

Referential alarm calling behaviour in New World primates

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Abstract There is relatively good evidence that non-human primates can communicate about objects and events in their environment in ways that allow recipients to draw inferences about the nature of the event experienced by the signaller. In some species, there is also evidence that the basic semantic units are not individual calls, but call sequences and the combinations generated by them. These two findings are relevant to theories pertaining to the origins of human language because of the resemblances of these phenomena with linguistic reference and syntactic organisation. Until recently, however, most research efforts on the primate origins of human language have involved Old World species with comparatively few systematic studies on New World monkeys, which has prevented insights into the deeper phylogenetic roots and evolutionary origins of language-relevant capacities. To address this, we review the older primate literature and very recent evidence for functionally referential communication and call combinations in New World primates. Within the existing literature there is ample evidence in both Callitrichids and Cebids for acoustically distinct call variants given to external disturbances that are accompanied by distinct behavioural responses. A general pattern is that one call type is typically produced in response to a wide range of general disturbances, often on the ground but also including inter-group encounters, while another call type is produced in response to a much narrower range of aerial threats. This pattern is already described for Old World monkeys and Prosimians, suggesting an early evolutionary origin. Second, recent work with black-fronted titi monkeys has produced evidence for different alarm call sequences consisting of acoustically distinct call types. These sequences appear to encode several aspects of the predation event simultaneously, notably predator type and location. Since meaningful call sequences have already been described in Old World primates, we suggest that basic combinatorial vocal communication has evolved in the primate lineage long before the advent of language. Moreover, it is possible that some of these communicative abilities have evolved even earlier, or independently, as there is comparable evidence in other taxonomic groups. We discuss these findings in an attempt to shed further light on the primate stock from which human language has arisen [*Current Zoology* 58 (5): 680–697, 2012].

Keywords Primate alarm calls, Functionally referential calls, Call combinations, New World monkeys, Old World monkeys

1 Primate Alarm Calls

Alarm calls are a common component of the anti-predator strategies employed by many species of birds and mammals. They usually function to announce threats to conspecifics and to communicate directly to the predator (Caro, 2005). Multiple explanations have been offered to understand the evolution and mechanisms of this potentially costly behaviour (see review in Wheeler, 2008). Some species, for instance, produce several acoustically distinct alarm calls in response to different predator types (vervet monkeys; Seyfarth et al., 1980a, b), but in others the nature of the danger is reflected by the number of calls per sequence (Guereza

colobus monkeys *Colobus guereza*; Schel et al., 2009), the rates of call delivery (Campbell's monkeys; Lemason et al., 2010), the acoustic features and intensity of calls (chacma baboons *Papio cynocephalus ursinus*; Fischer et al., 2001a, b), or certain combinations of calls (putty-nosed monkey *Cercopithecus nictitans martini*; Arnold and Zuberbühler, 2006a, b). Many of these utterances are elicited by specific external events, the 'referents' (e.g. eagles, leopards, snakes), and there appears to be some mediation by corresponding underlying mental concepts (Zuberbühler et al., 1999), the 'references', a process that can take place even in the absence of contextual information (Seyfarth et al., 1980; Macedonia and Evans, 1993; Evans and Marler, 1995).

Another interesting phenomenon is the bewildering range of acoustic structures that serve as alarm calls. One relevant factor here seems to be the perceptual abilities of the predators. Marler (1955) has proposed that low-pitched, broadband calls are conspicuous and easier to localise for predators than cryptic high-pitched, narrowband calls. Thus, prey animals that defend themselves by avoiding detection are likely to produce high-pitched calls that alert others to the danger without putting themselves at risk of detection (Wilson and Hare, 2006; Campbell and Snowdon, 2007). However, primate alarm calls are often conspicuously loud, especially the ones given by adult males, suggesting that they are also directed at neighbouring groups or directly at the predator, for instance to signal detection, an adaptive strategy if the predator relies on surprise hunting (Zuberbühler et al., 1997; Zuberbühler, 1999a). Conspicuous calling in the presence of predators is often related to mobbing behaviour, a behaviour that is fairly common in New World monkeys (Bartecki and Heymann, 1987; Fichtel et al., 2005; Digweed et al., 2005; Campbell and Snowdon, 2007; Clara et al., 2008). Mobbing behaviour is usually defined in terms of individuals making repeated and aggressive advances on a predator, typically while vocalizing and displaying in a conspicuous manner, which appears to distract or repel predators (e.g., Schel et al., 2010).

