions explained a significant amount of the variation in the acoustic structure of the call types (fig. 5.11). The first one, consisting mainly of the frequency at call end ($r=0.650$) and number of harmonics ($r=-0.589$) explained 53.8% of the variation (Wilks' $\lambda=0.419$, $\chi^2_{25}=211.124$, $P < 0.001$). The second one, consisting mainly of call duration ($r=0.876$) and frequency at the end ($r=0.217$) explained 26.1% of the variation (Wilks' $\lambda=0.650$, $\chi^2_{16}=104.313$, $P < 0.001$). Overall, only 43.4% of the original grouped cases were correctly classified and in a cross-validated analysis, the functions successfully classified only 38.6% of calls into the six categories. The highest classification success was the puma, with 71.8% of cases correctly classified, followed by the tayra (58.3%) and small snake (54.1%). The lowest percentages of correctly classified cases were with the big snake (10.0%) and the deer (27.0%). Acoustic measures of B calls given in response to six stimuli in experimental contexts are presented in table 5.6.

Table 5.6. Acoustic measurements (mean \pm SD) of call B given by adults in the five habituated groups of *C. nigrifrons* in response to various terrestrial disturbances

Acoustic feature	small snake (N=37)	big snake (N=40)	oncilla (N=48)	puma (N=39)	tayra (N=48)	deer (N= 37)
Group's contribution	A/10, D/11, M/9, P/5, R/2	A/10, D/10, M/10, P/10	A/8, D/10, M/10, P/10, R/10	A/10, D/9, P/10, R/10	A/10, D/9, M/10, P/10, R/9	D/10, M/7, P/10, R/10
Duration (s)	0.0327 \pm 0.005	0.030 \pm 0.007	0.031 \pm 0.006	0.030 \pm 0.005	0.025 \pm 0.005	0.028 \pm 0.006
F0 Onset (Hz)	3850 \pm 855	3994.2 \pm 508.0	4226 \pm 893	5054.5 \pm 485.7	4179 \pm 487.1	4536 \pm 692
F0 Middle (Hz)	3894 \pm 833	3997.9 \pm 501	4300 \pm 908	5114.9 \pm 503.5	4191.4 \pm 515.6	4620 \pm 748
F0 End (Hz)	4871 \pm 664	4994.7 \pm 452.3	5419.5 \pm 653.3	5926.4 \pm 429.4	5043.4 \pm 514	5271.4 \pm 543.6
Transition onset (Δ Hz)	44.6 \pm 175.6	3.7 \pm 89.3	74.6 \pm 106.9	60.4 \pm 105	12.4 \pm 99.3	83.4 \pm 138
Transition offset (Δ Hz)	977.2 \pm 413.8	996.8 \pm 413.7	1119.1 \pm 387.9	811.5 \pm 218.1	852 \pm 263.1	651.6 \pm 362.3
Overall transition (Δ Hz)	1021.7 \pm 437.2	1000.4 \pm 427.9	1193.8 \pm 387.7	872 \pm 167.9	864.4 \pm 244.6	735.0 \pm 368.8
# Harmonics	2.59 \pm 1.23	2.05 \pm 1.20	1.71 \pm 1.07	0.4872 \pm 0.60	1.54 \pm 1.13	1.43 \pm 0.93

Below each stimulus is depicted the number of calls measured, and with a standardized Z score less than 3.29, per stimulus. Group's contribution shows the number of calls per group considered for the analysis.

To examine whether each of the uncorrelated acoustic parameters varied between stimulus types, I conducted one-way related-samples analysis of variance tests with stimuli as the fixed factor and group as random factor. Only call duration varied statistically among model types ($F_{5,17}= 4.362$, $p=0.010$). The other parameters did not vary significantly between model types (frequency at call end: $F_{5,17}=2.468$, $p=0.074$, overall transition: $F_{5,17}= 1.548$, $p=0.227$; transition onset: $F_{5,17}=1.147$, $p=0.374$; and number of harmonics: $F_{5,17}= 2.325$, $p=0.088$). I also found that group identity varied consistently with call duration and frequency at call end: $F_{4,17}= 5.296$, $p=0.006$; $F_{4,17}= 3.466$, $p=0.030$, respectively. *Post hoc* pairwise Sidak-corrected comparisons revealed that mean call duration significantly discriminated between call B produced in response to tayra and all the other stimuli. Calls produced in response to puma have a higher frequency at the call end and a smaller number of harmonics than any other model. The number of harmonics was higher in calls produced to the small Boa, compared to all other stimulus. The overall transition of calls produced in response to oncilla was higher than to any other model. Table 5.7 and figure 5.12 summarize the results.

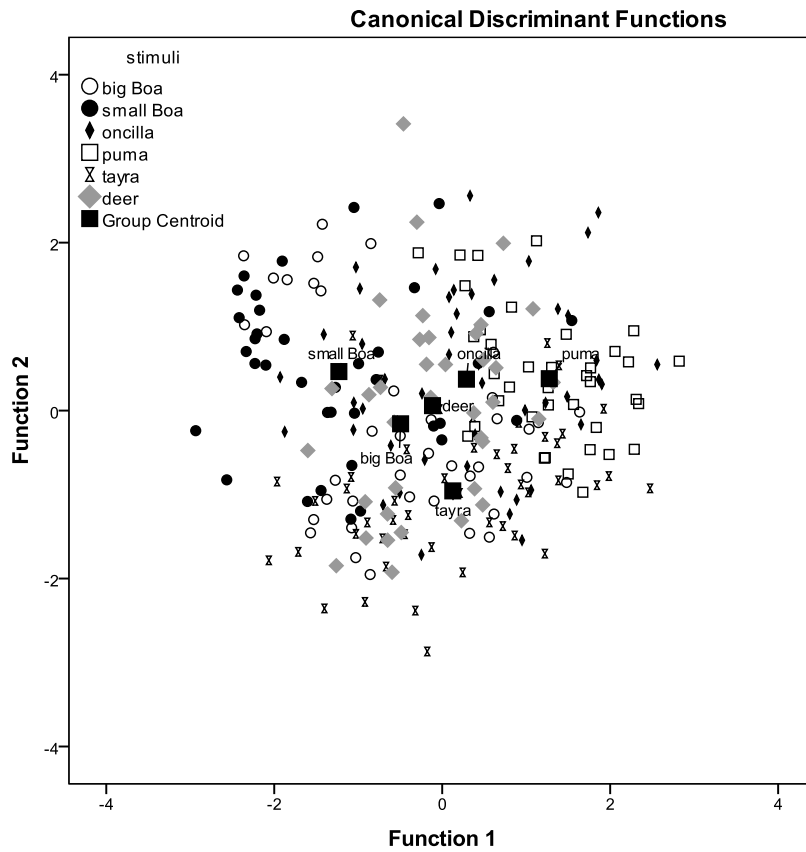


Figure 5.11. Distribution of discriminant scores along the two canonical discriminant functions to separate titi monkey terrestrial disturbances calls (Eigen values: Function 1 =0.553; Function 2 =0.269). Black squares represent group centroids.

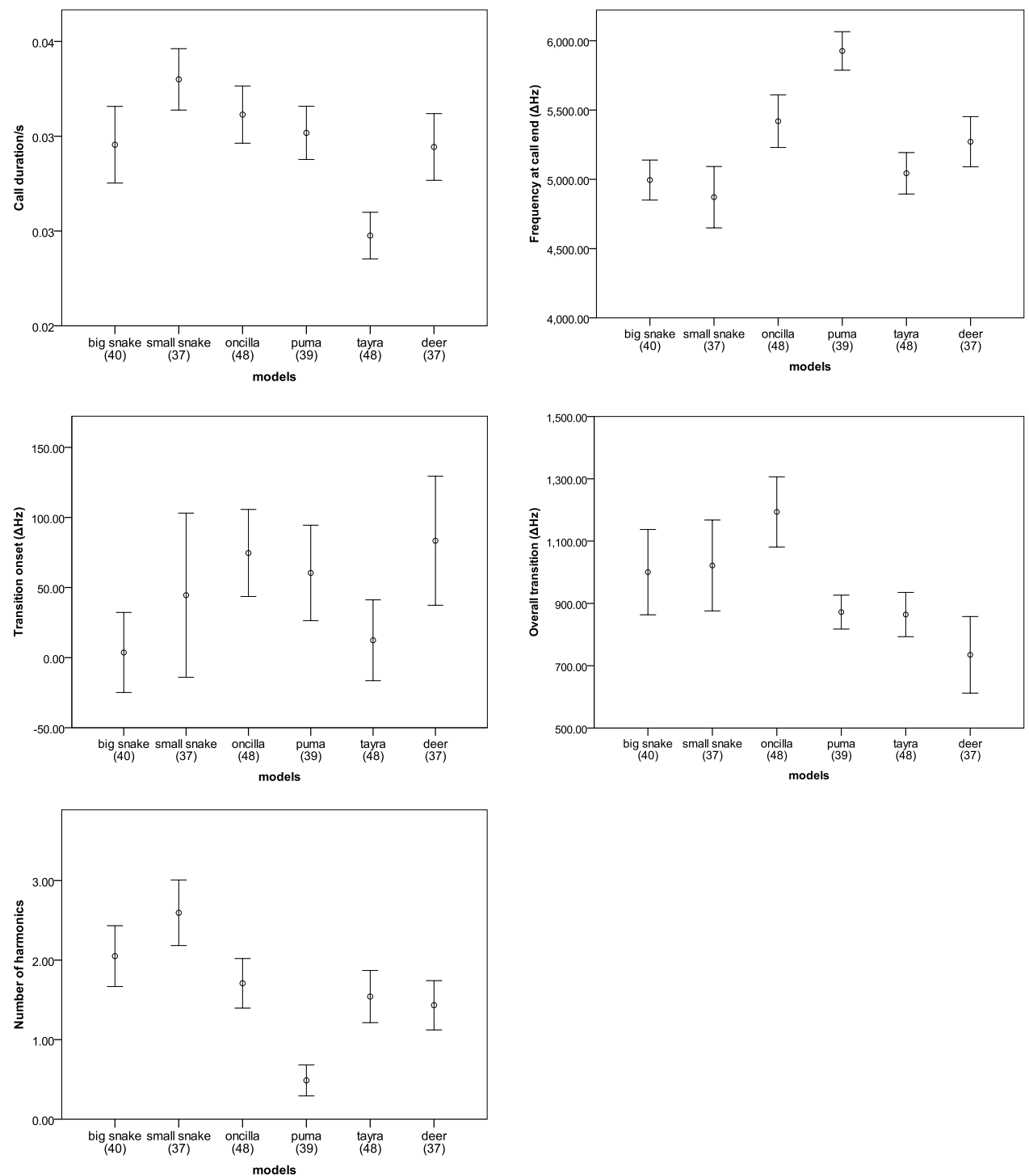


Figure 5.12. Mean values \pm SE for five acoustic parameters showing the similarities and differences between call B produced in response to different predator models (big and small Boa, oncilla, puma, tayra) and the control non-predator animal (deer): (a) call duration (s), (b) frequency of maximum energy at call end (Δ Hz), (c) transition onset (Δ Hz), (d) overall transition (Δ Hz) and (e) N harmonics.

Table 5.7. Results of *post hoc* Sidak-corrected comparison tests for differences between sample means of acoustic parameters of call B produced in response to six predator model and one non-predator control animal. (ca): caracara, (bs): big snake, (ss): small snake, (on): oncilla, (pu): puma, (ta): tayra and (de): deer.

Acoustic parameter	stimuli	ss	on	pu	ta	de
Call duration	bs	**	ns	ns	***	ns
	ss	-	ns	*	***	**
	on		-	ns	***	ns
	pu			-	***	ns
	ta				-	***
Frequency at call end	bs	ns	***	***	ns	**
	ss	-	***	***	ns	***
	on		-	***	***	ns
	pu			-	***	***
	ta					*
Transition onset	bs	ns	*	ns	ns	*
	ss		ns	ns	ns	ns
	on			ns	ns	ns
	pu				ns	ns
	ta					ns
Overall transition	bs	ns	**	ns	ns	***
	ss		**	ns	*	***
	on			***	***	***
	pu				ns	ns
	ta					ns
Number of harmonics	bs	**	ns	***	**	***
	ss		***	***	***	***
	on			***	ns	ns
	pu				***	***
	ta					ns

P-value: *<0.05; **<0.01; ***<0.001.

5.5 Discussion

5.5.1 Call function and meaning

Black-fronted titi monkeys (*Callicebus nigrifrons*) produced vocalizations in response to all predator models and to the control. All groups reliably uttered call A as a first response to the raptor (caracara) in the canopy and call B in response to all other species of predators (snakes, oncilla, puma and tayra) and to the control (deer) on the ground. In later parts of the sequence, groups produced other call types, especially in response to mammalian terrestrial predators. However, call A was never produced to any of the models presented on the ground, but only in response to the caracara in the canopy.

Vocal sequences in response to a perched caracara were composed only, or almost exclusively of call A, and monkeys usually went to a hidden place or left the area. During raptor presentations, only two individuals from two different groups approached the model after looking and calling at it for some time. It is reasonable to assume that encountering a motionless raptor represents an unusual event, while the continued lack of movement may influence the caller to approach for further inspection. This reaction was not observed in response to live raptors, possibly because monkeys can differentiate between still and moving animals. Another observation to support this interpretation comes from the two trials in which the caracara model was moved by the experimenter. In both cases, the caller, which was closest to the model, was affected by the movement and escaped quickly. The same behaviour was observed during all natural observations of raptor encounters and attacks. Listeners looked upwards and stayed still, probably in order to avoid being detected by the predator.

Vocal responses to predator models presented on or close to the ground, especially oncalla, puma and tayra, were longer and more complex than other responses. They contained several additional call types, including loud and low-pitched calls. The first caller always initiated the vocal sequence with call B, which seems to be produced primarily to inform or attract conspecifics' attention to a disturbance on the ground. Subsequently, the other listeners usually approached and also called towards the model. This behaviour, along with the production of loud calls, seems to be directed at the predator to inform that it has been detected (Zuberbühler et al., 1997, Zuberbühler et al., 1999ab, Clarke et al., 2006). This hypothesis is supported by the increase in production of low pitched and loud calls throughout the time and the mobbing behaviour performed towards these predator models by several individuals. Digweed et al. (2005) have suggested that capuchin alarm calls may also recruit conspecifics to mob. It seems also likely that once the group is together they try to intimidate the predator (Zuberbühler et al, 1999ab). Moreover, the use of different call variants and sometimes low-pitched calls may be important to inform group members the degree of threat they are facing. Another possible explanation for recruitment and mobbing would be an increase in the caller's fitness when a younger individual later recognizes a predator and alarms, thereby warning the original caller (Curio, 1978, revised in Wheeler, 2008).

Some calls produced in response to models on the ground, especially call B, are also produced in other contexts. In other studies, it has been reported that most of the major call types of *C. cupreus* occur in a wide range of social circumstances, including both hostile and non-hostile situations (Moynihan, 1966; Robinson, 1979a). However, it seems likely that some calls can be context-specific if the caller and listener are able to extract the relevant information from the event. For instance, some calls produced in long distance sequences consist of different vocal combinations that can have different functions if uttered separately (Marler, 1977). Robinson (1979) has also shown that in response to abnormal sequences *C. cupreus* produced more "moans", which are uttered in more disturbing situations. During this study, I recorded subjects uttering call B while

descending or foraging near the ground, when a human (the observer) was in their way, or in response to human observers by unhabituated animals (chapter four). This suggests that this call is also triggered by non-predatory events, a pattern common in other primate species (Wheeler, 2008, Arnold and Zuberbühler, 2006a). The loud calls given only to oncilla and tayra (and puma, not analysed) were observed during duets and other loud sequences during some intergroup encounters. Whether or not these calls produced in different contexts have a different meaning will have to be tested in the future.

Although monkeys are using the same call in different contexts, it may be possible that subtle differences, in acoustic features of the same call or call variation, are sufficient to inform others about the ongoing contexts or level of threat. For instance, while coding vocal responses I noticed that monkeys often produced multiples (such as doubles and triplets) of call B in response to terrestrial predators. However, due to overlap between different callers I could not reliably code this vocal behaviour as a unique call variant, which was rare or absent during non-predatory contexts. Variation in syllable number may be associated with particular predator types (Schell et al, 2009) and/or the caller's risk urgency (e.g. Templeton et al 2005), which may also explain titi's behavioural responses after hearing the presence of a predator. In contrast, there is no evident behavioural response from the rest of the group when a caller was descending, when human observers were in its way, or when it was foraging in the lower canopy. In those cases, listeners only looked towards the caller and continued with their current activities. In some cases, for example when the caller was feeding, other group members followed the first individual and fed in the same tree or bush, usually by producing call B (cheep) and other high-pitched calls, such as whistles and food calls (C. Cäsar, personal observation). In response to a human observer, unhabituated subjects seem to produce the same call types as habituated subjects give in response to predator models on the ground. However, their vocal sequences are usually shorter and the animals retreated more quickly (Cäsar, personal observation).