Predator-specific alarm calls are well described in Old World monkeys (see Zuberbühler, 2009 for a review), but this is not the case for New World monkeys, an independent radiation within the primate lineage with its own life history and socio-ecological characteristics (Strier, 2011). Therefore, discovering whether and how other Neotropical monkeys use vocal behaviour when interacting with predators has implications for evolutionary theories of primate communication and underlying cognitive processes.

There is evidence for alarm calls in almost all New World monkey species that have been studied in the wild. However, most records are from anecdotal observations with little or no systematic information on the types and function of calls and most reports are on responses to raptors (Digweed et al., 2005; Fichtel et al., 2005; Kirchhof and Hammerschmidt, 2006; Wheeler, 2010). Aerial alarm calls are usually very specific (given to a few species of dangerous raptors) while terrestrial alarm calls can be given to a range of disturbances on the ground and sometimes during non-predatory events (Digweed et al., 2005; Wheeler, 2010), a pattern also found in Prosimians (Fichtel and Kappeler,

2002; Fichtel and van Schaik, 2006) and Old World monkeys (Arnold and Zuberbühler, 2006). Table 1 provides an overview of all Neotropical primates known to produce at least one type of alarm call. This list is not exhaustive as there are further reports of predation on Neotropical primates (see for instance Boinski et al., 2000; Ferrari, 2009; Miller and Treves, 2011) and it is biased towards species that have been the subject of long-term research projects (Boinski et al., 2000; Miller and Treves, 2011). Table 1 illustrates how little is currently known about the type and function of alarm calls in Neotropical species.

Aotus, for instance, was first described to possess nine distinct vocalisations (Moynihan, 1964), including generalized alarms to alert group members of danger (Wright, 1981). To our knowledge, however, no further studies have been carried out to investigate these calls in more detail. *Chiropotes* is also known to have alarm vocalizations (Silva and Ferrari, 2008), but it is not clear how these signals are deployed to predators, which is partially explained by the fact that this genus is one of the most difficult primates to study (Pinto et al., in press). Other studies have generated vocal repertoires in some species but detailed information on alarm calling is typically missing. For captive cotton-top tamarins *Saguinus oedipus oedipus*, Cleveland and Snowdon (1982) identified eight context-specific acoustic variants of ‘chirp’ calls, one of which was used during mobbing behaviour. In a playback study, Bauers and Snowdon (1990) investigated two variants of the chirp call, one given to unfamiliar groups and another given during within-group call exchanges, and found contextually appropriate responses by recipients. Interestingly, the chirp variant produced during mobbing behaviour was also uttered to preferred foods by some groups, but it is currently not known whether listeners can discriminate these variants.

Other reports have indicated that individuals do not always produce alarm calls in response to predators, while some calls that function in long-distance communication are also given to predators, similar to what has been found in some African forest monkeys (e.g. Schel et al., 2010; Zuberbühler et al., 1997). *Alouatta*’s roaring vocalizations, for instance, are used during predator encounters (Eason, 1989), for example by *A. palliata* in response to crested caracaras (*Caracara planctus*; McKinney, 2009). However, *A. caraya* has not been observed to produce loud calls in response to natural encounters with ocelots (*Leopardus pardalis*; da Cunha and Byrne, 2006).

Table 1 Overview of predation records and anti-predator responses from Neotropical primate species

| Genera/Species | Predator | Reported anti-predator response | Source |
|--|---|--|---|
| <i>Alouatta clamitans</i> | <i>Leopardus pardalis</i> | not available | Miranda et al. (2005) |
| <i>Alouatta clamitans</i> | black-hawk eagle <i>Spizaetus tyrannus</i> | loud call/ descend trees | Miranda et al. (2006) |
| <i>Alouatta palliata</i> | crested caracara <i>Caracara plancus</i> | call/hide | McKinney (2009) |
| <i>Alouatta palliata</i> | harpy eagle <i>Harpia harpyja</i> | call/hide/vigilant | Gil-da-Costa et al. (2003) |
| <i>Alouatta seniculus</i> | crested eagles <i>Morphnus guianensis</i> | call | Julliot (1994) |
| <i>Aotus</i> | Unspecified | call/mobbing | Wright (1981) |
| <i>Ateles</i> | harpy eagles | call | Janson's pers. obs. in Robinson and Janson (1987) |
| <i>Ateles paniscus</i> | jaguar and terrestrial non-predators | call/mobbing (aggressive display) | van Roosmalen (1985) |
| <i>Ateles paniscus</i> | terrestrial predators | alarm call | Symington (1987) |
| <i>Brachyteles hypoxanthus</i> | Owl | call/infants ran | Dias and Strier (2002) |
| <i>Brachyteles hypoxanthus</i> | tayra <i>Eira Barbara</i> | call/mobbing | Dias and Strier (2002) |
| <i>Brachyteles hypoxanthus</i> | tayra, grey-headed Kite <i>Leptodon cayanensis</i> | call | Printes et al. (1996) |
| <i>Brachyteles hypoxanthus</i> | dogs, tayra, coati, lizard | call/ascend trees | Mendes (1997) |
| <i>Brachyteles hypoxanthus</i> | flying bird, raptor | call | Mendes (1997) |
| <i>Cacajao</i> | flying hawks (other large bird), cats and raccoons | call/unspecified | Fontaine (1981) |
| <i>Cacajao calvus</i> | Raptors | call/alert and look up | Bowler (2007) |
| <i>Cacajao calvus</i> | Tayra | call/mobbing | Bowler (2007) |
| <i>Callicebus discolor</i> | harpy eagles | call (loud calls) | de Luna et al. (2010) |
| <i>Callicebus discolor</i> | Tayra | call/ hide/piloerection | de Luna et al. (2010) |
| <i>Callicebus moloch</i> | tufted capuchin <i>Cebus apella</i> | call/agitated | Sampaio and Ferrari (2005) |
| <i>Callicebus discolor</i> | Boa <i>Boa constrictor</i> | call/unknown ¹ | Cisneros-Heredia et al. (2005) |
| <i>Callicebus nigrifrons</i> | Raptors, including crowned eagle <i>Harpyhaliaetus coronatus</i>) black-chested buzzard-eagle <i>Geranoaetus melanoleucus</i> , black hawk-eagle <i>Spizaetus tyrannus</i> , along with several species of falcons, caracara <i>Caracara plancus</i> and vultures. | alarm call/hide/descend trees | Cäsar et al. (2012a); Cäsar et al. (2012b) ² |
| <i>Callicebus nigrifrons</i> | tayra, spotted cat | alarm call/approach and mob | Cäsar et al. (2012a); Cäsar et al. (2012b) ² |
| <i>Callimico</i> | human | call/ mobbing | Pook and Pook (1979) in Heltne et al. (1981) |
| <i>Callithrix jacchus</i> | domestic dog | call/stay motionless | Bezerra and Souto (2008) |
| <i>Callithrix jacchus</i> | Raptors | call/hide | Bezerra and Souto (2008) |
| <i>Lagothrix lagotricha</i> | black-and-chestnut eagle <i>Spizaetus isidori</i> | call/descend | Lehman (1967) in Ramirez (1988) |
| <i>Lagothrix lagotricha</i> | overflying birds | none | Ramirez (1988); Durham (1975) |
| <i>Cebuella</i> | Squirrels, snakes, humans | call/mobbing | Soini (1988) |
| <i>Cebus</i> | eagles and hawk eagles | alarm call | Terborgh (1983) in Robinson and Janson (1987) |
| <i>Cebus capucinus</i> | avian predators | alarm call/scan the sky/ descend trees | Fichtel et al. (2005) ² ; Gros-Louis et al. (2008); Digweed et al. (2005) ² |
| <i>Cebus capucinus</i> | snakes and terrestrial | alarm call/ascend trees/ look and sometimes mob | Fichtel et al. (2005) ² ; Gros-Louis et al. (2008); Digweed et al. (2005) ² |
| <i>Cebus capucinus</i> | unfamiliar humans | alarm call/remain hidden in trees | Fichtel et al. (2005) ² ; Gros-Louis et al. (2008) |
| <i>Cebus capucinus</i> | unfamiliar monkey or other group | alarm call/look towards them | Fichtel et al. (2005) ² ; Gros-Louis et al. (2008) |
| <i>Cebus capucinus</i> | Caiman | alarm call/scan the river | Fichtel et al. (2005) ² ; Gros-Louis et al. (2008) |
| <i>Cebus nigrinus</i> | aerial threats, raptor | alarm call | Wheeler (2010) ^{2,3} |
| <i>Cebus nigrinus</i> | Agouti <i>Dasyprocta azarae</i> , other capuchins | alarm call | Wheeler (2010) ^{2,3} |
| <i>Chiropotes satanas</i> | harpy eagle | not available | Rettig (1978) |
| <i>Chiropotes utahicki</i> | Unspecified | alarm call | Fernandes (1991) |
| <i>Chiropotes utahicki</i> | <i>Boa constrictor</i> | alarm call | Ferrari et al. (2004) |
| <i>Chiropotes</i> | Unspecified | alarm call | van Roosmalen et al. (1981); Silva and Ferrari (2009) |
| <i>Leontopithecus rosalia</i> | Tayra | call/mobbing | Stafford and Ferreira (1995) |
| <i>Pithecia</i> | harpy eagle | not available | Rettig (1978) |
| <i>Saguinus Geoffroyi</i> | Hawks | alarm calls/mobbing | Moynihan (1970) |
| <i>Saguinus oedipus</i> | unspecified (sudden animated stimuli) | mobbing | Cleveland and Snowdon (1982) |
| <i>Saguinus fuscicollis</i> | ornate hawk-eagles <i>Spizaetus ornatus</i> | not available | Robinson (1994) |
| <i>Saguinus mystax</i> and <i>S. fuscicollis</i> | <i>S. ornatus</i> , other raptors and other birds | alarm calls/looking up and falling down from trees | Heymann (1990) |
| <i>Saguinus fuscicollis</i> and <i>S. mystax</i> | aerial and terrestrial predators | alarm call | Kirchhof and Hammerschmidt (2006) ⁴ |
| <i>Saimiri fuscicollis</i> | crested eagles | not available | Robinson (1994) |
| <i>Saimiri</i> spp | raptors and other flying birds | alarm call | Baldwin and Baldwin (1981) |
| <i>Saimiri</i> spp | dogs, snakes, cats and humans | call/mobbing | Baldwin and Baldwin (1981) |
| <i>Saimiri oerstedii</i> | raptors, collared forest falcon <i>Micrastur semitorquatus</i> | mobbing | Boinski (1987) |
| <i>Saimiri oerstedii</i> | tayra and opossum <i>Didelphis masupialis</i> | alarm call | Boinski (1989) |