Context-specific information can be also conveyed in subtypes of a general alarm call (Fichtel et al, 2005). The acoustic differences I found in call B produced in response to predators and the control (tables 5.6, 5.7 and figures 5.10, 5.12) may convey information about different types of terrestrial threats. For instance, call B with high frequency at the call end and less number of harmonics may inform of a presence of puma, while a shorter version would indicate the presence of tayra. Unfortunately, I did not measure any suitable independent variables that would allow me to address this hypothesis more systematically; and at this point my results showed no behavioural differences (e.g. all monkeys approached and mobbed) in response to puma, oncilla and tayra, even though the calls were apparently context-specific. One possibility to explain this would be that the acoustic variants within call B do not provide sufficient evidence for a communicative function. In a playback study with meerkats (*Suricata suricatta*), for instance, Townsend et al (2010) showed that receivers did not perceive the group signature present in their ‘close calls’, possibly because they used other sensory systems to identify non-group members. Whether or not titi monkeys can discriminate between the acoustic differences present in their B calls is still unclear and will require further investigation. Nonetheless, the data presented here indicate that monkeys may be able to extract the meaning from the subtle differences in the acoustic structure of call B and/or by examining the behaviour of the caller (e.g. Fisher and Hammerschmidt, 2001). While still not apparent how these differences may or may not be understood by the listeners, some evidence suggests monkeys may be able to cue in one or more of these differences (e.g. during encounters with terrestrial predators monkeys approach and mob the models; during encounters with deer model, monkeys look and call while monitoring the model; and during foraging monkeys look and continue with their activities).

An important additional point is that all contexts in which B-calls were given are conceptually similar. They all relate to situations in which the caller is vulnerable to threats from the ground.

5.5.2 Anti-predator behaviour of titi monkeys

As expected, the vocal responses to caracara were shorter than given to other animals and monkeys did not approach or mob the raptor. This behaviour suggests that raptors may represent a bigger risk to the monkeys, as several species of raptors are very manoeuvrable (Templeton et al, 2005) and could pursue the monkeys in the canopy. An event recorded in 2008 supports this hypothesis. I witnessed an attack by a small raptor, *Accipiter* sp., on group R, in response to which all five individuals in the group behaved as if they were in danger. The raptor tried to catch a monkey six times and almost succeeded, and even provoked the fall of an adult individual. During attacks, at least one individual produced A calls (chirps), which were also given to the caracara model and other raptors. The only noticeable difference in this event was that monkeys produced triplet chirps, which could also indicate the degree of threat. After the first attack, all group members, which were foraging in a relatively open area, ran to a more protected place (e.g. close to the trunk and under the tree branches). This and other observations suggest that black-fronted titi monkeys in this area suffer from predation pressure, especially by raptors. My long term study has revealed a relatively high mortality rate for infants – one group lost its last three infants over consecutive years and another group lost at least one infant, all of them between birth and 2 months of age (C. Cäsar, unpublished data), possibly caused by predation. These patterns seem to be common in other New World monkeys, where the intensity of the selective pressure exerted by raptors is illustrated by a relative large number of recorded events (reviewed in Ferrari, 2009).

In response to terrestrial predators, subjects produced BW and some loud calls within alarm-calling sequences, regardless of the type of the predator. There were small differences in the proportion of each call type; however, the differences between the different types of terrestrial predators (e.g. *oncilla* and *tayra*) were not statistically significant. This suggests that titi monkeys might be categorizing the two species as the

same type of threat (terrestrial predators), although other variables, such as the acoustic characteristics of the same call may still play a role in context discrimination.

Contrary to my expectations, call rates in response to predator species and the control were not statistically different. A possible explanation would be that since young Cervids with spotted coats are hidiers (that is, they are sequestered during the first weeks after birth: Caro, 2005), their presence would be perhaps unexpected by the monkeys, which could generate an initial confusion. It is also possible that monkeys, at least at the beginning, confused the deer with a spotted cat, as the baby deer model may resemble a spotted cat with its light spots. Misclassification of non predators as potential threats is expected in a dense forest where callers may not be able to see a stimulus well enough to correctly identify it (Evans 1997). This possible confusion may explain the similar call rate produced in response to the control and to other terrestrial predators (oncilla, puma and tayra) during the first minute after detection. However, soon thereafter monkeys were able to differentiate between the different species (maybe by cueing in on other anatomical features), as evidenced by different behavioural and vocal responses after the first minute.

Responses to snakes were not very strong and groups never approached or, mobbed the stimuli. This pattern was also found in the buffy-headed marmoset (*Callithrix flaviceps*), which approaches snakes with extreme caution and uses continuous low-volume intragroup communication calls, whereas they aggressively mob carnivores, such as tayras, with loud “tsak-tsak” calls (Ferrari and Lopes 1990). It is important to remember that most snakes, especially boids, do not depend on either visual or auditory cues to locate their prey (Pough et al 2004), therefore, visual displays and calls from potential prey would most likely not have a dissuasive effect on snakes.

5.5.3 A mixed system?

The two alarm calls produced by black-fronted titi monkeys showed varying degrees of specificity: the production of call A was highly specific, being elicited exclusively by a raptor in the canopy, while call B was given both in response to terrestrial predators and a non-predator model. These results are in line with earlier work of primates that indicate the aerial and terrestrial predators elicit distinct alarm calls (e.g. Seyfarth et al, 1980, Zuberbühler, 2000, Fichtel et al 2005, Kirchhof and Hammerschmidt, 2006, Digweed et al 2005, Ouattara et al., 2009 a, Schel et al 2009, Wheeler 2010). Likewise, the regular production of terrestrial predator-associated calls in non-predatory contexts appears to be common, especially with New World Monkeys (Fichtel and Kappeler 2002; Fichtel et al 2005, Digweed et al 2005, Kirchhof and Hammerschmidt, 2006). There are also some examples in Old World Monkeys (Arnold and Zuberbühler 2006a, Ouattara et al 2009). Although the monkeys' first response to disturbances on the ground was always the production of a B call, the later parts of call sequences often contained different call types, suggesting that they might discriminate between different types of terrestrial threats. Moreover, differences in the acoustic structure of B calls produced for various predators and non-predator animal may as well convey information on different contexts and/or threat levels. These results, together with the propensity to use the same call type in different contexts, indicate no fundamental difference to the vocal patterns reported in Old World monkeys and apes. Primate alarm call behaviour is likely to be phylogenetically old, with an early origin within the primate lineage. Additional research is needed to determine if variation within call types affect the call receiver's perception of threat or risk urgency.

CHAPTER 6: Signalling of predator type and location

Abstract

Animal alarm calls can encode information about a predator's type, general class, size, distance and degree of threat. In primates, alarm calls typically encode something about the predator type ("leopard") or general class ("terrestrial predator"). In some non-primate species, such as chickadees or meerkats, individuals can encode not only information about the predator type but also the distance or size of the predator, a pattern not yet described for non-human primates. In this chapter, I present the results of a field experiment designed to explore the information content of titi monkeys alarm call system. I found that titi monkeys produced uniquely composed alarm call sequences, consisting of two main call types that conveyed both information about the location and type of predator within the same utterance. In responses to a felid predator, the locational information was conveyed by the first call of each sequence. In responses to predatory raptors, the locational response was conveyed by later parts of the sequence. To my knowledge, this study is the first systematic demonstration of a sequence-based predator signalling system in a nonhuman primate capable of conveying both the location and type of predatory threat.

6.1 Introduction

Some species of mammals and birds produce alarm calls that convey information either about predator types or the level of response urgency. For example, various primate species produce acoustically distinct alarm calls in response to different predator types which evoke accurate and adaptive responses in recipients (e.g. vervet monkeys, *Chlorocebus aethiops*: Seyfarth et al., 1980a, 1980b, Diana monkeys, *Cercopithecus diana*: Zuberbühler et al., 1997, Campbell's monkeys, *Cercopithecus campbelli*: Zuberbühler, 2001). Such signals are then said to be 'functionally' referential because they are produced in context-specific ways and evoke appropriate responses from the listeners in the absence of eliciting stimuli (Macedonia and Evans, 1993). Some other species use the same basic call type to various predator species or situations, but vary the acoustic fine structure in context-specific ways (Campbell's monkeys, *Cercopithecus campbelli*: Ouattara et al., 2009). A third pattern observed in primates is to use more complex utterances. For instance, male putty-nosed monkeys (*Cercopithecus nictitans*) produce series of loud and conspicuous calls combined in predator- and context-specific ways (Arnold and Zuberbühler, 2006a, 2006b).

In Diana monkeys, alarm calls encode predator type while the level of threat and direction of attack appear to be less important. In field playback experiments, animals reacted with predator-specific alarm calls regardless of whether they heard the 'shrieks' of a predatory crowned eagle from the ground or from above within the canopy (Zuberbühler, 2000c). In some non-primate species, however, the location (distance) or level of threat is encoded. For instance, the alarm calls of California ground squirrels convey information about distance or threat experienced by the caller, rather than predator type. 'Whistles' are generally given to raptors and 'chatter-chats' to terrestrial predators, but it is not uncommon for callers to produce whistles to a sudden attack by a ground predator or chatter-chats to a distant eagle (Leger et al., 1980). Another

interesting example comes from research on domestic chickens, *Gallus gallus domesticus*. These animals produce two acoustically distinct alarm calls for disturbances from the air or the ground, respectively, while playbacks of these call types were sufficient to evoke appropriate responses in listeners (Gyger et al., 1987, Evans et al., 1993). Systematic manipulations of the location of attacks by typical ground or aerial predators, such as a raccoon or a hawk from the ground and the air, revealed that chickens responded to the spatial characteristics of the threat rather than the predator category (Evans et al., 1993). Finally, Griesser (2008) demonstrated that Siberian jay (*Perisoreus infaustus*) calls convey information about predator behaviour to conspecifics, instead of predator type or level of urgency.

A couple of remarkable examples of an alarm call system that combines referential information and also information on the level of urgency come from studies with the black-capped chickadees (*Poecile atricapilla*) and the suricates (*Suricata suricatta*). Chickadees, for instance, produce a high-frequency low-amplitude “seet” call when detecting flying raptors, and a loud broad-band “chick-a-dee” when detecting perched raptors. Moreover, they vary the number of notes per call depending on of the perceived predation risk (e.g. predator size) (Templeton et al., 2005). Suricates, produce different alarm calls in response to aerial and terrestrial predators, and also vary the acoustic structure depending on the distance of the predator (Manser, 2001).

These examples show that a variety of psychological processes appear to underlie animal alarm calls, ranging from categorical assessment of predator types to judgements of distance and movement vectors. However, none of these studies have yet tested whether the acoustic structure of alarm calls, or call series, varies simultaneously with predator type and location.

In previous chapters, I found that black-fronted titi monkeys produced sequences consisting of two basic alarm call types to predators in context-specific ways. To raptors, titi monkeys produced high-pitched, low amplitude “chirp” calls (call A), while

terrestrial predators and other disturbances on the ground triggered high-pitched “cheep” call of variable amplitude (call B). A number of observations suggested, however, that the alarm calling behaviour in these monkeys goes beyond responses to the basic predator types. For example, call A was not only given to raptors but also produced as part of sequences to predatory capuchin monkeys within the canopy. To explore the communicative function of these monkeys’ alarm call system, I conducted a field experiment during which I systematically presented models of a terrestrial and aerial predator (oncilla, caracara) to different groups of black-fronted titi monkeys on the ground or within the canopy to investigate how individuals encoded information concerning the predators’ biological category and relative location in their call sequences.

6.2 Methods

6.2.1 Predator models and presentation

Experiments were conducted with an oncilla model (*Leopardus tigrinus*), to represent a predatory threat by a mammalian ground predator, and a caracara model (*Caracara plancus*) to represent an aerial predatory raptor. I selected caracara and oncilla for use in this study based on the list of predators to whom monkeys alarm called during natural and experimental conditions, my personal observations in the field, and on the availability of stuffed animals to use in an experimental setting. Although often encountered on the ground, oncillas are expert climbers while raptors are sometimes encountered the ground, for example when feeding on a carcass.

The models were positioned either on or close to the ground at an elevation of 20-180 cm or within the canopy at 6-10m height, in a relatively open location to increase chances of detection (Fig. 6.1). The order of presentations was randomized for each group and within-group trials were separated by at least 10 days (Table 6.1). The presentation protocol was the same used in chapter 5.

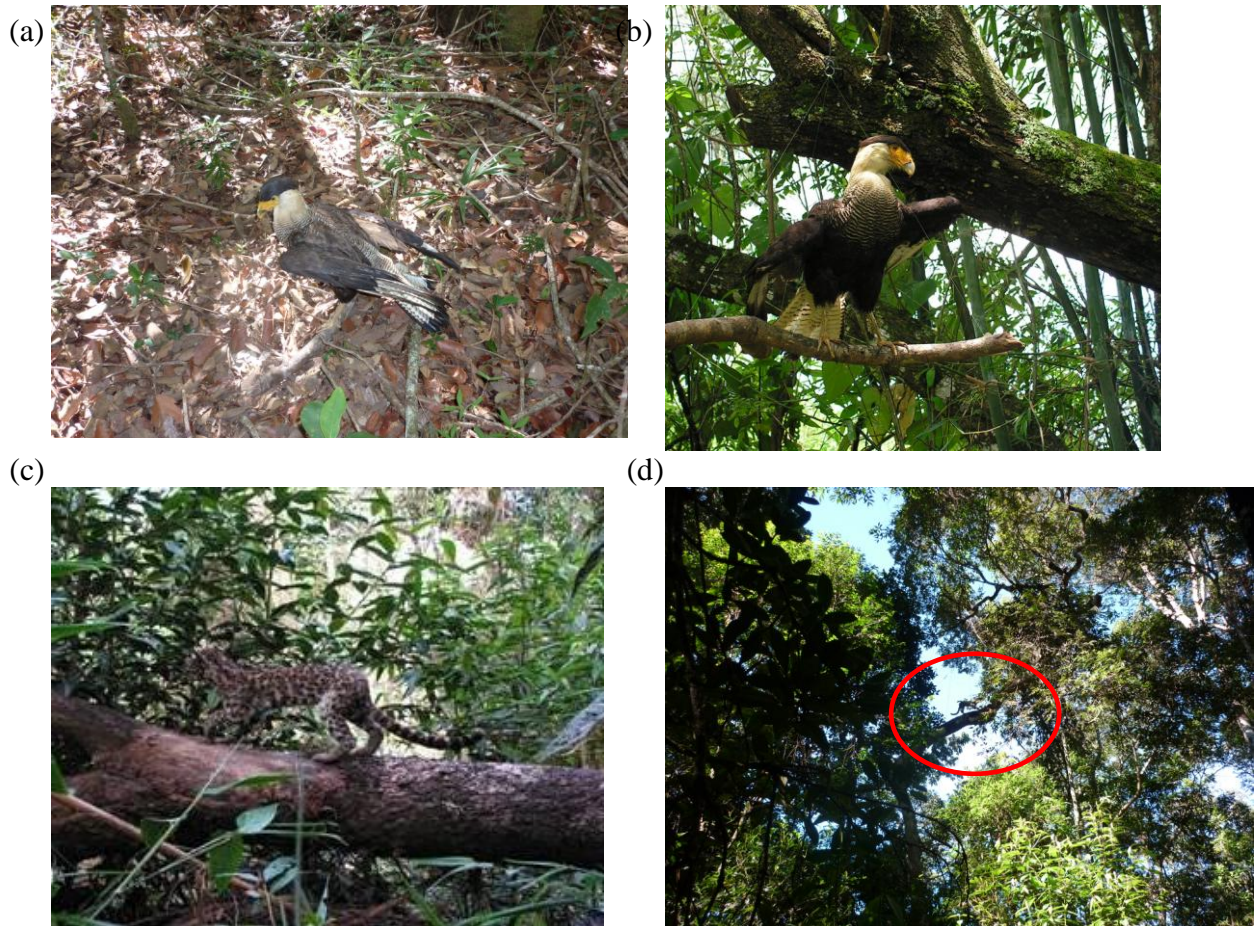


Figure 6.1. Photographs of predator models: (a) caracara (*Caracara plancus*) on the ground and d (b) on the canopy; (c) ocella (*Leopardus tigrinus*) on the ground and (d) in the canopy. Photos by Cristiane Căsar.

Table 6.1. Description of experimental trials conducted with 5 different black-fronted titi monkeys in Caraça Private Reserve, Minas Gerais, Brazil.

Model	Date	Experiment time	Group	N of Individuals*	First caller	Duration (min)	Valid
Caracara in the canopy	25/09/2008	12:25	GA	5 (+1)	AF	1.00	DS
	19/09/2008	15:00	GD	3	AM	6.65	DS
	14/09/2009	13:20	GM	4 (+1)	J or AM/I	18.48	DS
	11/11/2008	09:05	GP	4 (+1)	AF2	2.50	DS
	19/09/2008	08:50	GR	5	AF	3.40	DS
Caracara on the ground	09/06/2010	13:00	GA	6	AM2	1.28	DS
	24/06/2010	9:50	GD	3	AF	0.02	-
	17/06/2011†	10:55	GD	3	AF	1.50	DS
	31/05/2010	11:50	GM	5	AM	23.23	DS
	13/05/2010	9:21	GP	3	Ad?	10.50	DS
	19/05/2010	13:43	GR	2	AF	3.03	DS
Oncilla on the ground	14/08/2009	12:29	GA	5	AM	48.05	DS
	06/08/2009	13:11	GD	2	AM	26.37	DS
	22/09/2009	14:51	GM	4 (+1)	AF2	33.85	DS
	23/07/2009	13:21	GP	4 (+1)	AM?	68.90	D
	25/05/2010†	13:00	GP	3	AM?	35.45	S
	07/08/2009	13:29	GR	4	AF	59.35	DS
Oncilla in the canopy	29/05/2010	14:05	GA	6	AM2	24.13	DS
	28/05/2010	10:30	GD	3	AF	48.10	DS
	14/07/2010	9:08	GM	5	J	106.13	DS
	23/06/2010	12:40	GP	3	AM	24.00	DS
	17/06/2010	8:53	GR	2	AF	111.33	DS
	01/07/2010	11:40	GB/R	3/2	AM	42.12	S

AM = paired adult male, AM/I = adult male carrying infant, AM2 = unpaired Adult male, AF= paired adult female, AF2= unpaired adult female, J = juvenile, I = infant; * group sizes varied due to births, migration and disappearances; number in brackets represent the presence of dependent infant being carried mainly by the father (paired adult male). Valid trials for analyses (D: duration of vocal response; S: first sequence composition). † Repetitions.