¹No behaviour, but calling, was observed after the observers arrived at the event. ²These studies describe both the production and perception of alarm calls. ^{3,4}For this table we present only responses to natural contexts. ⁴Describes the perception of alarm calls.

2 Reference in Primate Calls?

A key question in animal communication research concerns the function and meaning of signals (Fitch, 2010), where ‘meaning’ is typically inferred from a recipient’s response (Smith, 1968). Evidence of such semantic signals in primate communication has come from several species in different contexts, including rhesus macaques’ recruitment screams (*Macaca mulatta*; Gouzoules et al., 1984), food calls in chimpanzees (*Pan troglodytes*; Slocombe and Zuberbühler, 2005), tufted capuchin monkeys (*Cebus apella nigritus*; di Bitetti, 2003), Geoffroy’s marmoset (*Callithrix geoffroy*; Kitzmann and Caine; 2009) or rhesus monkeys (Hauser, 1998), and various studies on predator-specific alarm calls, including vervet monkeys (*Chlorocebus aethiops*; Seyfarth et al., 1980), Diana monkeys (*Cercopithecus diana*; Zuberbühler et al., 1997), Campbell’s monkeys (*Cercopithecus campbelli*; Zuberbühler, 2001), ring-tailed lemurs (*Lemur catta*; Macedonia, 1990; Pereira and Macedonia, 1991), moustached tamarins (*Saguinus mystax*, Kirchof and Hammerschmidt, 2006), blue monkeys (*Cercopithecus mitis stuhlmanni*, Papworth et al., 2008), and tufted capuchin monkeys (*Cebus apella nigritus*, Wheeler, 2010).

Research on the meaning of animal signals requires detailed studies of how individuals respond to each other’s calls. Much of this kind of research has been carried out with primate alarm calls, which has led to evidence not only for some flexibility in vocal production, that is, the ability to actively control and learn vocal production (Zuberbühler, 2000a; Zuberbühler and Jenny, 2002) but also for a widespread ability to correctly infer the eliciting context from the calls of conspecific and hetero-specific individuals (Seyfarth and Cheney, 1990; Zuberbühler, 2000 a, b, c; Kirchof and Hammerschmidt, 2006). Vervet monkeys, for instance, respond with appropriate anti-predator behaviour to alarm calls by superb starlings, a bird that inhabits the same area (Cheney and Seyfarth, 1985). Studies with Diana monkeys have shown some similarity to how humans interpret certain sounds as indications of the presence of external events. In one study, monkeys were primed with a playback consisting of a series of predator vocalisations or conspecific predator alarm calls (the prime stimulus). After a period of silence, a second series of corresponding or non-corresponding predator vocalisations were played from the same location (the probe stimulus). In the key condition, Diana monkeys primed with conspecific predator alarm calls no longer