6.3 Results

6.3.1 General responses

All groups reliably produced calls in response to both models. Predator type, but not location, affected the duration of vocal responses (Friedman Test: $\chi^2=12.120$, $df=3$, exact $p=0.001$; fig. 6.2a), a pattern also found for the number of calls produced per individual during the first minute (Friedman Test: $\chi^2=12.120$, $df=3$, exact $p=0.001$; fig.

6.2b). Post hoc Wilcoxon comparisons, however, did not reach significance after a Bonferroni correction.

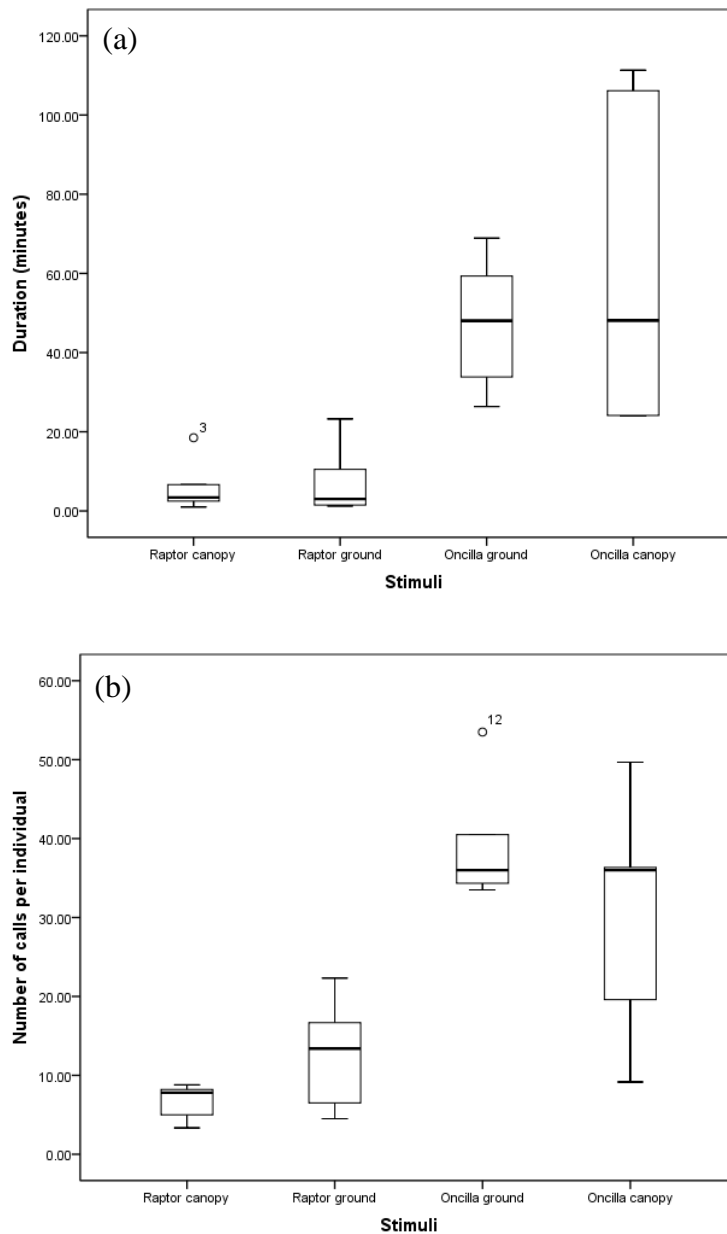


Figure 6.2. Box plots indicating the: a) duration of calling behaviour when encountering two species of predators in the canopy or on the ground; b) number of calls produced per individual based on the number of adults and juveniles in the group during the experiments. Box plots represent medians and upper and lower quartiles. Outliers are marked with circles.

6.3.2 Context-specificity of call production

The proportion of A and B calls given to each of the model types was dependent on the predator type and location, with more A-calls given to the raptor, regardless of its location. A-calls were also produced to the cat model, but only if encountered within the canopy (Figure 6.3).

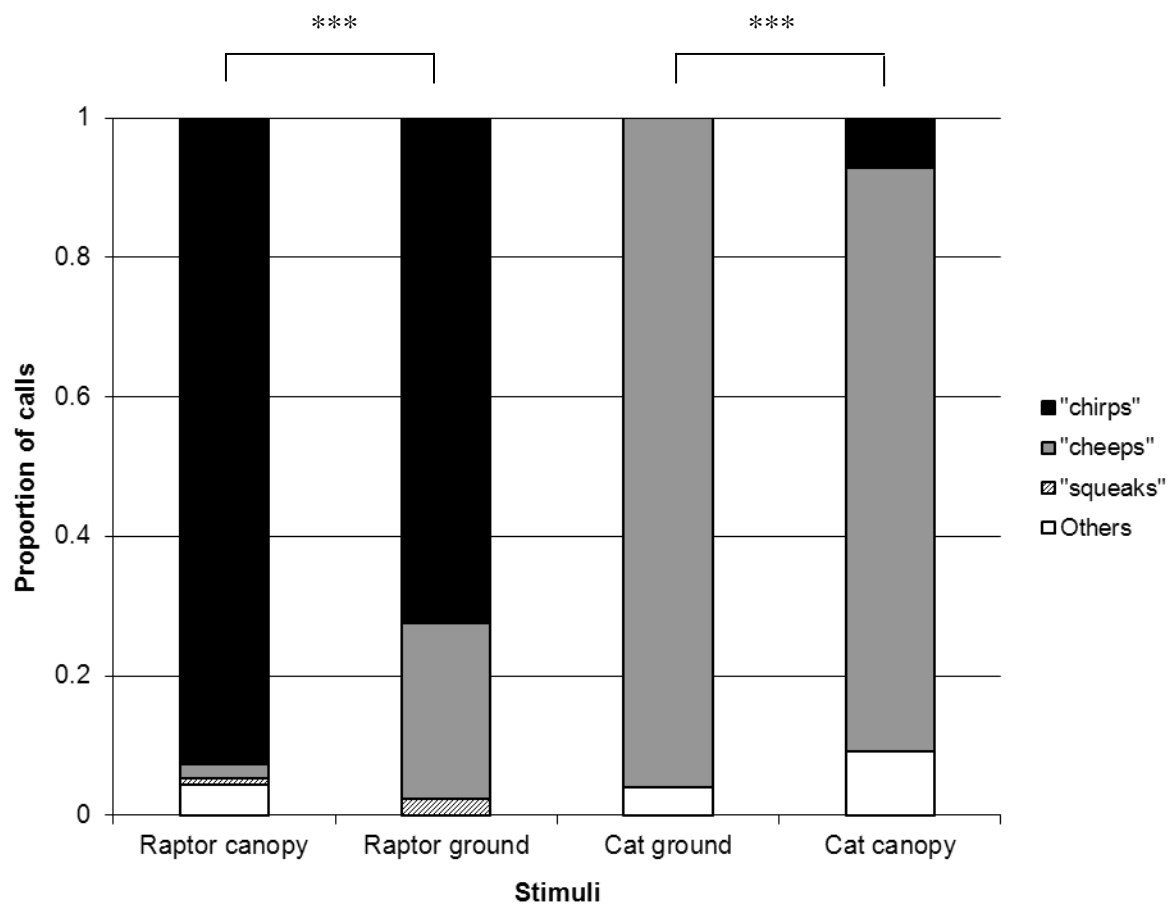


Figure 6.3. Proportion of each call type during the first minute (n=5). “Squeaks” were produced only in response to the raptor, other calls included B+ and grunts. I compared only the first minute as some of the monkeys’ responses lasted only one minute. Differences in frequency of occurrence of calls A and B between contexts: *** $p < 0.001$: (Fisher’s Exact Test, $\alpha = 0.05$, two-tailed).

Analyses of call sequences revealed that combinations of predator type and location generated unique patterns of calling behaviour (Fig. 6.4, table 6.2). Raptor encounters within the canopy systematically caused A-call series. Raptor encounters on the ground also caused A-call series, but these were always interspersed with B call series (range 1 to 13 calls), usually after an initial A-call sequence of at least four 4 calls (except one group, that produced one A followed by two Bs, Appendix A). Conversely, cat encounters on the ground systematically elicited B-call series, while cat encounters within the canopy consisted of combined sequences starting with only one call A followed by a B series.

Distance of detection was not significantly different for both predator types whether they were in the canopy (raptor= range 6- 15m, cat=10-20m) or on the ground (raptor=5-15m, cat=5-15m; Chi-square: $\chi^2=3.607$, df= 4, p= 0.462 each comparison).

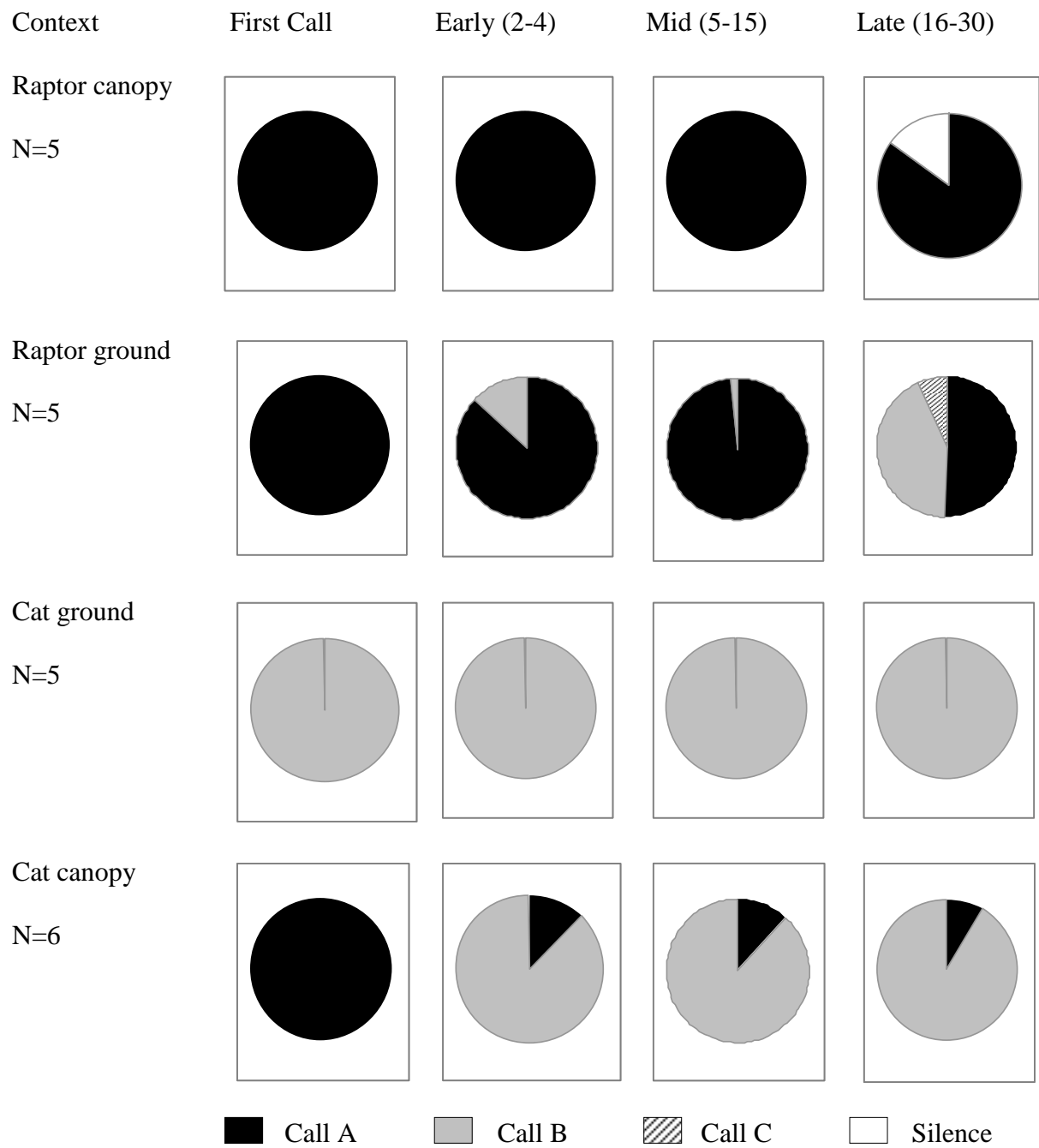


Figure 6.4. Sequential analyses of the first 30 calls produced in predatory contexts.

Table 6.2. Number of calls coded to describe the first 30 calls produced in response to predator models.

Stimuli	N	First call	Early (2-4)	Mid (5-15)	Late (16-30)
Raptor canopy	5	5/5	20/20	50/47	75/75
Raptor ground	5	5/5	20/20	50/50	75/75
Oncilla ground	5	5/5	20/20	50/50	75/75
Oncilla canopy	6*	6/5	25/25	60/60	90/90

N: number of groups tested per predator stimuli recorded and analysed. Values on First, Early, Mid and Late calls, represent firstly the total number of calls produced (which are the result of multiplying the number of events by the number of calls in each category), and secondly the total number of calls codeable and used to illustrate the differences on Figure 6.4. * Includes one response from a semi-habituated group, increasing the sample to 6 groups in this context.

6.3.3 Call interval

The interval between the first and second call was longer when the raptor was on the ground than in the canopy, for all five groups (Wilcoxon: $z=-2.023$, $n_1=n_2=5$, $p=0.043$; fig 6.5a). Likewise, the interval between the first and second call was significantly longer when the cat was in the canopy in comparison to when it was on the ground (Wilcoxon: $z=-2.023$, $n_1=n_2=5$, $p=0.043$, figure 6.5b).

In response to the raptor, there were no differences in the mean call interval within the first 30 calls, according to whether it was in the canopy or on the ground (Wilcoxon: $z=-0.724$, $n_1=n_2=29$, $p>0.46$). In response to the cat, there were likewise no differences according to whether it was in the canopy or on the ground ($z=-1.741$, $n_1=n_2=29$, $p=0.082$).

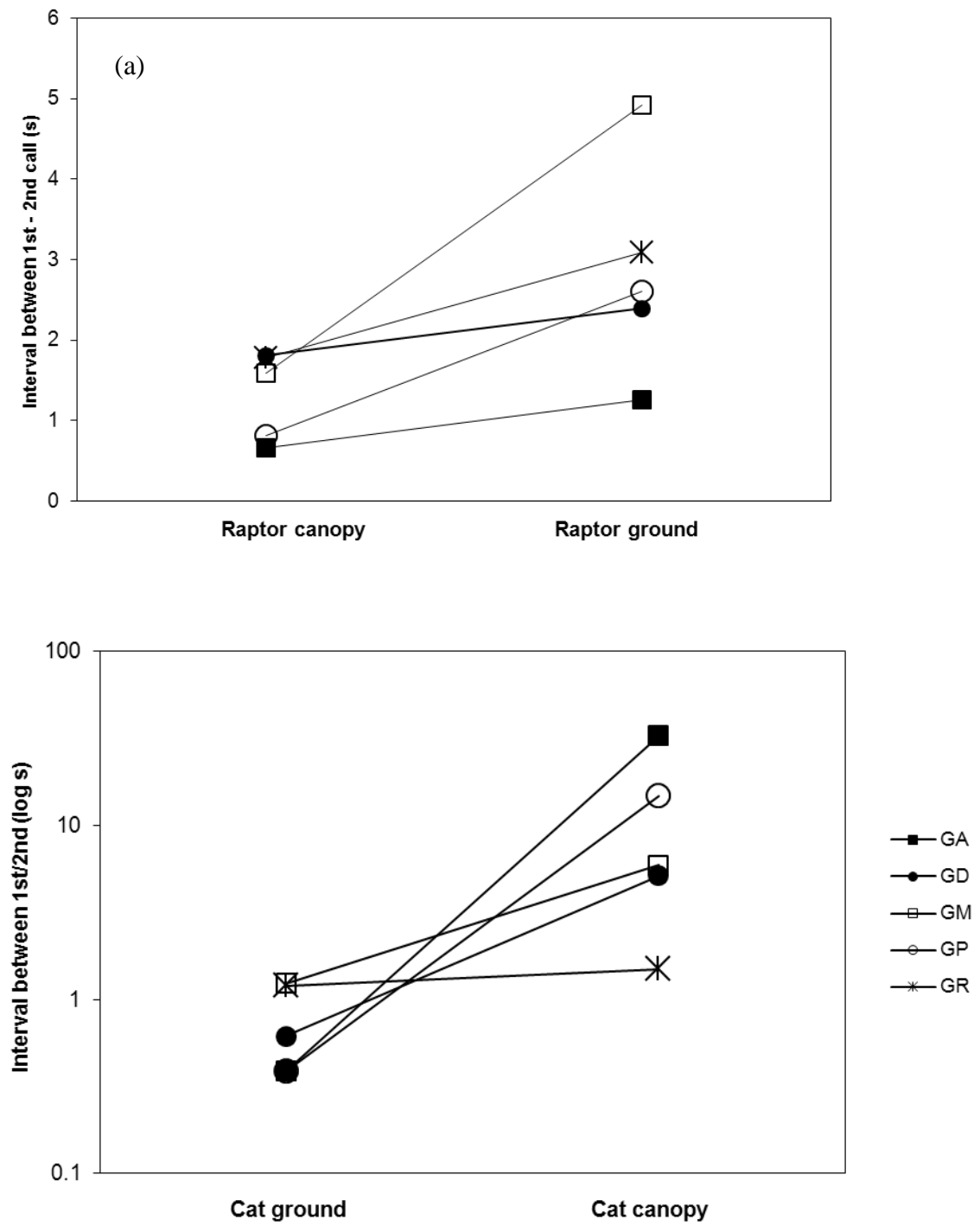


Figure 6.5. Call interval between the first and second call in response to the (a) raptor and (b) cat on different locations.