responded to the vocalizations of the corresponding predator, even though the acoustic features of the two playback stimuli were completely different. In other words, monkeys responded to a predator as if they already knew about its presence, suggesting that the phenomena normally associated with the prime stimuli, not their acoustic features alone, drove the monkeys’ response patterns, possibly because recipients had formed a mental representation of the corresponding predator (Zuberbühler et al., 1999a). In related studies, listeners responded in similar ways if listening to playbacks of Campbell’s monkey or chimpanzee calls put in relation with matching and non-matching predator vocalisations (Zuberbühler, 2000a, b).

The classic example of meaningful predator-specific alarm calls is apparent in vervet monkeys. These primates give distinct alarm call types to predators, such as leopards, eagles and pythons (Struhsaker, 1967). Subsequent playback studies have shown that receivers respond to these predator-specific alarm calls by taking evasive reactions appropriate to the hunting technique of the predator, even in the absence of the predator (Seyfarth et al., 1980a, b). On hearing an eagle alarm call, for instance, monkeys may escape into dense vegetation, whereas they climb into a nearby tree after hearing leopard alarm calls, or adopt a bipedal posture and scan the ground after hearing python alarm calls.

Such signals have been termed ‘functionally’ referential, based on their context specificity in production (calls are given to a limited range of objects or events) and perception specificity (calls are sufficient to evoke appropriate responses from listeners in the absence of the eliciting stimulus; Macedonia and Evans, 1993). This type of behaviour has been found in a number of other primates, such as ring-tailed lemurs (*Lemur catta*; Macedonia, 1990; Pereira and Macedonia, 1991), Diana monkeys (Zuberbühler et al., 1999a), Campbell’s monkeys (Zuberbühler, 2001), or blue monkeys (*Cercopithecus mitis*, Papworth et al., 2008). In New World monkeys, there is evidence for functionally referential calls in moustached tamarins (*Saguinus mystax*, Kirchof and Hammerschmidt, 2006), tufted capuchin monkeys (*Cebus apella nigritus*, Wheeler, 2010) and black-fronted titi monkeys (*Callicebus nigrifrons*; Cäsar et al., 2012a, b).

In many primate and non-primate species, patterns of alarm calling behaviour are also consistent with the hypothesis that calls indicate degrees of threat experienced by the caller, rather than something about the predator category. This has been shown with studies on call

morphology, which often show structural differences in response to the perceived urgency during a predator encounter. In non-primate species, such analyses have revealed relations between call structure and the size of a predator (e.g. Templeton et al., 2005), its proximity (e.g. Leger et al., 1980) or other factors that presumably have an impact on the caller's psychological states (e.g. Baker and Becker, 2002). Urgency-related alarm calling is particularly important for species that rely on a single escape strategy to deal with all threats of predation, such as running into a burrow, because the level of threat appears to be the only relevant piece of information required for selecting an appropriate response (Macedonia and Evans, 1993). An interesting finding in this context is that one call type can be given to any predator that is about to attack and another one to any predator spotted at a distance, which does not require a locomotor response. It has been argued that living in a three-dimensional habitat may have been a crucial factor selecting for the evolution of functionally referential signals because of the need to make rapid and adaptive locomotor responses when confronted with different predators, which is different for species living in essentially two-dimensional habitat (Blumstein, 1999). However, there is evidence that species living in a two-dimensional environment can also evolve functionally referential calls. Suricates, for instance, have functionally referential alarm signals, which are attributed to social factors, such as coordinating group movements, allowing them to increase their foraging efficiency in an open and dangerous habitat (Furrer and Manser, 2009).

In primates, urgency-dependent alarm calling has been proposed for bonnet macaques (*Macaca radiata*, Coss et al., 2007), red-fronted lemurs *Eulemur fulvus* and Verreaux's sifakas (*Propithecus verreauxi*; Fichtel and Kappeler, 2002, Fichtel and Hammerschmidt, 2002). These species produce calls to aerial and terrestrial threats, with interesting acoustic variation within the terrestrial predator-associated calls that is related to urgency. A similar pattern is suggested for capuchin's terrestrial predator alarm (Wheeler, 2010).