6.4 Discussion

Titi groups systematically produced series of A calls during raptor encounters, regardless of location. However, when the raptor was encountered on the ground, monkeys systematically interspersed a small number of A calls with a series of B calls. During cat encounters, on the other hand, monkeys systematically produced B-call series, but if the cat was encountered within the canopy this series was introduced by **one** A call. To my knowledge this study provides the first evidence for a non-human primate using call compositions to convey both predator location and biological category within the same utterance.

Alarm call systems conveying information about predator type or levels of threat have been described in numerous species [primates (e.g. (Seyfarth et al., 1980a, Macedonia, 1990, Zuberbühler et al., 1997, Zuberbühler, 2000), marmots (Blumstein and Armitage, 1997, Blumstein and Arnold, 1995) and squirrels (Owings and Virginia, 1978)]. In primates, many species appear to discriminate between aerial and terrestrial predators (Macedonia, 1990, Macedonia and Evans, 1993, Zuberbühler et al., 1999, Zuberbühler, 2001, Kirchhof and Hammerschmidt, 2006, Fichtel et al., 2005, Digweed et al., 2005), although some show additional specificity in terms of predator types (Seyfarth et al., 1980a, 1980b, Zuberbühler et al., 1997). In playback experiments, different alarm calls typically evoke specific predator-specific responses in receivers, demonstrating that receivers have learned something about the different links between acoustic structures and eliciting context (Seyfarth et al., 1980a, Seyfarth et al., 1980b, Zuberbühler et al., 1997, including in New World monkey species, Digweed et al., 2005, Fichtel et al., 2005, Kirchhof and Hammerschmidt, 2006, Wheeler, 2010).

Reports on encoding spatial location or direction of attack are less common, and seemingly restricted to alarm calling in birds. One of the best demonstrations is for chickens in which signallers produce alarm calls in relation to the spatial characteristics

of the threat while largely ignoring predator category (Evans et al., 1993). Results of this study show that spatial information is also encoded by titi monkey alarm calls in addition to predator class.

These results illustrate a yet unknown set of multiple strands of information in an animal alarm call system, by encoding both the type of predator and the spatial location, as opposed to predator type and level of urgency or predator type and behaviour. In meerkats, for instance, callers produce acoustically different alarms to different predator types, but call structure is also influenced by the level of urgency, i.e. by the distance of detection (Manser, 2001, Manser et al., 2002). Another well studied example is the graded alarm call system of chickadees with evidence for a functionally referential system that encodes both predator type (flying versus perched raptor) and level of threat, where size and maneuverability of a raptor is conveyed through some acoustic structure of the “chick-a-dee” alarm calls. (Templeton et al., 2005). Griesser (2008) has also found that Siberian jays have specific calls depending on the predator behavior (i.e. whether the hawk was perched, prey searching or attacking). I believe that the responses found in this study were not based on the predator behavior as I used the same models either on the canopy or on the ground. In one experiment with primates, the acoustic structure of individual Diana monkey alarm calls was not majorly affected by predator location (Zuberbühler, 2000). In some non-primate species, however, the location or level of threat is readily encoded. For instance, the alarm calls of California ground squirrels convey information about distance or threat experienced by the caller, rather than predator type. ‘Whistles’ are generally given to raptors and ‘chatter-chats’ to terrestrial predators, but it is not uncommon for callers to produce whistles to a sudden attack by a ground predator or chatter-chats to a distant eagle (Leger et al., 1980). Although it could be argued that the locational component of titis’ call-sequences reflects the situation-specific risk, I found no difference in the distance of detection within and between trials, indicating that monkeys were signalling the location of the predator and not the level of threat.

The titi monkey alarm call system is unusual in that it combines aspects of a more traditional referential warning system, as repeatedly described for primates, with information on predator location at the call sequence level. Contrary to my prediction, monkeys did not use the same syntactic rule for both predators, however. Instead, spatial information of raptor encounters was conveyed by adding (or omitting) series of B-calls within the raptor-typical A call series. Hearing a call series beginning with at least four A calls, in other words, provides reliable information that the caller has spotted a raptor, while a subsequent optional change to B-calls indicates that the event is taking place on the forest floor. The rule for more typical terrestrial predators, such as the oncilla, is slightly different. Here, the predator type is conveyed by the production of a B-series, while spatial information is conveyed by the optional addition of one A call prior to this series.

It is difficult to hypothesize about the underlying processes involved in this calling system. It seems that call A, primarily given in response to raptors regardless of their behaviour (perched, flying, calling), is also used when this predator is encountered on the ground. A possible explanation for that pattern is that, although raptors can attack at any height, they mostly attack from within the canopy or from the sky. Responses from playback studies have shown that primates' first responses to indications of raptors is to look up and scan the sky and descend to a protected place (e.g. Wheeler, 2010, Kirchhof and Hammerschmidt, 2006, Seyfarth et al., 1980a, Seyfarth et al., 1980b, Fichtel et al., 2005). Thus, if A functions to inform about raptor presence, then it is reasonable to assume that monkeys would use the same call if they want to, first, convey information of the location of a threat (canopy or sky) and then switch to other calls types, when appropriate.

The ability of these monkeys to switch between call types has also been observed in cases where they responded to two independent events. In pilot trials I presented a puma model on the ground (C. Cäsar, unpublished data), which triggered, as expected, a series

of B calls, in addition to other loud calls. During the experiment, the group was surprised by an eagle swooping rapidly over them, which caused an immediate switch to an A-call.

It is also relevant to point out that B-call series can be produced not only to felid predators, but also to tayra and other non-predatory disturbances, such as deer and other unidentified events on the ground. Interestingly, monkeys also produce B calls when descending within the canopy, when foraging close to the ground, when their intended travel path is blocked by an observer, during inter-group encounters and, for unhabituated groups, in response to humans. Although these contexts differ strongly in content and risk, one unifying feature is that they are all given to disturbances close to the ground. Thus, in contrast to A-calls, hearing a series of B-calls does not seem to carry much referential specificity, suggesting that listeners will have to take additional information into account before deciding on how to respond (see also: Arnold and Zuberbühler, submitted). However, this assumption must be treated cautiously, as differences in the acoustic structure of call B may still play an important role in different contexts.

I also found evidence suggesting that the call interval may convey additional information on the location of a predator. The call interval between the first and second call was significantly longer when the raptor was on the ground than when on the canopy. Likewise, the interval between the first and the second call in response to the cat in the canopy was significantly longer than on the ground. Whether or not these differences are also significant between predator types could not be tested here and will require further work and/ or a larger sample size to account for multiple comparisons. Despite this, my key finding was that callers systematically used the same pattern within predator types, suggesting that different locations were also meaningful to them.

In sum, the vocal repertoire of black-fronted titi monkeys is remarkably versatile and organised in complex context-specific sequences, something that has already been noted

by the pioneering work by Moynihan (1966), who suggested that *Callicebus* vocalisations might represent “the maximum elaboration and complexity which can be attained by a species-specific language.” My findings corroborate this statement by providing evidence of a basic syntactic communication system in a New World Monkey capable of conveying information about the location and type of a predator. The fact that information on both type and location of a predator can be communicated by changing the order, and number, of calls, raises some fascinating questions about the evolution of communication in this species and primates more generally and how these monkeys categorise different aspects of their environment.

CHAPTER 7: The information that receivers extract from alarm calls in black-fronted titi monkeys

Abstract

In chapters four to six I found that black-fronted titi monkeys, *Callicebus nigrifrons*, produce acoustically inconspicuous vocalizations in response to different predator species. Call A was produced during encounters with raptors (whether flying, perched or calling) and capuchins and stuffed oncilla in the canopy. Call B was produced during encounters with predators on the ground, but also in response to a non-predator terrestrial animal, a deer, and during other non-predatory contexts. In this chapter I investigate whether conspecifics are able to extract meaning from these high-pitched quiet calls produced in predatory contexts. Playbacks of call series recorded in response to a perched raptor (caracara) and two terrestrial predator mammals (oncilla and tayra) were conducted. Listeners' gaze directions and locomotor behaviours were recorded and compared before, during and after exposure to stimuli. Gaze direction was highly predator specific. Listeners looked significantly longer upwards when hearing raptor-related calls than terrestrial predator-related calls, while they looked significantly longer towards the caller when hearing terrestrial predator-related calls. The first gaze was particularly strongly related to the emission context. After hearing raptor-related stimuli 11 of 11 listeners looked upwards, while after hearing terrestrial-related stimuli eight of 12 looked towards the speaker, two downwards and two in another direction, but never upwards. Only few individuals moved after hearing these playback stimuli, but if they moved then it was in the expected direction. Overall, results showed that black-fronted titi monkeys can discriminate between calls given to raptors and terrestrial predators on the basis of acoustic features of these calls alone, even if they are produced by non-family conspecific individuals.

7.1 Introduction

According to the current literature, animal signallers do not intend to inform others about a distinct object or event in the environment (e.g. Arnold et al., 2011), although there are many examples where the vocal signal alone is sufficient to evoke the appropriate response from listeners in the absence of the eliciting stimulus (Macedonia and Evans, 1993, Evans and Marler, 1995, Seyfarth et al., 1980ab; Zuberbühler et al, 1997; Zuberbühler, 2001; Manser, 2001, Templeton et al., 2005). These signals, usually referred to as ‘functionally’ referential, are typically produced in a context-specific way, where the ‘referents’ (e.g. eagles, leopards, snakes or terrestrial versus aerial predators) may be related to corresponding mental concepts, the ‘references’ (Odgen & Richards, 1923, Seyfarth and Cheney, 1980, Macedonia and Evans, 1993). The classic example comes from studies of vervet monkeys (*Chlorocebus aethiops*), which produce several acoustically distinct alarm calls, each of which is tightly associated with detection of a distinct predator type, e.g. pythons, eagles or leopards (Struhsaker, 1967). Locomotor responses elicited by playbacks of the different alarm call types are mostly appropriate to the hunting technique of the predator that originally triggered the calls, as if the listeners had spotted the predator themselves. Upon hearing an eagle alarm call, for instance, vervet monkeys respond by descending into dense vegetation, whereas they climb into nearby trees in response to leopard alarm calls (Seyfarth et al., 1980a,b).

Evidence of functionally referential communication in animals has come from several other species, including various birds (e.g. Templeton et al., 2005), Gunnison's prairie dog (Slobodchikoff et al., 1991), and suricates (Manser, 2001, Manser et al., 2002), but specially prosimians and Old World primates: ring-tailed lemurs (Macedonia 1990), Diana monkeys (Zuberbühler 2000), Campbell's monkeys (Zuberbühler, 2001) and Guereza colobus monkeys (Schel et al., 2010). Such observations are interesting from an evolutionary perspective because of the parallels with symbolic reference in human language (e.g. Seyfarth et al., 1980). Furthermore, Snowdon (1997) suggested that New

World Monkeys (NWM) offer greater promise for the understanding of speech and vocal language than any of the great apes or baboons, arguing that, because all of them are severely constrained in their use of visual communication, they are expected to have evolved complex vocal communication systems. However, only few New World Monkeys have been described to produce at least two call variants to external disturbances with differences in their acoustic structure accompanied by functionally distinct behavioural responses. Kirchhof and Hammerschmidt (2006), for instance, have shown that two sympatric species of tamarins (*Saguinus fuscicollis* and *Saguinus mystax*) responded with adequate anti-predator reaction after hearing playbacks of calls originally given to aerial and terrestrial disturbances. However, differences between the two species suggested there might be more factors, other than taxonomic, involved. For instance, while aerial and terrestrial alarm calls of *S. mystax* were both functionally referential, *S. fuscicollis* had a combined system of one functionally referential aerial alarm call and one non-specific terrestrial alarm. In a more recent study, Wheeler (2010) provided evidence that tufted capuchin monkeys (*Cebus apella*) also showed appropriate responses after hearing “barks” (aerial predator calls) and “hiccup” (generalized disturbance call), which were produced in the appropriate contexts.

In the previous chapter, I have shown that black-fronted titi monkeys (*C. nigrifrons*) produce two different alarm calls to predators in relatively complex ways (chapter 4-6). A high-frequency, low amplitude A-call (chirp) was given specifically during predatory encounters with raptors (whether flying, perched or calling), and in sequences to capuchins and a stuffed oncilla in the canopy. On the other hand, in response to different terrestrial predators, and a non-predator terrestrial animal, monkeys initially produced another high-frequency call, the variable amplitude B-call (cheep). Although call A was strongly associated with predators (mainly raptors), call B was also produced in non-predatory contexts, such as when descending or feeding in the lower canopy and during some intergroup encounters, although most contexts tend to be related to threats

monkeys may face when close to the ground. Whether or not these quiet alarm calls are enough to inform listeners of the presence of a predator is still unknown.

To test if the acoustic information of these alarm calls is sufficient to elicit predator-specific reactions (i.e. if call perception matches call production) in black-fronted titi monkeys I conducted playback experiments with the same undisturbed individuals who had given alarm calls to predator models. If the calls denote predator type and/or location (e.g. raptor in the canopy versus cat on the ground), I predict that monkeys will respond as if they have themselves seen the predator, which elicited the call during the first experiment. Thus, after hearing call A I expect monkeys to scan the sky and either hide under a tree branch or descend rapidly within the canopy. On the other hand, in response to cheeps I expect monkeys will scan the lower canopy and approach the speaker to mob the potential predator, as observed during natural encounters and predator model presentations (chapter 4). Likewise, because it is still unknown if variants of call B are context dependent, and the visibility in a tropical forest is low, I expect monkeys will mainly look towards the speaker as to acquire both information from the caller and from the immediate vicinity as far as possible, and not look upwards.

7.2 Methods

7.2.1 Subjects

Eleven individuals of four groups of black-fronted titi monkeys (*Callicebus nigrifrons*) were tested between July 2009 and July 2010. Individuals could be identified by a combination of visual features, such as body size and fur characteristics as well as other body parts. All individuals were fully habituated to the observer's presence, so that they could usually approach the animals up to approximately 3m.

7.2.2 Playback stimuli and experimental procedure

All calls used as playback stimuli were recorded from the same groups that have already participated in the previous experiments with model predators (chapter 5). Playback stimuli of conspecific alarm calls were extracted (with the program Adobe Audition) from complete vocal responses to presentations of a raptor (caracara) perched in the canopy and two mostly terrestrial predators (tayra and oncilla) positioned close to the ground. Because call rate varies in response to the three predators (chapter 5, fig. 5.5) I kept the total length of the playback stimulus the same (30 sec) but varied the absolute number of calls. For one stimulus (call A-series GD), the call rate was smaller than the minimum number of calls produced in the experimental condition; although it remained within the natural range, as determined by a response to live perched raptor encounters (minimum of 4calls/30s, table 7.1). I used only calls of satisfactory acoustic quality that were recorded from members of the study groups. When possible, I used the original recording. However, in most cases I had to remove some calls due to heavy background noise or interference with other calls of the same type produced by other individuals. To reduce pseudo-replication each playback stimulus consisted of unique exemplars of calls produced by the same group in the same event.

Table 7.1. Mean call rate produced by different groups in response to natural and model predators, during the first 30 seconds of alarm calling, which were later used as playback stimuli.

Stimuli	Mean	Range
Chirp - series		
Perched live raptor (n=4)	7.75	4-16
Perched model raptor (n=5)	19.2	8-29
<i>Playback stimuli</i> (n=5)	13.0	7-24
Cheep - series		
Spotted live cat (n=1)	51.0	51
Oncilla (n=5)	54.4	39-83
Tayra (n=5)	45.6	15-79
<i>Playback stimuli</i> (n=3)	69.0	55-83

These call rates represent the total number of calls produced by each group during the first 30 seconds (mainly by one, but sometimes two or more individuals) in response to both natural and stuffed predators.

I initially intended to generate 10 different playback stimuli; one from each call recorded from each of the five groups. However, due to low quality recordings I was not able to edit some of their responses, which then resulted in a final sample of eight different playback stimuli (five A- and three B-calls series). Thus, some call series were used in more than one playback experiment, but not more than four times. Each individual was tested only once for a given stimulus type (A-series and B-series). To avoid habituation, individuals were not retested for at least 10 days, with one exception (Roberto who was retested after three days). I attempted to test only one individual per trial, and a member of the same group would be only tested on the same day if it was out of range (more than 40m away) during the first playback with a family member. Using this criterion, in only two cases were different members of the same family group

tested on the same day. On two other occasions, a family member was near the focal individual and was, therefore, recorded at the same time. In these cases, I scored the first glance of both individuals, but the whole response of the focal individual only.

All playbacks were broadcast in areas regularly visited by both the call provider and recipient, i.e. an overlapping zone. This was to keep the experience realistic by removing possible side effects of simulating the presence of a conspecific intruder in the subject's core area. Playback stimuli were broadcast with an Apple iPod Nano, connected to a Kenwood KAC-5203 Power amplifier and a PRO-BASS SF 250 speaker. During broadcasting of the predator stimuli the speaker, attached to an extendable pole, was positioned at an elevation of 3 metres above the ground, circa 12-20m from the vocal animal, beyond its visual range. The volume of the iPod was adjusted so that all playback stimuli were broadcast within their natural amplitude range, and sounded natural to a human observer at a distance of about 20m. I videotaped all playback trials using a camcorder CANON MD205 (36x/2000x Advanced zoom/Digital zoom; 2.7" Wide LCD & Wide EVF; Quick Start; Mini DV; 16:9 High Resolution).

7.2.3 Behavioural Measures

All videos were viewed and coded with ADOBE PREMIERE PRO CS4 software with a time resolution of 25 frames per second (duration of a single frame = 0.04s). The following measures were taken from the videos: a) the latency to the first reaction of the focal animal (mostly a turn of the head) by counting the frames, beginning from the first call during the call series; b) direction of the first glance and c) the looking duration, by counting the frames the focal spent looking in different directions during approximately 30s of playback. Directions of glance were exclusively classified as: a) 'Looking up', which was defined as looking beyond the immediate substrate, with the head oriented at least 45° above the horizontal line, when located in the lower canopy, b) 'looking towards the speaker', defined as looking beyond the immediate substrate, with the head oriented within 45° relative to the axis formed with the speaker, c) 'looking down',

defined as looking below immediate substrate, with the head oriented at least 45° below the horizontal line; d) 'looking elsewhere', defined as looking in any other direction, including scanning . Because of the density of the forest and the fact that the playbacks often elicited movement in the focal animals, causing them to get out of view, the duration of looking in a direction was coded only during the first 15 seconds of each trial. The relative looking duration was then calculated by dividing the time a subject spent looking in each direction by the total time looking to any direction. Thus, the time in which they were moving, hidden or not visible were not considered for the proportion of each looking direction. Locomotor responses were scored as 'movement' vs. 'no movement'. If movement occurred, I scored whether it was in the horizontal or vertical plane. To test if a subject's looking direction was in response to the stimulus, I compared monkeys' looking behaviour in the 15 s before and 15 s immediately after the end of a playback.

To estimate the accuracy of the coding, I carried out an inter-observer reliability test between me and a second coder (EM), who was naïve to my hypotheses. EM recoded the first gaze direction of all trials (N=24) and, unaware of the speaker's location was instructed to score the direction (left, right, front, behind) and angle (straight line, up, down) of the first head movement immediately after the first call.

7.2.4 Statistical analysis

For differences in the direction of the first gaze (upwards, downwards, towards speaker, other) I considered all trials (n= 24, including family and non-family member) by using a Chi-square and binomial test. For differences in latency and duration of looking I only considered individuals tested with stimuli produced by a non-family member. Because more individuals of Group A were tested in comparison to other groups, I conducted a first Generalized Linear Mixed Model to test if 'group' membership was a predictor of the monkeys' responses. Since the results were not significant I also ran additional models with 'individuals' as a random factor, which took into account the fact that

multiple observations from the same individuals contributed to the dataset. I used proportional data that were transformed to normality using ASIN transformation. For significance test I used the conditional t-test (Pinheiro and Bates, 2000). Analyses were performed on SPSS 18 for Windows and R 2.13.1 (The R Foundation for statistical Computing, Vienna, Austria). Alpha-levels were set at 0.05.

7.3 Results

A total of 24 playback experiments were conducted with 11 different individuals. Individuals were tested at least once in both conditions (raptor alarm call and terrestrial predator alarm call), with playback stimuli sourced from either a family member or a non-family member (i.e. a member of a neighbouring group) (Table 7.2).

Table 7.2. Individuals tested with the playback of alarm calls (A- vs B-series) produced by a family member or a neighbouring group.

Subject	Age-sex	Group	Affiliation ^a	Condition	Group provider
Apolo	Adult male	GA	AN (paired)	1 - 2	GD - GD (o)
Ana	Adult female	GA		1 - 2	GD - GD (t)
Aquiles	Adult male	GA		2 - 1	GP - GD
Aguirre	Adult male	GA		1 - 2	GD/ GA - GD(o)
André	Juvenile male	GA	AP/AN (parents)	1 - 2	GR - GD (o)
Desbotado	Adult male	GD		1 - 2	GR - GA (o)
Diego	Adult male	GD	DE (presumably father)	1 - 2	GD - GA(o)/GD
Roberto ^b	Adult male	GR	RS (paired)	1 - 2	GA -GD
Rosa	Adult female	GR		1 - 2	GA -GD (o)
Rafael ^c	Adult male	GR	RB (presumably father)	1 - 2	GD - GD
Marion ^d	Adult female	GM		2 - 1	GA - GP

Bold: completed trials of subjects tested with a non-family stimulus in both conditions, used for GLM analysis.

^a Affiliative relations based on the individual responsible for breast feeding and carrying (potential father) the new-born, and paired couples during this study. Two different paired couples were independently tested (GA: Apolo/Ana, GR: Roberto/Rosa).

^b During playback of A-series to Roberto the female (Rosa) was seated next to him, and although they both had the same reaction only Roberto was included in the analysis of duration.

^cRafael's responses to chirp-series were recorded during playback to another family member (RS). He was already looking towards the speaker before the stimulus started, and might have seen it in advance. In the second condition trial (B-series) Rafael was lower than the speaker and spent most the time looking upwards, although towards the speaker: thus, I could not use the same coding protocol, i.e. his head was upwards about 45°, but he was looking towards the speaker and not just upwards. Because of the possibility for misinterpretation, I decided to exclude the trial from analysis.

^dDuring the playback of A-series, Marion was on the upper canopy and the direction of looking could not be confirmed during most of the playback. Although I could see she was scanning the canopy, I excluded her responses also because I could not use the same coding protocol.

Because I had more recordings of A-series most individuals were first tested with this stimulus, followed by B-series after an interval of a few days. Despite this bias in presentation order, the latency and duration of looking upwards, downwards and towards the speaker, of the two individuals tested first with call B did not differ from

the others in any comparison (all comparisons $p > 0.05$). Thus, I assume that presentation order did not influence on listeners responses, but only the call type.

7.3.1 Latency

There was no significant difference in the latency to respond after hearing playbacks of A-series in comparison to B-series (Mann-Whitney $U = 29.5$, $n_1 = 9$, $n_2 = 11$, exact $p = 0.133$, figure 7.1). Likewise, matched-sample comparison was also not significant (Wilcoxon: $z = -.987$, $n_1 = n_2 = 8$, exact $p = 0.391$).

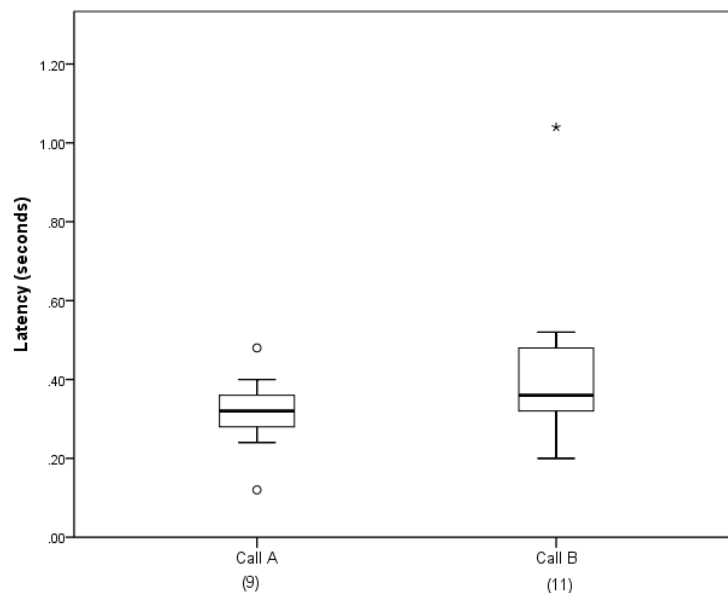


Figure 7.1. Box plots indicating the latencies in response to the different playback types. Thick lines represent medians, box edges represent the upper and lower quartiles; whiskers represent the adjacent values. Outliers are marked with circles and extreme case with asterisk.

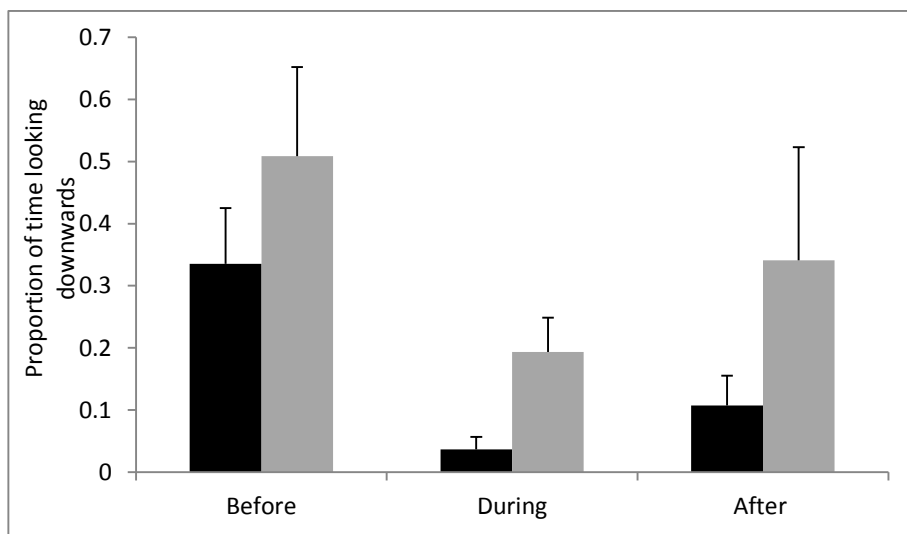
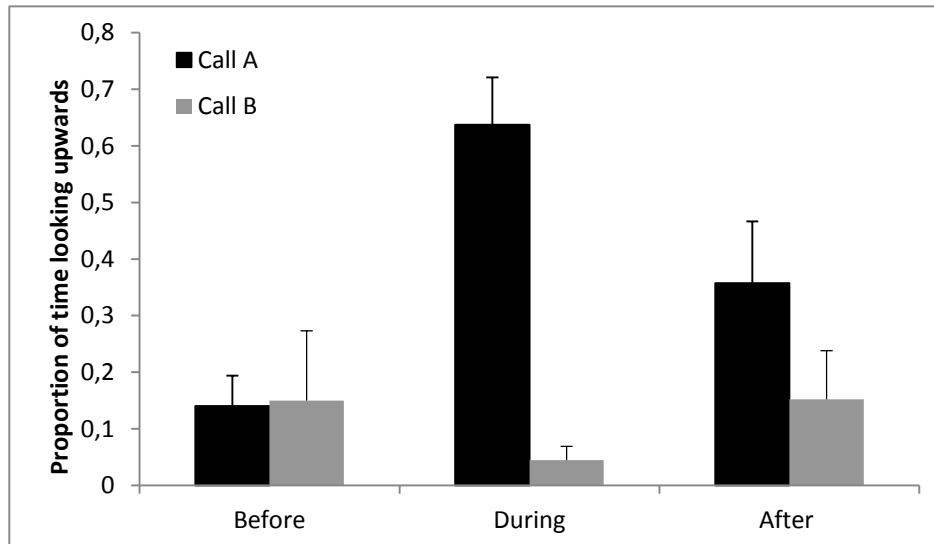
7.3.2 Looking durations

Listeners looked significantly longer upwards in response to recordings of call A than call B ($t=4.45$, $df=32$, $p<0.001$, figure 7.2a). Moreover, in response to call A they looked significantly longer upwards during the playback condition in comparison to before the stimulus (baseline, $t=3.84$, $df=32$, $p=0.0005$). Duration of looking upwards after the end of stimulus was not statistically different than before the stimulus ($t=1.58$, $df=32$, $p=0.125$). Furthermore, there was no difference in the time spent looking upwards after hearing call B across all conditions ($p>0.05$).

Although listeners looked slightly longer downwards after hearing call B than after call A the difference was not significant ($t=0.90$, $df=32$, $p=0.374$, figure 7.2b). Listeners looked significantly less downwards during playbacks of call B in comparison to before the stimulus ($t=2.56$, $df=32$, $p=0.016$). There were no differences in the duration of looking downwards across other conditions for call B, both before versus after ($t=0.98$, $df=32$, $p=0.333$) and during versus after trials ($t=1.25$, $df=32$, $p=0.220$). Although monkeys looked downwards for more time after compared to during the playback of this call, the difference was not significant ($t=1.801$, $df=32$, $p=0.081$).

Monkeys looked significantly longer towards the speaker direction while hearing call B than after hearing call A ($t=3.53$, $df=32$, $p=0.001$, figure 7.2c). They also looked significantly longer towards the speaker during ($t=4.611$, $df=32$, $p=0.0001$), but not after ($t=1.245$, $df=32$, $p=0.222$), playbacks of call B than before the stimulus started. Monkeys spent less time looking towards the speaker after the playback of call B in comparison to during the playback of this call ($t=2.786$, $df=32$, $p=0.0089$). For call A, there were no differences on the time spending looking towards the speaker in all conditions ($p>0.05$).

There were no differences in time spent looking in other directions in all comparisons (($p > 0.05$), figure 7.2d).



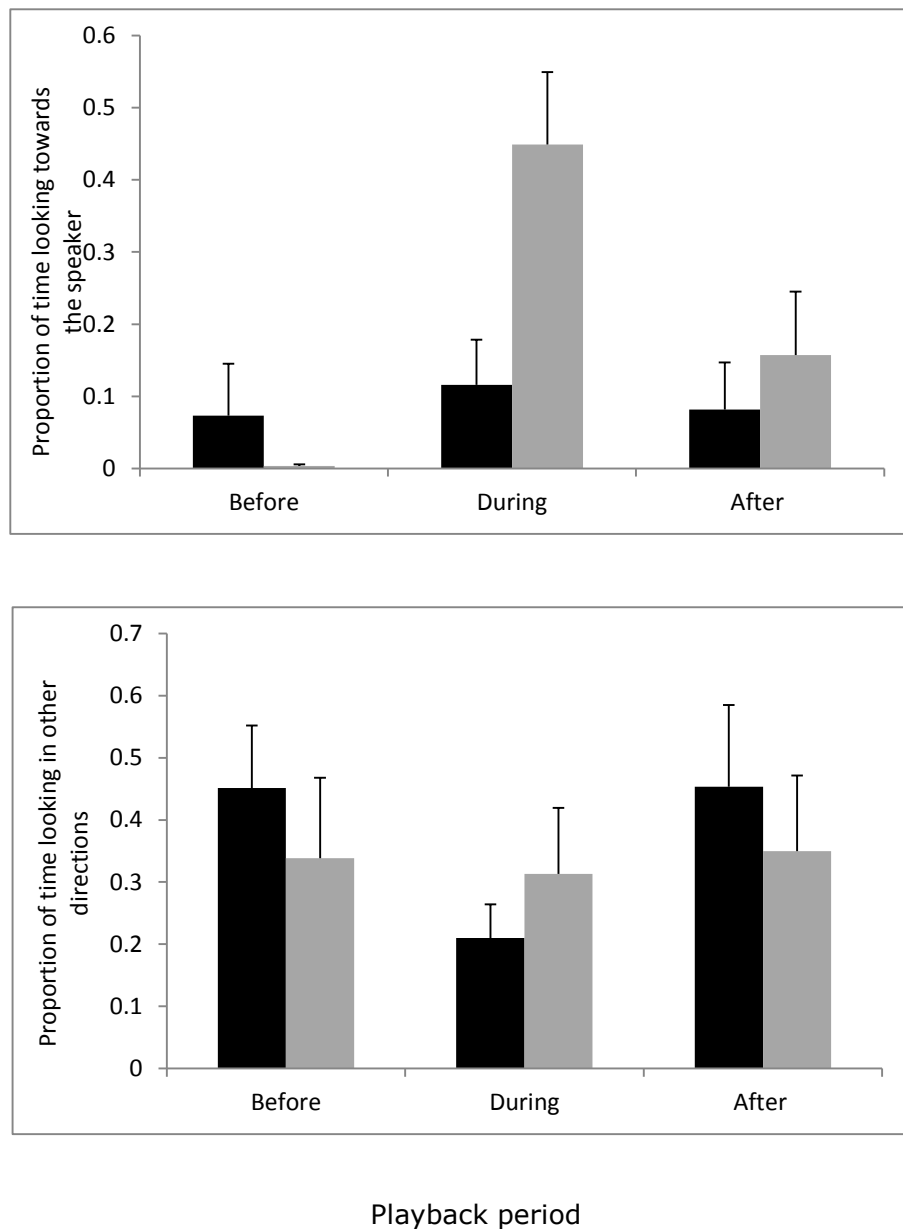


Figure 7.2. Mean \pm SE duration of looking durations: a) upwards, b) downwards, c) towards the speaker and d) other directions.

The inter-observer reliability between the CC and the second coder (EM) reached 100% of accuracy, confirming that direction of looking was completely reliable.

7.3.3 Direction of first gaze

Direction of first gaze was very obvious and not difficult to score. Typically, individuals immediately changed their looking direction after the first call was played back. In two cases, however, individuals apparently failed to hear the first call and only reacted after a few seconds, when they obviously changed the looking and locomotor behaviour. In these cases, I moved the beginning of their response to fit the moment when they clearly heard the stimulus. The volume of the stimuli was the same in all cases, and in these two cases I only heard the stimuli before them because I was closer to the speaker than the focal individual. Interfering noise were moving branches by wind and an unidentified terrestrial mammal walking nearby before the stimuli, which got the attention of the focal animal.

After hearing the first call in a sequence, the monkeys' direction of first gaze depended on the predators' type and most likely location (table 7.3). Listeners never looked immediately down after hearing playbacks indicating the presence of a raptor, and never looked immediately up after playbacks indicating the presence of a terrestrial predator (chi-square two-tailed: $\chi^2=20.444$, $DF=3$, $p>0.0001$).