Some authors have argued that their data may be interpreted as evidence for a 'mixed' system. This is because of evidence for one alarm call for raptors and another one for disturbances on the ground and during non-predatory events (Fichtel and Kappeler, 2002; Digweed et al., 2005; Fichtel and van Schaik, 2006). The system has been called 'mixed' because - following Macedonia and Evans' (1993) definition - responding to a wide range of events does not meet one of the two

criteria (i.e. specificity in production) for functional reference. Equally, it could be argued that this criterion is not very useful. In human language, evidently, words can refer to very different things but no one would doubt their referential nature (e.g. chair in "departmental chair" versus "patio chair"). A more basic problem with Macedonia and Evans' notion of referential signals is that some species use the same basic call type for various predators or situations, but vary the acoustic fine structure in context-specific ways (e.g. Ouattara et al., 2009a). These acoustic differences can be important to receivers, as demonstrated experimentally, suggesting that discrete call types are not a prerequisite for encoding specific external events (Fischer et al., 2001b).

Examples of an alarm call system that combines information regarding external events and perceived urgency come from studies with black-capped chickadees *Poecile atricapilla*, suricates *Suricata suricatta* and fowl *Gallus gallus*. Chickadees produce a high-pitched, low-amplitude "seet" call when detecting flying raptors and a loud, broadband "chick-a-dee" call when detecting perched raptors. In addition, they vary the number of notes per call depending on the perceived predation risk (e.g. predator size) (Templeton et al., 2005). Suricates also produce different alarm calls in response to aerial and terrestrial predators and vary the acoustic structure depending on the distance to the predator (Manser, 2001). Other systems consist of a single alarm signal to simultaneously encode external and urgency information (Manser, 2001; Wilson and Evans, 2012). This has been shown in suricates changing the acoustic structure of the alarm calls depending on whether they are facing non-dangerous animals (herbivores and non-raptors) or predators at different distances (i.e., very close, close or far away; Manser, 2001). Wilson and Evans (2012) have also found that male fowl *Gallus gallus* communicate changes in size, speed and proximity of aerial stimuli through amplitude changes in the acoustic signal.

What psychological states do primates experience when responding to a predator? Some authors have argued that differences in alarm call behaviour reflect differences in a caller's levels of arousal ('affect', 'fear', 'emotion'), usually because of evidence that calls given to predators are sometimes given in non-predatory contexts when callers appear to be in a state of high arousal. Although it has been difficult to independently quantify 'arousal' (e.g. Rendall, 2003; Fichtel et al., 2001), the notion has been embraced by a number of authors for explaining differences in the amplitude, resonance and

fundamental frequency of calls due to changes in respiration, facial musculature activity, or vocal fold behaviour (Morton, 1977; Owren and Rendall, 2001). Others have found evidence that there are links between vocal behaviour and physiological measures, such as cortisol levels (common marmosets: Cross and Rogers, 2006; Clara et al., 2008).

Although it is possible to generate lists of external events that primates respond to with specific calls, this cannot fully resolve how callers classify events, mainly because individuals sometimes commit errors, possibly try to deceive others, or vary in their ontogenetic experience within and across populations. In sum, the key question is how callers perceive and classify external events, a basic problem that have hardly been addressed and is far from being resolved.

In conclusion, examination of both call production and perception is important because context-specificity in call production does not always lead to distinct responses in receivers (Blumstein 1995). Another important point is that many species produce the same basic alarm call type to a range of events, some of which are not linked with the presence of a predator. Also, anti-predator responses can sometimes be elicited by calls that are not normally given to predators (e.g. Fitchel and Kappeler, 2002), suggesting that context plays an important role for recipients of alarm calling behaviour (e.g. Zuberbühler, 2000). Reliance on what may be called ‘pragmatics’ (that is, the aspects of meaning that are dependent on the context of the utterance, such as the composition and identity of the audience) is an important but under-researched field of future investigation in primate communication (see Wheeler and Fischer, 2012).

The best-studied alarm call system in Neotropical primates is in capuchin monkeys (*Cebus* spp.). From the 1960s it has been suggested that capuchins might use distinct alarm calls for different predators (Oppenheimer, 1968). More recent studies have investigated call diversification and functional significance in the different species. For example, Fitchel et al. (2005) described seven subtypes of alarm calls in *Cebus capucinus* that could be grouped into two main categories based on acoustic features. The first category, consisting of three subtypes, was produced in response to aerial predators, humans and other monkeys, while the second category was given to snakes, caimans, other terrestrial predators (e.g. canids and felids) and conspecific aggressors (Fitchel et al., 2005). Working with the same species, Digweed et al (2005) found three call types given to