Table 7.3. Direction of first glance presented as the frequency of the different looking directions immediately after hearing the first call of the stimulus. Responses to chirps included two individuals videoed at the same time of the focal.

Looking direction	Canopy (raptor)	Ground (cat or tayra)	Binomial test one-tailed p
Up	11 ^a	0	p= 0.0005
Down	0	2	p= 0.2500
Towards Speaker	1 ^b	8	p= 0.0195
Other	0	2 ^c	p= 0.2500

Significant one-tailed *P* values are shown in bold.

^a Includes one response of an adult female (Rosa) recorded at the same time of Roberto's trial. Both individuals remained in the same place the whole time, however I did not code all her responses as my focal was Roberto.

^b Response of an adult male (Rafael) recorded at the same time of Rosa's trial. Rafael was already looking towards the speaker before the start of the stimulus and might have seen it in advance, which interfered in his first response. Nonetheless, he looked up after the second and third call, but since the focal moved in opposite to hide I could not code all his responses.

^c Responses from two non-paired adult male, which are presumably offspring of the paired male.

7.3.4 Locomotor responses

Monkeys were equally likely to remain where they were than move after hearing call A ($N_{\text{Move}} = 2$; $N_{\text{Not move}} = 6$, two-tail *P* value= 0.2891, binomial test). Both individuals that did move went away from the caller and hid. Monkeys were also equally likely to remain where they were after hearing call B-series ($N_{\text{Move}} = 3$, $N_{\text{Not move}} = 5$, one-tail *P* value is 0.3633). When moving they were more likely to move further ($n = 2$, 67%) or to move up in trees ($n = 1$, 33%).

7.3.5 Family- versus non-family (neighbouring) member

Responses of one subject (Aguirre) after hearing playbacks of call A-series produced by a family member were significantly different upon hearing a call A-series produced by a neighbouring group (chi-square: $\chi^2 = 73.442$, $df = 3$, $p = 0.000$, table 7.4). Responses of one

subject (Diego) after hearing playbacks of call B-series produced by a family member were significantly different upon hearing a call B-series produced by a neighbouring group (chi-square: $\chi^2 = 112.823$, $df=4$, $p=0.000$, table 7.4).

Table 7.4. Frame counts of latency to respond and looking directions in response to Call A on B with two individuals tested with both a family and non-family member, l= looking.

	Latency	l up	l down	l speaker	l other	NV	Move(up)	Total
Aguirre								
Non-family	12	277	0	57	29	0	0	375
Family	4	348	0	0	15	8	0	375
Diego								
Non-family	13	18	15	236	41	52	0	375
Family	7	6	112	133	24	0	93	375

7.4 Discussion

Titi monkeys' responses to playbacks of two of their own calls given to different predator types were related to the type and most probable location of the predator, suggesting that the two call types designated different external objects or events to hearers. This was evident for A calls given to raptors, normally detected within the canopy, and B calls to medium cats or tayras, normally detected on the ground. In addition, A calls elicited anti-aerial predator behaviours, while B calls elicited behaviours typical for terrestrial predators.

Call A is spontaneously produced to raptors (flying, perched or calling), but also to other predators in the canopy (chapters 4-6). Playbacks of A calls elicited longer looking in the upwards direction, indicating monkeys were anticipating an important event, such as a raptor attack, from above. From the available data it seems safe to

conclude that call A (chirps) are functionally referential signals to danger within the canopy, specially raptors. Future work will have to determine if there are acoustic difference in chirps produced to raptors and other predators in the canopy (mainly capuchins), and raptors on the ground.

Call B is spontaneously produced to terrestrial predators, but also to other disturbances on the ground, while descending or foraging near the ground and during some intergroup encounters (chapter 4). Playback elicited longer looking towards the caller, indicating monkeys were anticipating an attack/event from near the caller. This reaction may be explained by a few options. It is possible that listeners were looking for cues from caller's behaviour and/or body orientation. Arnold and Zuberbühler (submitted) have shown that after hearing 'pyows' (a call produced in different contexts, but also to predators on the ground) putty-nosed monkeys spent more time looking towards the caller than when contextual information was also given, suggesting that the call alone is not enough to inform the monkeys of the correct context and that they were seeking for the caller's accompanying behaviours. In addition, it would make sense for a listener to look towards the speaker's direction, because it is most likely that the 'referent' will be in the caller's direction, as the caller is evidently able to see it. Looking towards the speaker would thus increase the chances of the listener seeing the threat. Given the range of circumstances that elicit call B, and the yet unknown function of the acoustic variation according to context, a cautious scenario would be to define this call as a "generalized terrestrial disturbance call", rather than a functionally referential call, as it does not seem to refer to one or even a similar group of 'referents'. Nonetheless, although call B only seems to indicate a threat near the ground (as listeners mostly looked towards the speaker (caller) and towards the lower substrate), the results strongly suggest that this call almost certainly does not refer to raptors.

Previous chapters showed that black-fronted titi monkeys usually give very different vocal and locomotor responses to raptors and terrestrial predators. After hearing the first

caller spotting a raptor, monkeys mostly scan the canopy or sky, freeze or show rapid flight usually descending or moving towards a protected place, while in response to mostly terrestrial predators they scan the forest ground or lower canopy, look for and approach the first caller and usually gather to harass the predator cooperatively (chapters 4 and 5).

While this study examined only situational variation in call type, acoustic variation and call rate may also be associated with context of production, especially for terrestrial threats (e.g. Manser 2001) and receivers may be able to cue in on these differences (e.g. Manser et al., 2001). Contrary to my expectation, monkeys did not approach the speaker while hearing call B, and that may be explained by few possible scenarios. It is possible that listeners did not have enough information/time to approach the caller, as their behaviour was only considered during 15 seconds of stimulus. Monkeys' vocal responses to terrestrial predators can last up to an hour and the time to other members approach and join in calling also depends on the distance they are from the caller - a second caller would join in the first one from as quickly as a second to about a minute (C.Cäsar, unpublished data). If approaching the caller also depends on caller's behaviour, and since they could not see the caller, listeners would be constrained by the lack of this further cue. Alternatively, if monkeys can recognise other individual calls, and since stimuli were call-series produced by a non-family member, listeners may not have been stimulated to approach and help mobbing the potential predator. Call B seems to be a variant of a mostly two-syllable call "chirrup" of *C. cupreus* described by Moynihan (1966) and Robinson (1979) and these authors found individual differences in "chirrup". Thus, if call B also carries individual identity, it may be possible that monkeys recognise these variations and did not approach because the stimulus came from a non-family member. One observation to support this theory comes from a second trial with Diego, who was played back to a B-series produced by Desbotado, presumably his father. Diego, who looked faster towards the speaker, than after hearing a series by a non-family member, also moved up and closer while hearing

his family member calling, apparently also to have a better view of the caller's surrounding area, and may have only not approached and called because he probably saw Desbotado moving towards the speaker. These explanations are not exclusive and it may be possible that two or even all of them play a role on listeners' response after hearing a terrestrial predator related alarm call. Moreover, it also explains why listeners did not produce their own alarm calls after hearing a terrestrial predator alarm call series. Monkeys did not respond with alarm calls to the raptor stimulus either. In this case, however, the avoidance was expected, as usually only the first individual to see a raptor calls, and others would only call if they are out of range of the first caller and see the predator afterwards (chapters 4 and 5).

It is also interesting to note that, although both call type series were produced by a neighbouring group member, listeners did not present any conspicuous display behaviour usually observed during intergroup encounters, such as pilo-erection, tail lashing and body arch (Moynihan, 1966, CC personal observation). Because their gaze direction differed between conditions, I assumed that individuals were reacting to the predator information conveyed by the stimuli, instead of a simply reaction to the presence of a conspecific intruder.

7.5 Proposed future study

A first aspect that merits attention in a more systematic study is to verify the behavioural differences after hearing alarm calls provided by a family versus a non-family member. A pilot study has illustrated the possibility that family members elicit a quicker and stronger response than non-family members, which suggests monkeys are able to discriminate between different providers.

With respect to experimental design for field studies, a few improvements would appear useful. First, to control for the influence of other variables, such as call rate, one should keep this variable fixed in both conditions. Because, call rate of A-series is usually lower than B-series, another experiment which manipulates call rate would be interesting to test if these differences are also meaningful to the monkeys.

CHAPTER 8. General Discussion and Future Directions

8.1 Aims of the study

Although titi monkeys have been renowned for their complex vocal abilities, there have been very few systematic efforts in studying them. With the exception of loud calls during intergroup interactions, they are a mostly cryptic species which may explain the relative lack of research efforts. One consequence has been that little is known about whether any part of their vocal repertoire functions as predator alarm calls, and if so, how. In addition, early studies may have underestimated the role of predation, and consequently not much attention has been given to this type of vocal behaviour.

A first aim of my thesis was to present a detailed description of the form and function of anti-predator behaviour of black-fronted titi monkeys, with a special focus on their alarm call behaviour. A second aim was to determine the exact mechanisms of alarm calling behaviour, with an emphasis on their production and comprehension. I have addressed these questions by describing the monkeys' natural responses to potential predators and then by experimentally eliciting and playing back their alarm calls.

I have presented a detailed description of the vocal and locomotor behaviour of one population of black-fronted titi monkey in response to natural predators and artificial predator models, as well as their responses to alarm calls produced by conspecifics. To this end, I used both established and new protocols to increase our understanding of the vocal and physical anti-predator behaviour and associated cognitive capacities of this species in particular, and, by extension, those of the primate lineage in general. Here I summarise the key empirical results, before drawing some general conclusions concerning titi anti-predator behaviour and its wider relevance for the evolutionary and comparative study of primate communication and, more specifically, human language.

8.2 Summary of the key empirical findings

8.2.1 Do titi monkeys have a predator alarm call system?

Titi monkeys are cryptic and agile New World primates, and although they are well known for their complex vocal behaviour, almost nothing was known about their anti-predator strategies. Chapter 4 aimed to describe the monkeys' responses to natural disturbances including predators. I was able to describe a large number of predation attempts and corresponding anti-predator responses by the monkeys. A first unexpected finding was that cryptic behaviour was observed only in a few cases. Instead, the monkeys' most common response to raptors was to produce one very short and high-pitched call (call A or 'chirp') and then hide. Predation attempts by raptors occurred at least once a day, suggesting that these predators are likely to represent the greatest threat to this population of titi monkeys. Moreover, predatory raptors varied drastically in size, ranging from small accipiter species to the big black-chested buzzard eagle, which suggested that monkeys might both be chased inside the canopy (Căsar, personal observation) and also experience sudden surprise attacks, requiring different anti-predator strategies (e.g. Templeton et al 2005). It is possible that titi monkeys still use cryptic behaviour to avoid an initial encounter, but this appears to be a problem in need of systematic testing.

Although relatively rare, anti-predator responses to terrestrial predators were very different from the ones to raptors. In response to a predatory cat or a tayra, the monkeys' first reaction was to produce a distinctive high-pitched call (call B or 'cheep'), which was acoustically different from the call produced to raptors. Following these initial predator-specific responses, monkeys produced a range of other vocal and behavioural patterns, generally characterised by a gradual increase in the production of loud and low-pitched calls, with occasional instances of predator mobbing until the predators left the area. Intriguingly, the monkeys also produced alarm calls to another primate, the capuchin monkey. Here, both call types were given as combinations,

suggesting that titi monkey alarm calling behaviour might convey information on both the type and location of a predator.

I tested hypotheses from these natural observations systematically, using both established and new experimental protocols, and showed that titis did indeed possess an unusually sophisticated alarm call system that conveyed information on both predator category and location.

8.2.2 Do titi monkeys respond to visual predator models with predator-specific behaviour?

Black-fronted titi monkeys' responses to experimentally presented predator models were consistent with natural observations. Call A was only given in response to the raptor model presented in the canopy whereas call B was given in response to all terrestrial predators, but also to a control stimulus (deer). These findings matched well with many previous studies of primate alarm calling behaviour, by demonstrating that aerial and terrestrial predators elicit acoustically distinct alarm call types (e.g. Seyfarth et al., 1980, Macedonia and Evans, 1993, Zuberbühler, 2000, Fichtel and Kappeler 2002, Digweed et al., 2005; Wheeler, 2010). In this way, non-human primates, appear to be different from sciurid rodent and avian taxa that have been investigated in similar ways (Caro, 2005, Blumstein, 2007).

Conceptually, some of the predators used as models in this study (tayra, puma, oncilla and snakes) may be classified as exerting the same type of threat - that is, danger from the ground - even if they might vary in how dangerous they are for a monkey. It was interesting that in this context the monkeys produced the same alarm call in response to terrestrial predators and to the non-predatory deer, which supported this conceptual interpretation. My results showed that monkeys were producing the same call type to any major disturbance on the ground, suggesting that they perceived this as categorical information.

In some ways, this generates somewhat of a conundrum. Why is it adaptive for monkeys to respond to predatory and non-predatory disturbances with the same type of vocal behaviour? One possibility is that there were consistent differences in the acoustic characteristic of the B calls, given in response to different terrestrial threats. Alternatively, the monkeys may be using additional pragmatic cues, such as the callers' behaviour, as an indicator of the call eliciting context. A number of behavioural observations in response to real predator species and non-predator models suggested that monkeys discriminated between different types of terrestrial threats, indicating that at least one of these two mechanisms played a role. First, it was common that titi monkeys mobbed and produced loud low-pitched calls only in response to the oncilla, puma and tayra models, but not to the deer or to snake models, indicating that they clearly discriminated between the different types of terrestrial disturbances. Although the monkeys' first response to all disturbances on the ground was the production of at least one call B, later parts of their vocal responses varied in predator-specific ways, which further demonstrated that they discriminated between different types of threats or risks.

There was also evidence for the use of B calls in other non-predatory contexts, particularly by individuals descending to feed or when foraging close to the ground. This finding further illustrates the fact that the B call appears to convey information about a terrestrial source of danger, i.e. locational information, but that listeners would require more information from the ongoing context before being able to decide on an adaptive behavioural response, such as joining in to chase or mob a predator or knowing about the whereabouts of a group member. This would be important as they are usually not visible to each other when foraging close to the ground. Playback experiments will be needed to address these hypotheses more thoroughly.

8.2.3 Are there predator-specific alarm calls within the terrestrial category?

Acoustic analyses revealed consistent differences in the acoustic structure of B calls produced in response to oncilla, puma, tayra and snakes (chapter 5, table 5.6 and figures 5.9, 5.10). However, it is not clear whether listeners can discriminate between the subtle acoustic differences. The acoustic differences in call B given in different terrestrial contexts may be a way of reliably convey information about different situations. Evidence of context specificity in a graded system was provided by Cleveland and Snowden (1982). They found eight different ‘chirps’ produced by cotton-top tamarins (*Saguinus oedipus oedipus*) that were closely associated with different behaviours and contexts. In a subsequent study Bauers and Snowden (1990) played back two of the most similar in acoustic structure and most different in context (alerting to a strange group of animals versus maintaining vocal contact within an unaroused group). They found not only that receivers discriminated between the two chirp types, but also gave contextually appropriate response to each one of them. On the other hand, the presence of acoustically different calls or calls variants does not always mean that receivers can recognize them (Townsend et al 2010).

From a functional perspective, it would not seem very useful for titi monkeys to discriminate between oncillas and, for instance, tayras, since both require similar anti-predator responses. On the other hand, it would seem useful to know from the calls if the caller has spotted an oncilla in the canopy or an oncilla on the ground. In order to discriminate if the documented acoustic differences are communicatively functional, i.e. whether these calls convey information about the predator type and degree of risk, a systematic playback study will be needed.

8.2.4 Are titi monkeys’ alarm calls meaningful to conspecific recipients?

Results from chapter 7 showed that listeners attribute different meaning to A and B calls, the two main alarm calls. In response to playbacks of A-call series, monkeys

scanned the sky or canopy and descended to the lower canopy or hid in a protected place. A-calls can thus be considered functionally referential signals (that indicate specific danger within the canopy, especially raptors).

In response to B calls, listeners' main responses were to look towards the speaker, and sometimes to move up or approach the speaker. Again, this was an appropriate and adaptive response to the type of predator which normally elicited the calls. However, since B calls are given in several different contexts, they are perhaps better interpreted as generalized terrestrial disturbance calls with no predator-specific referential function. Thus, black-fronted titi monkeys' alarm calls refer to at least two different types of external events, the presence of a raptor within the canopy and an unspecific disturbance on the ground. In the case of call A, there is evidence that the signal functions in a contextually narrower way, by only referring to predators located within the canopy. In the case of call B, results need to be interpreted more cautiously, as it is still unclear whether or not the documented context-specific acoustic differences are perceived and meaningful to listeners. In terms of the monkeys' responses to B calls produced to predatory *oncillas* and *tayras*, the listeners' main response was to look towards the speaker. As mentioned before, these responses appear to be adaptive as examining the behaviour of the caller will provide additional cues about the eliciting context (Fischer and Hammerschmidt, 2001). Also, given the impaired visibility of a tropical forest, the chances of a terrestrial disturbance being near the caller are very high, and therefore, looking towards the caller is the most likely place to find the eliciting reason of the call.

8.2.5 Sequences

Results presented in chapters 4-6 indicate that the different communicative functions and meanings are not necessarily only conveyed by single calls but also by sequences of one or different call types (see also Robinson, 1979a, for loud call-sequences; appendix A). I described seven different call combinations that were context specific. The majority of these sequences were produced by single individuals, indicating the

composition was based on the context and not on different individual contributions. The general pattern was that titi monkeys produced different call sequences when detecting different species of predators while receivers responded to raptor alarm series and two terrestrial predator series in context-specific way. The diversity of call combinations illustrated a rather large flexibility which in turn increases the number of messages that can potentially be conveyed. Repetitions may function to intensify the meaning of an individual call or to represent new meanings from that of individual calls (Cleveland and Snowdon, 1982, and see below). More specific studies will be required to explore the role of call sequences but so far results suggest that different call sequences were meaningful to them, in ways that fulfilled the criteria of functionally referential signals (i.e. context specificity of call production and perception specificity in call response; Macedonia and Evans, 1993).

Table 8.1. Overview of the main empirical results

<i>Event</i>	<i>Localisation</i>	<i>Call A</i>	<i>Call B</i>
<i>Natural disturbance</i>			
Flying raptors	Sky/canopy	YES	NO
Perched Raptors	Canopy	YES	NO*
Capuchins in tree	Canopy	YES	NO*
Other flying birds	Sky/canopy	NO	NO
Spotted cat	Ground	NO	YES
Adult deer	Ground	NO	YES
Humans (blocking route)†	Lower canopy	NO	YES
Humans (unhabituated monkeys) †	Ground	NO	YES
Unidentified threats †	Ground	NO	YES
Unidentified threats †	Canopy	YES	NO
<i>Experimental disturbance</i>			
Caracara (raptor on the canopy)	Canopy	YES	NO
Snakes	Ground	NO	YES
Oncilla	Ground	NO	YES
Puma	Ground	NO	YES
Tayra	Ground	NO	YES
Deer	Ground	NO	YES
<i>Specific monkey behaviours†</i>			
Descending	-	NO	YES
Foraging close to ground	Lower canopy	NO	YES
Intergroup encounters	-	NO	Sometimes
<i>Additional Experiments</i>			
Raptor on ground	Ground	YES	YES
Oncilla in tree	Canopy	YES	YES

* Monkeys descending - YES; † Not analysed

8.3 General discussion of the results

8.3.1. Predation pressure and vocal flexibility

Black-fronted titi monkeys face a wide array of predator species in Caraça, and during my study period at least seven individuals were presumed killed by predators (table 2.2, chapter 2). Predation is known to influence the evolution of several traits, such as body size, group size, and vocal behaviour (Anderson, 1986).

Larger primate species may be relatively less vulnerable to predation by raptors (Ferrari, 2009) but titi monkeys are small to medium sized, with consequent high vulnerability to predation. They are a cryptic and agile species that forages mostly in dense vegetation, although they are commonly seen on the tree-tops sunbathing, especially during cold mornings (Cäsar, personal observations). This behaviour is probably risky as it exposes them to several species of raptors. However, some of their traits, in particularly pelage coloration, cognitive abilities and rapid behavioural responses, appear to help compensate for their small body size and aid their survival.

When detecting raptors, titi monkeys responded very quickly with alarm calls and hiding, suggesting that the cognitive abilities required to identity the predator type and take the appropriate responses are operating rapidly to enhance their chances of survival. Accurate and immediate responses to raptors are an effective way to avoid predation by these predators (Ferrari, 2009).

Also, as raptors rely on visual cues to locate their prey (Jones et al. 2007) evolution is likely to select for cryptic coloration in primate species occupying the upper canopy. According to that, *Callicebus nigrifrons* have a mostly cryptic coloration, with most of its body being brownish agouti, with a black forehead and crown, and an orange tail

(van Roosmallen et al., 2002). *C. nigrifrons* prefer the middle to upper canopy and very often are seen foraging in emerging trees (Cäsar, personal observation).

Callicebus monkeys are characterised by relatively small group sizes. Whether this is a result of predation pressure is difficult to decide but is perhaps less likely. Instead, in all species bi-parental care and monogamy are obligatory, which by default will lead to small group size (Wright, 1986, Fernandez-Duque, 2007). Small group size is likely to complement other cryptic features seen in these species, including coloration and behaviour.

An important and relevant aspect of titi monkeys seems to be the ability to deal with a large range of predator species, as seen in Caraça. Perhaps as a consequence it was possible to document a complex alarm system with some evidence of referentiality, due to a specific alarm call type to raptors (and other predators within the canopy). Call sequences appear to convey information on the predator's behaviour, because flying raptors consistently triggered fewer calls than perched raptors. When followed by series of B calls, the sequences were usually indicative of the canopy location of non-raptor predators. Moreover, preliminary evidence suggested that acoustic differences in B calls given in response to several disturbances on the ground might be context-specific.

A more general question therefore is whether high degrees of vocal flexibility in the predatory context are representative of titi monkeys in general or whether this is an effect of high predation pressure. It is possible that the variety described in this study represents one of the biggest elaborations of predator signalling in titi monkeys. If that is the case, it is still possible that titis living in areas with less predator species do also have the ability to recognise, and signal about, different predator or risk situations. Evidence from a study with Guereza colobus monkeys suggests that this may indeed happen. By comparing two populations with different predator pressure, Schel et al (2009) found that where leopards have been locally extinct for decades the monkeys still reliably produced appropriate anti-predator responses to a leopard stimulus. On the

other hand, differences in exposure and experience may influence the existence of different vocal repertoires. Captive female Campbell's monkeys, for instance, did not produce two variants of 'RRA' calls (RRA3 and RRA4) which reliably indicate the presence of a crowned eagle and leopards and snakes in the wild. On the other hand, another variant RRA2 was only produced by captive animals, in response to a familiar caretaker (Lemasson et al 2004 in Ouatarra et al, 2009).

A related question is whether the increase in number of predators within the same category (i.e. aerial vs. terrestrial) increases the importance of call combinations, perhaps to provide more information about specific types of predators within a class (Seyfarth, personal communication). Hauser (1997) described an event that supports this theory. While working in the study population established by Cheney and Seyfarth, Hauser witnessed some vervet monkeys alarm calling in response to a lion, a predator that they have never observed preying. The interesting point was that, although the calls seemed typical of leopard alarm calls, they had a slower delivery rate (see also Lemasson et al 2010). He hypothesized that vervets appeared to have added lions into the general category of large predatory cat, but used a distinct delivery rate. Thus, it would appear that there was flexibility in the system, both in terms of altering call structure and in classifying exemplars into a category with certain definitional features. As Hauser (1997) further suggested, such changes may be observed over the course of an individual's lifetime or over the course of several generations.

Titi monkeys in general are known for their complex vocal behaviour but the lack of systematic studies on the function of most vocalizations prevented definitive conclusions on much of their vocal behaviour. A proper way of studying the influence of the predation pressure on vocal flexibility would be to test different populations that differ in predator densities and predation risks.

8.3.2Vocal repertoire

A few aspects of the vocal repertoire of *Callicebus nigrifrons* during anti-predator responses particularly need discussion. (1) The number and complexity of calls seemed similar to the described to *C. cupreus*. (2) Most of the major call types that occurred during predator signalling also occurred in a wider range of different non-predatory contexts. (2) Like Moynihan (1966) and Robinson (1979a), I also found gradation within and between most of the call types.

In this study, I described 11 different call types produced during predatory contexts, which encompasses almost all call types I observed in the field. Only a few other calls were either not (screams, sneezes and food calls; Căsar, unpublished data), or only very rarely (whistles, trills) produced during encounters with predators. **Whistles** and **trills** were produced only once, during an encounter with capuchin monkeys, and they do not seem to be predator related. Whistles and some trills were often produced when an individual was isolated or when other groups were calling; whereas some trills were also produced before duet sequences. **Screams** were usually observed during inter and intra group disputes, while the motivation for **sneezes** were unclear. Another vocal pattern observed was what I termed **food calls**. These were very quiet, short and high-pitched calls which were given in rapid sequences, sometimes together with Bs and whistles.

Conversely, with the exception of call A, all calls registered during anti-predator responses were also produced in non-predatory contexts. Thus, to be able to convey information about different contexts, titi monkeys appear to be using a combination of these subtle acoustic differences within call types and different call combinations.

Despite the acoustic variation on call B according to context, I also found evidence of gradation within contexts. Variation in terms of frequency modulation and number of bands (see figures 3.1 and 3.10b-c), may be a result of a different motivational

continuum throughout time. For instance, in my perception, monkeys appear to produce narrow band variants at the beginning of their responses, while broader band variants are more frequent later on, suggesting that may be a difference in message (Smith, 1968). The same pattern appears to happen with call BS (see chapter 5).

Fischer et al (2001a) described different variants of female baboons' barks which were given in different situations. Tonal barks, for instance, were typically given to regain group contact, while harsher barks (or alarm barks) were given in response to mammalian carnivores and crocodiles. As in the titi monkey repertoire, they also found intermediates between different contexts. In a follow up playback study, Fisher et al (2001b), found that listeners responded only to the harsh alarm barks, but failed to distinguish between clear contact barks and intermediate alarm barks. One possibility raised by the authors was that adult listeners may perceive these variants but have a lack of motivation to react; and playbacks with infant baboons have shown that infants do indeed discriminate between alarm barks and clear contact barks (Fisher et al 2000). Another possibility raised was that the "baboons propensity to respond to alarm barks depends as much on the context in which the call is given as on the call's acoustic features" (Fischer et al., 2001b).

Studies with several nonhuman primates have shown that listeners' responses are influenced by different variables, including caller identity (Hammerschmidt and Fisher 1998), context (Macedonia and Evans 1993) and perceived risk (Zuberbühler et al 1999). Preliminary evidence suggested that caller (or group) identity may also play a role in call and context recognition in titi monkeys (table 7.4, chapter 7). Another possibility is that monkeys may use the olfactory sense to help with discrimination between contexts. A study with red-bellied tamarins (*Saguinus labiatus*) found that chemicals from predators elicited higher rates of sniffing and avoidance of the scent source than those of the non-predators or controls (Caine and Weldon, 1989). Additionally, subjects gave alarm calls only to margay scent, a response not observed

with the other predator extracts (jaguar or jaguarondi), suggesting a different assessment of risks. Since there are some indicators that titi monkeys have a rather well-developed sense of smell (Moynihan, 1966), this possibility should be also kept in mind in future experiments.

Other evidence of gradation can be seen in the loud calls. By looking at spectrograms of the loud calls (figures 3.6, 3.7, 3.8) it appears that one syllable of one call sometimes resembles one of the syllables of a different call. For instance, the first syllable of a “honk” is structurally similar (i.e. has the same shape) to the second syllable of a resonating and to the two syllables of pumps, and visually the main differences appear to be the duration and number of harmonics. These variations can be treated either as a unique category of calls (as the resonating calls described by Moynihan, 1966) or as different call types (as the honks, bellows and pants described by Robinson, 1979a). In this study, I used the terms resonating calls and honks. The important point is that despite differences on denomination, both authors found evidence for different call sequences with these calls in *Callicebus cupreus*. Moreover, Robinson (1979) also found significant differences in the acoustic structure of the last syllable (thereafter, “climax”) of each one of these calls, which prompted him to split them into different call types. These loud calls are often used during intergroup encounters ((Moynihan, 1966, Kinzey et al., 1977, Kinzey, 1981, Kinzey and Robinson, 1983, Robinson, 1979b, Robinson, 1979a, 1981, Robinson et al., 1987, Müller, 1995a,b, Müller and Anzenberger, 2002; this study), but also in some predatory encounters (this study). Evidence of context dependent sequences during different social contexts (Robinson, 1979a), suggests that sequence specificity may also apply for predatory contexts. Preliminary evidence suggests that this may be the case (appendix B).

The existence of a relatively complex call structure in most of the major components of titi monkeys’ repertoire has been long suggested to be a primitive trait (Moynihan, 1996). According to Moynihan, all the major acoustic signals of *Callicebus* have

homologues in the repertoire of species of many genera, including *Aotus*. However, he argued that the acoustic signals of titi monkeys were more elaborated than other species. The view of complex call structure as a primitive trait is also shared by Fischer et al (2001b). These authors suggested that the graded system of female baboons may constitute an ancestral form of call system that has not been subject to as much selection pressure as the vervet's alarm calls, for instance. They also suggest that species with graded vocal repertoires may provide a better model for the evolution of human speech than do species with a more discrete alarm call system. The fact that vervet monkeys, which live in relatively open habitats, have a rather discrete repertoire, and that baboons' long distance calls are acoustically graded, challenge the hypothesis that there is simple relationship between the morphology of a species' vocal repertoire and its physical and social environment. At the very least, species with graded vocal system, such as titi monkeys, "provide intriguing comparative data that may force us to rethink previous hypothesis about signal design and evolution" (Fischer et al 2001b).

Altogether, these results suggest that although most titi calls are used in several different contexts (see also Moynihan, 1966, Robinson, 1979a), and which does not point strongly to their use as vehicles of semantic context, different call sequences appear to provide sufficient information for receivers to select appropriate antipredator responses. Whether or not acoustic variations (found in call B) are communicatively important or represent differences in arousal is unclear and will require further investigation.

8.3.3 Arousal and vocal behaviour

Another point that deserves attention is whether arousal (or affect intensity) influences the behaviour of the monkeys during predator encounters. A problem with interpreting the results of predator experiments is that they may be influenced by more neophobic propensities (Miller and Treves 2011). It is therefore important to analyse carefully the monkeys' responses to non-predatory control stimuli.

In this study, I was able to reliably distinguish between alarm calling and other behavioural responses to predator and to non-predator models. Call types (A and B) and certain sequence compositions appeared to be a stable and reliable feature that indicated to recipients the predator type encountered by a signaller, and this did not appear to be well explained by underlying differences in arousal. This point was well demonstrated when monkeys detected raptors, or predators from above, compared to disturbances on the ground. Some observations also illustrated that monkeys did not simply call to any novel stimulus. For example, I recorded the responses of three groups (GA, GD and GP) to predator models covered by a black plastic bag. In these three cases, the monkeys detected the stimulus but produced no conspicuous behaviour, such as alarm calling, hiding, fleeing or approaching. In some sense, these unplanned mistakes acted as additional control conditions, confirming that monkeys did not simply respond to novelty or unfamiliar large objects on the ground. Instead, they observed the large black objects for a few seconds and then continued with their previous activities.

Other measures with some promise to detect differences in arousal were the duration of responses and response rates. Judging by these measures, the titi monkeys were most aroused in the presence of oncillas, especially when encountered in the canopy (chapter 5 and 6). Ideally, physiological measures of arousal, including hormonal variables, such as cortisol, should also be examined to allow for more meaningful conclusions about the role of arousal in predator responses (Cross and Rogers, 2006, Clara et al., 2008).

Another interesting finding was that some other call types that are related to the basic alarm calls, such as the BS call, were much louder than the basic B calls. The BS call type was never given in the early parts of a sequence but was more common in sections of monkeys' responses (chapters 4 and 5), i.e., after some or several B calls. BS calls consist of a B call with an additional suffix (or syllable), which is perhaps a result of increased amplitude during call production, similar to the inhalation element of chimpanzee pant-grunt sequences (Laporte, 2010). If this is the case, then arousal

variations may be helpful in interpreting titi monkey vocal responses to terrestrial predators. It has been argued that arousal (or affect) influences some acoustic variables of animal calls, most notably noisiness and the overall calling effort (as measured by duration and response rate) (e.g. Fichtel et al, 2001, Riede et al, 2001, Rendall, 2003, Clara et al, 2008). However, some other results also suggest arousal and context specificity interpretations of calling behaviour are not necessarily mutually exclusive. In my recordings, BS calls were mostly restricted to responses to oncilla, tayra and puma, in contrast to responses to deer and snakes. Whether or not such differences should be interpreted as differences in affect and general arousal will continue to remain an unresolved issue until more useful variables of affect and arousal are found and put in relation to vocal behaviour. Until then, vocal behaviour will be equally well “explained as mediated by differences in cognitive capacities concerning the adaptations to specific anti-predator techniques or recognition of visual patterns” (Schel et al, 2010).

In terms of locomotor responses, the observed behavioural patterns appear to be highly adapted to the different predators’ hunting techniques, whereas arousal-based explanations are unable to account for the patterns. Whether or not the notion of arousal is necessary and whether it should be seen as an alternative explanation to the notion of referential meaning is a matter of ongoing debate (Seyfarth and Cheney, 2003). A reasonable position seems to be that they interact with one another.

8.3.4 Caller identity and individual variation

I found no sexual differences in the behaviour of individuals during predator detection, suggesting that in this species both sexes play a similar role in detecting and communicating about the presence of predators (see Ouattara et al, 2009c, for a different pattern in Campbell’s monkeys). In general, both sexes produced A calls in response to raptors and B calls in response to disturbances on the ground. This is in line with earlier work on titi monkeys that highlighted that both sexes produced the same calls, although with significant acoustic differences between them (Moynihan, 1966,

Robinson, 1979a, Müller & Anzenberger 2002). However, I also found that some individuals deviated in their responses. For instance, the adult female Denise showed a different response pattern to presentations of the raptor on the ground, compared to the other individuals tested. Instead of producing a few A calls followed by some B calls, she only produced one call A in the first trial and one call A, followed by few Bs in the second trial. During the first trial, Denise was far away from the other group members when she detected the model, which may have influenced her response. In the second trial, again she only produced one A call; however, this time it was followed by few B calls, as if to indicate the location of the predator. Interestingly, on this occasion, the two other group members were near her.

Another deviation from the normal patterns was produced by the adult male Michael, who produced a long series of A calls in response to a raptor model on the ground, while the other group members were more than 20 meters away. These examples may simply be part of natural biological variation. On the other hand, they raise some intriguing questions about the possibility of audience effects in titi monkeys' responses, something that has been studied more systematically in other species (Cheney and Seyfarth, 1990a, Zuberbühler, 2007, Slocombe & Zuberbuhler, 2007, Papworth et al 2008, Townsend & Zuberbühler, 2009). Future research will have to address this possibility. Until then no further conclusion can be made at the moment.