aerial predators, snakes and terrestrial threats, suggesting that the environment has some influence on the ontogeny of alarm calling behaviour in this species, since large mammalian predators (e.g. puma, jaguar, coyote) were not present in the second study (Digweed et al., 2005). A study with tufted capuchin *Cebus apella nigritus* has found three different call types, ‘barks’, ‘hiccups’, and ‘peeps’ regularly produced to predators (Wheeler, 2010). ‘Barks’ were elicited exclusively by aerial threats, while ‘hiccups’ were produced in response to terrestrial threats and some non-predatory contexts, such as when foraging close to the ground. Responses to playbacks of these two calls were relatively specific. ‘Peeps’, finally, seemed to be specific to terrestrial threats, but here there was no clear evidence for specific anti-predator responses (Wheeler, 2010). These calls appear to be directed both at conspecifics and to the predator, especially as part of predator mobbing, a well documented behaviour in *Cebus* monkeys (*C. capucinus*: Chapman, 1986; Boinski, 1988; *C. apella* and *C. albifrons*: van Schaik and van Noordwijk, 1989).

Other evidence for functionally referential communication in Neotropical primates comes from studies with tamarins (*Saguinus* spp.). Kirchhof and Hammerschmidt (2006) have shown that *S. fuscicollis* and *S. mystax* responded with adequate anti-predator reaction after hearing playbacks of alarm calls originally given to aerial and terrestrial disturbances. In addition, both species behaved as if they correctly classified the alarm calls of the other sympatric species, a pattern also found in some Old World primates (Zuberbühler, 2000b) and a possible benefit for mixed-groups associations (Peres, 1993; Heymann and Buchanan-Smith, 2000). However, little is known about the range of contexts that lead to the production of these calls. From the available evidence it appeared that both aerial and terrestrial alarm calls of *S. mystax* are fairly predator-specific, while *S. fuscicollis* appears to have a specific aerial alarm and a non-specific, terrestrial alarm call. In light of these findings, Kirchhof and Hammerschmidt (2006) conclude: “Thus, it seems that, although ecological conditions and predator-specific reactions are important, they may not be sufficient to explain the evolution of a certain type of alarm call system.” It would be interesting to investigate more species in similar ways to find out what causes differences in predator-specificity.

3 Meaningful Call Combinations

According to many scholars, one of the defining as-

pects of language and ‘what it means to be human’ is syntactic communication (Chomsky, 1957). Syntax has been defined as “...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, p. 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, p. 26). One way to study the evolution of complex behaviour, such as syntactic communication, is by direct comparisons across species. Hauser et al. (2002) have made this point as a way to study language evolution, based on the idea that mechanisms involved in linguistic behaviour - memory, sequencing, vocal production and perception - are to various degrees shared with other species. An example, as mentioned before, is the ability to communicate about objects or events in the environment, which appears to be relatively widespread in animal communication (e.g. Seyfarth et al., 1980; Zuberbühler et al., 1999; Manser, 2001; Templeton et al., 2005). How exactly these animal examples relate to the human ability to extract meaning from linguistic utterances is not well understood, but it is possible that the cognitive processes are very similar.

There is good evidence that some species combine existing calls into meaningful sequences, which increases the variety of messages that can be generated (e.g. Arnold and Zuberbühler, 2006; Cleveland and Snowdon, 1982; Marler et al., 1992). Such syntax-like patterns have been demonstrated in titi monkeys (Robinson, 1979), capuchins (Robinson, 1984), Campbell’s monkeys (Zuberbühler, 2002), putty-nosed monkeys (Arnold and Zuberbühler, 2006a, b), gibbons (Mitani and Marler, 1989, Clarke et al., 2006) and colobus monkeys (Schel et al., 2010). Lar gibbons *Hylobates lar*, for instance, use different orderings of song units when singing as part of their regular morning duets or when singing in response to terrestrial predators (Clarke et al., 2006). Likewise, red titi monkeys *Callicebus cupreus* produce different call sequences when interacting with neighbouring groups. Here, variation was due to the number of individuals calling and the location and distance between the groups (Robinson, 1979).

Another type of sequence-based calling system is grounded in differences in the number of call units per utterance. A recent example is Guereza colobus monkeys that produce roaring sequences consisting of few

call units per utterance to leopards and many call units per utterance to eagles, a difference that is recognised by receivers (Schel et al., 2010). Similarly, Moynihan (1970) suggested that the number of alarm calls in tamarins *Saguinus Geoffroyi* might be correlated with vulnerability to predation and that combinations of different call types “...may provide more precise information about the positions and probable intentions of potential predators, and/or may be more effective in attracting and retaining attention of the predators and/or other tamarins, than even a multitude of variation on a single type of signal”.