8.3.5 Call structure

An intriguing aspect of titi monkey alarm calls (A calls and some variants of B calls) is their acoustic structure. Compared to other primates, these are very quiet and high-pitched calls, which is rather different from the loud and conspicuous alarm calls of most other species (e.g. Seyfarth et al 1980, Macedonia 1990, Ouattara et al 2009, Schel et al 2009, 2010, Arnold and Zuberbühler, 2006a, Zuberbühler et al 1997, but see Kirchhof and Hammerschmidt 2006, for examples of quiet alarm calls). All alarm calling responses begin with these quiet calls; later in their calling sequences, usually

after having examined the terrestrial predators, titi monkeys switch to different calls which are typically loud and conspicuous and seem to be directed to the predator. It has been argued that high-pitched quiet calls are used by callers that need to avoid detection by the predator (Marler, 1955): thereby, callers can convey predator-specific meanings by alerting others without putting themselves at risk (Campbell and Snowden 2007). Based on these observations, it seems plausible to conclude that the titi monkeys' first alarm calls primarily function to inform conspecifics about the presence and type of a predator. Subsequent calls may then function to rally other group members if more aggressive responses to the predator are needed. Similarly, Digweed et al (2005) has proposed that the "aerial predator alarm" call of capuchin monkeys is less localizable than the "alerting call", which is shorter and less tonal. This is especially true if comparisons are between different alarm calls within a species' repertoire. However, if comparisons are made of the alarm call structure between species, then titi monkey chirps and initial cheeps to raptors and terrestrial predators are even less localizable than capuchin's alarm calls (see chapter 4 for call spectrograms and measures, and Digweed et al., 2005 for comparison). It is also remarkable how similar are the titi monkeys' quiet alarm calls in their general acoustic structures, which essentially only vary in shape. Nevertheless, they function to convey strong differences in meaning. This naturally raises the possibility that other primate species' quiet calls may also function in similar ways. Moreover, the fact that *Callicebus* possess a complex vocal repertoire, perhaps even more complex than those of many other primates living in similar environments with similar social organization (Moynihan, 1966), raises interesting questions about the relation between vocal complexity and underlying cognition.

Most *Callicebus* vocalizations are part of a graded continuum with many intermediate stages (Moynihan, 1966), which could potentially increase the ambiguity of their meaning. However, even though monkeys probably rely on external context, this will not be always possible, especially in a constrained environment such as a dense forest. Natural selection is thus expected to favour the evolution of vocal behaviour that

provides reliable information in urgent situation, such as the presence of a predator. Moreover, the unexpected presence of quiet, yet functionally referential alarm calls, in a primate species known for its acoustically variable and graded calling behaviour suggests a need for further investigation into the function of inconspicuous calls in other forest dwelling primates.

8.3.6 Conspecific warning and predator deterrence

As outlined earlier, the two main alarm calls (call A and B) were produced in very different situations, that is, in raptor and ground predator contexts. In addition, I found that listeners' responses to series of A calls (indicating a raptor in the canopy) and series of B calls (indicating a tayra or oncilla on the ground) were identical to the responses normally given to the predators that elicited these calls, suggesting that alarm calls served a warning function by providing nearby listeners with information about the type of predator or threat spotted by the caller. However, in most cases callers continued producing their vocalisations for long periods. Why would a monkey continue to alarm call even though all group members already know about the presence of the predator? It seems reasonable to assume that sustained calling is costly, because it could attract additional predators or permit the initial predator to monitor the prey at a distance (Miller and Treves 2011). One possibility is that sustained calling functions to communicate directly to the predator. One of the assumptions of predator-detering calls is that they should only be given to predators that depend on surprising their prey (e.g. Zuberbühler et al 1997). In this case, sustained alarm calling should be more efficient in response to oncillas, tayras and pumas than to raptors and snakes. In all experimental trials reported in this thesis, the monkeys engaged in continuous alarm calling, sometimes combined with predator mobbing, only in response to ambush predators. Durations ranged from 8 minutes to almost two hours (figures 5.1. and 6.2). Acoustically, titi monkeys' vocal behaviour to terrestrial predators was characterised by repetitions of loud low-pitched calls and mobbing. Natural observations demonstrated

that monkeys kept on calling only in cases when the predator was nearby and therefore still posed a danger. This was observed from monkeys responding to a spotted cat (chapter 4) and tayras (not sound recorded). Individuals persistently called and mobbed these predators as long as they were close to them. As expected, this highly conspicuous behaviour soon induced the predators to leave the area, an effect also demonstrated with monkey-hunting leopards (Zuberbühler et al 1999b). In natural cases, monkeys stopped calling and returned to their previous activities some minutes after the predator has departed. In response to the predator models, groups generally called and mobbed for longer periods than during natural encounters, probably because the disturbance remained stationary (until removed by the experimenter).

Conspicuous behaviour may be less effective with raptors, although larger monkeys are sometimes able to dissuade raptors with aggressive chasing behaviour (Zuberbühler et al, 1999b). During my study, I only saw conspicuous behaviour once towards a raptor. This was with group R, while chased by two large unidentified eagles (chapter 4). The beginning of their response was a standard reaction to perched raptors, i.e. a series of A calls. However, soon after the first encounter the eagles started to actively chase the monkeys, in response to which they started to produce AS calls and several loud calls (honks, resonating and pumps), similar to when responding to terrestrial predators. Nevertheless, the frequency and acoustic structure of calls produced to these eagles were different from the ones produced to terrestrial predators, such as the spotted cat or models of oncilla, tayra and puma (see Appendix B). Although these are only pilot data, it is very likely that titi monkeys also use loud calls to convey information about category or location of threat, in addition to the patterns with calls A and B at the beginning of monkeys' responses. This is something else that deserves attention in future studies.

8.3.7 Referential or urgency-related?

In the animal communication literature, referential signals are usually defined as ‘encoding information about specific external events’ (e.g. Seyfarth et al 1980). A signal qualifies as ‘referential’ if it is produced in a context-specific way, that is, the eliciting stimuli belong to some common category (e.g. ‘leopard’ or ‘ground predator’). A further criterion is that the signal alone should be sufficient to evoke the appropriate response from the listeners in the absence of the eliciting stimulus (Macedonia and Evans, 1993). Although titi monkeys produce at least two acoustically distinct alarm calls, only one (call A) was given exclusively to a specific predator type, raptors (chapters 4-6); and listeners behaved as if they had seen the predator themselves. Thus, this acoustically distinct alarm call fulfilled both criteria for functionally referential signals. Moreover, the monkeys assembled A and B calls into longer sequences that differed between predator contexts. Some of these sequences appeared meaningful to conspecific receivers, at least at the level of general predator class, or location of threat (chapter 7). In contrast, the fact that the same call and call sequences (series or phrases of B-calls) are used to a range of different disturbances on the ground suggests that some titi monkey alarm calls denote the immediacy of predation or the perceived threat of the situation (Arnold et al 2008). There were no significant differences between the distances of detection; neither there were any apparent differences in local visibility during experiments. The only determinant of groups’ response was predator category and location, and subtle differences between terrestrial contexts may also represent different levels of risk. Differences in acoustic features, call rate, and call composition may indicate different levels of threat experienced by the callers when a risk response is required to potential threats. Thus, my study showed that titi monkeys have a complex alarm call system, with evidence for both referential and risk-based communication, similar to what has been reported for some birds (Paridae: Templeton et al 2005, Sieving et al 2010), but also primates (Fichtel and Kappeler 2002).

8.3.8 Call combinations and their implications for the theory of language evolution

One relevant finding of this study was that alarm sequences appeared to convey information on both the type and location of a predator. The fact that titi monkey calls were organized into sequences, as combinations of one or more vocal signals, is not a novel finding (e.g. Robinson, 1984, 1979a). However, very few systematic studies have been conducted to examine the communicative function or meaning of such vocal sequencing, which has been referred to as instances of ‘zoo-syntax’ (Zuberbühler, 2002, Arnold and Zuberbühler, 2006a, b, Clarke et al 2006, Schel et al 2010).

In human language, syntax refers to the capacity to produce an infinite number of meaningful messages (phrases and sentences) by assembling a set of basic sounds, the morphemes (the smallest unit that has semantic meaning), according to structural rules (Fitch, 2010). From a comparative approach, Marler proposed two different types of syntax, a phonetic syntax that is equivalent to the formation of different words from phonemes and a lexical syntax that is equivalent to the formation of phrases or sentences from different words (Marler, 1977). Syntax can be further examined at both structural and functional levels, and even if a syntactical system does not allow for an infinite number of utterances to be produced, identification of a simpler kind of syntax can still be informative from the perspective of precursors to human speech and language (Snowdon, 1997).

In this thesis, I found that the main alarm calls produced by titi monkeys (calls A and B) during the early parts of predatory encounters differed in functionality and meaning if analysed at the sequence level. Structural analyses of these sequences revealed the following rules:

Call A was the only one produced singly. It was also the only one that had a referential meaning attached to it, individually. One (or few) A calls was common in response to flying raptors, whereas several A calls (e.g. AAAAAAAAA) indicated the presence of a

perched raptor. However, if multiple A calls were combined in a sequence with B calls (e.g. **AAABBBB** or **AAABBAAB**), then it indicated the presence of a raptor on the ground. Raptor “meaning”, in other words, was conserved. Finally if one A call was immediately followed by series of calls B (e.g. **ABBBBBBBB**), then the meaning of the A call appeared to change to indicate the location of the danger (i.e. within canopy or from above), instead of referring to the presence of a raptor.

Call B does not seem to possess a separate meaning, mainly because it is not usually produced singly; instead, its interpretation apparently depended on other calls that might precede or follow it. For example, series of B calls (**BBBBBBBBBB**) were common when monkeys detected a disturbance on the ground, typically a snake; combinations of series of B calls with C calls (**BBBCCBBC**) were common in response to a non-predator animal (deer); while sequences of Bs, BSs, BWs and loud calls (e.g. **BBBBB_BSBW_Loud calls**) indicated the presence of mammalian terrestrial predators, such as an oncilla, puma, or tayra.

Thus, titi monkey call sequences appear to be organised by a simple form of syntax, with some evidence of both lexical and phonetic syntax (Marler, 1977). Both A and B can be given alone, but only A appears to have its own independent meaning. When given in sequences with phrases of As followed by Bs, it continues to refer to raptors but also has a new meaning attached to it. However, when one call A is followed by Bs, the new sequence means the location of the danger (i.e. within canopy or from above), instead of referring to the presence of a raptor. Thus, individual calls and sequences have their own individual meanings but obtain a different meaning when combined into other sequences. A similar type of semantic combination was well demonstrated in an experimental study with putty-nosed monkeys, *Cercopithecus nictitans*, by Arnold and Zuberbühler (2006). These animals regularly produce ‘pyows’ when encountering a leopard and ‘hacks’ in response to crowned eagles. Furthermore, they combine these predator-specific call sequences in a third structure, a ‘pyow-hack’ sequence that in turn

stimulate group movement. Such vocal complexity illustrates monkeys' cognitive abilities and reflect the underlying neurological organisation of the animal; they may also further our understanding of the evolutionary pathways to the development of modern human language (e.g. Lieberman, 2001; Gil da Costa et al., 2006). Further research will be required to describe the full range of realised call combinations and their contextual meanings.

8.4 Conclusion

To conclude, the black-fronted titi monkeys have evolved a complex vocal alarm calling system that has the capacity to communicate predator class and the location of a predator to conspecifics, by the use of various specific call sequences. The acoustic features of the individual component calls differ from each other, which suggested that individual calls served as the main vehicles of this combinatorial communication system to convey semantic content. The black-fronted titi monkeys' vocal system thus provides another example of zoo-syntax, in which acoustically fixed units of a vocal repertoire are combined into higher order sequences that are meaningful to recipients. The system is functionally referential, at least at the level of one predator type and a general predator class, or location. As such, this is the first systematic empirical study to demonstrate a sequence-based alarm call system which conveys information on both predator category and location, perhaps one of the most complex examples of communication within the primate lineage.

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APPENDIX A

Signalling predator type and location

Figure A.1. Raw data of calling patterns of the first 30 calls given in response to visual models of a raptor and a cat, either on the canopy or on the ground. I used the first 30 calls because we understand that important information on the type of threat would be probably present at the beginning of a sequence. * Group D gave only one call and moved away during the first trial. ‡ In this case, the first individual to see and call was the adult male, which gave only calls A for a few minutes, while the rest of the group was more than 20m away, and could possibly being out of range to listen. Later on, the other group members (n=3) also called when saw the stimuli and did it so in a similar pattern of the other groups (i.e. several calls A first and calls B and A on later parts of their sequences). † We were able to test a semi-habituated group but not able to record the first call given by it in response to the cat on the canopy. However, from the second call its response was the same of other groups. As soon as the group B started calling in response to the cat, another group already tested (GR) approached and also saw and responded to the stimuli by giving 4 calls A and then only calls B. This result illustrate that although this group was seeing this stimulus for the second time, its response was the same as in the first trial, and therefore, represents a reliable response. GR: groups tested; A: call A; B: call B; C: call C; O: other calls; ?: uncodable call; blank cell: no call/silence.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
GR	Raptor on the canopy																														
A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	
D	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A												
M	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	
P	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	
R	A	A	A	A	A	A	A	A	A	O	O	A	O	A	A	A	A	A	A	O	A	A	A	A	A	A	A	A	A	A	A
Raptor on the ground																															
A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	B				B	B	
D*	A																														
D	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
M†	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	
P	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A		A		A	A	A	B	B	B	B	B	
R	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	B	B	B	B	B	A	A	A	B	B	B	
Cat on the ground																															
A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
D	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
M	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
P	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
R	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
Cat on the canopy																															
A	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
D	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
M	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
P	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
R	A	A	A	B	B	A	A	A	A	B	B	B	A	A	A	A	B	B	B	A	A	B	A	A	A	B	A	A	B	B	B
B†	?	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	

APPENDIX B

To investigate the possible existence of differences during mobbing of a terrestrial and an aerial predator I compared two natural events; one event in which two eagles were mobbed for 11 minutes and one event in response to an unidentified spotted cat.

Methods and results

Comparisons were made following the coding protocol described in chapter 2.

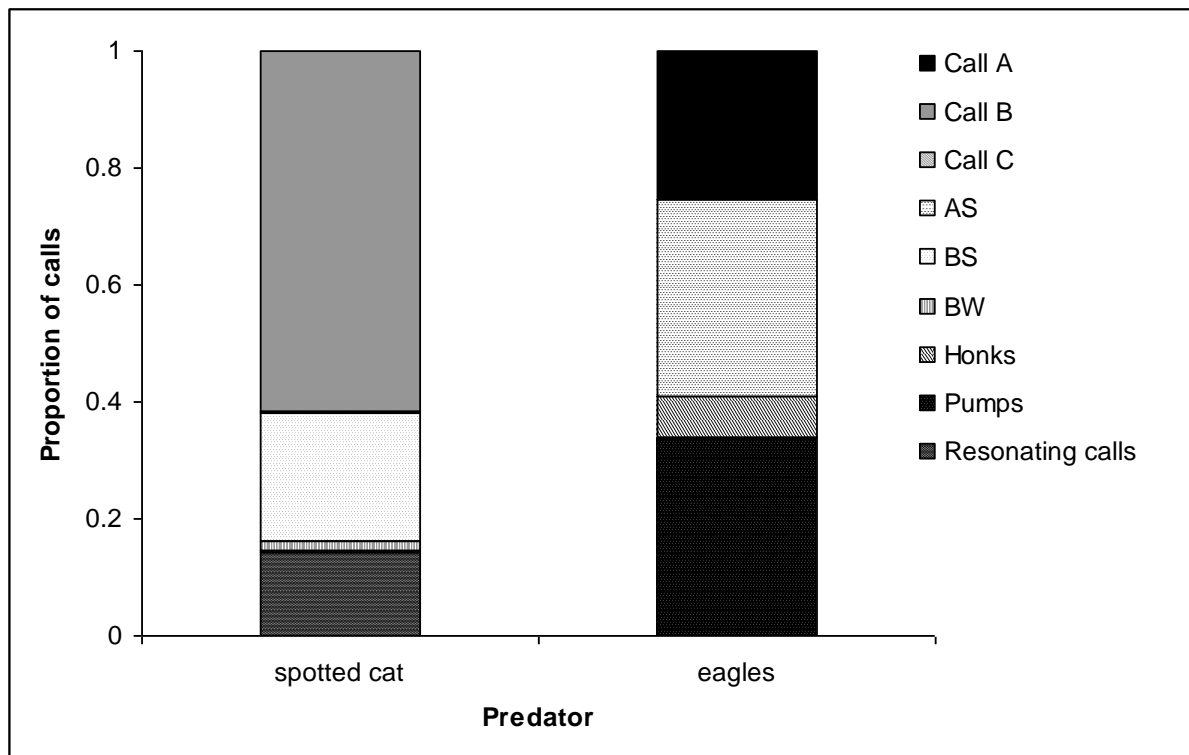


Figure B.1. Proportion of calls produced within the first five minutes after detecting two species of predators.

In the first five minutes after detection the most common call in response to a spotted cat was call B, followed by BS (Fisher's test < 0.0001). In response to eagles, however, the most common calls were AS and pumps (Fisher's test < 0.0001). Resonating calls were more common in response to the cat, while pumps were more common in response to eagles (Fisher's test < 0.0001).