One of the first attempts to categorise such phenomena in animal communication was by Marler (1977), who distinguished two types of zoo-syntax. Specifically, ‘phonological syntax’ refers to phenomena that are roughly equivalent to linguistic morphology. Here, meaningless units are rearranged into meaningful sequences, similar to how phonemes are arranged into morphemes and words. ‘Lexical syntax’, in contrast, is equivalent to the formation of phrases or sentences with different words so that the resulting sequence somewhat retains the meaning of the individual components. Robinson (1979, 1984) then interpreted field observations adopting this framework. In red titi monkeys, loud calls with apparently no independent meaning are organised hierarchically into ‘phrases’ that form the basis of more complex context-specific sequences, and this has been interpreted as ‘phonological syntax’ (Robinson 1979). In a playback study, Robinson (1979) then arranged utterances so that they mimicked both normal and abnormal sequence types, which were discriminated by listeners. In response to abnormal sequences, for example, subjects produced more “moans” -- a signal normally given to disturbing situations -- than in response to normal sequences. In wedge-capped capuchins, Robinson (1984) found that some calls were combined to create novel utterances, which were given in intermediate situations, relative to the component calls. Similarly, in tamarins, alarm and alert calls can be produced in combination, usually in contexts that are intermediate relative to the contexts in which the component calls are produced alone (Cleveland and Snowdon, 1982).

What is clear from these studies is that, in terms of production context, these call combinations are very closely related to the component calls, which is different from the hierarchical complexity of grammar in human speech (Byrne, 1982). An example of contextually unrelated combinations comes from studies with free-ranging putty-nosed monkeys. Here, the males produce two

alarm call types, ‘hacks’ and ‘pyows’, but these calls are not individually related to specific predator types, as both calls are given to eagles and leopards. Instead, the monkeys concatenate the two calls into longer sequences, which can be highly predator-specific but are also used in communicating non-predatory information (Arnold and Zuberbühler, 2006b). The cognitive proce-

sses underlying this behaviour are currently unknown.

In conclusion, in response to predators primates use different types of communication systems, including acoustically discrete and graded call types and some rule-governed combinations thereof. This range of behaviour has subsequently been classified as functionally referential, urgency-dependent, or mixed (Table 2).

Table 2 Studies that investigated the alarm call systems of different primate species, organized by the type of alarm call system used by these species

| PRIMATES Family ¹ /Genus | Alarm Call system | | | Signal type | | |
|--|---|-------------------------------|--|------------------|-----------------------|----------------|
| | Functionally Referential | Urgency Response | Mixed | Discrete signals | Graded signals | Call sequences |
| Indriidae | | | | | | |
| <i>Propithecus verreauxi</i> | | | Fichtel and Kappeler (2002) | + | | |
| <i>P. v. coquereli</i> | | | Fichtel and van Schaik (2006) | + | | |
| Lemuridae | | | | | | |
| <i>Lemur catta</i> | Macedonia (1990) | | | + | | |
| <i>Eulemur f. rufus</i> | | | Fichtel and Kappeler (2002) | + | + | |
| <i>Varecia variegata</i> | | Macedonia (1990) | | + | | |
| Cercopitheciidae | | | | | | |
| <i>Cercocebus atys</i> | | Range and Fischer (2004) | | | + | |
| <i>Chlorocebus aethiops</i> | Struhsaker (1967), Seyfarth et al. (1980) | | | + | | |
| <i>Cercopithecus campbelli</i> | Zuberbühler (2001), Zuberbühler (2002) | | | + | | + |
| <i>C. diana</i> | Zuberbühler et al. (1999) | | | + | | |
| <i>C. nictitans martini</i> | | Arnold and 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> | Kirchhof and Hammerschmidt (2006) | | | + | | |
| <i>S. mystax</i> | | | Kirchhof and Hammerschmidt (2006) | | | |
| Cebidae | | | | | | |
| <i>Cebus capucinus</i> ² | | | Fichtel et al. (2005), Digweed et al. (2005) | | + | |
| <i>Cebus nigrinus</i> | | | Wheeler (2010) | + | | |
| Pitheciidae | | | | | | |
| <i>Callicebus nigrifrons</i> | Cäsar et al., 2012b | | | + | possibly ³ | + |

¹Primate families according to Strier (2011). ²The authors did describe the calls and behavioural responses to predators, but no playback experiment was performed. ³It needs to be tested still.

Signal type indicates the type of signal used in the alarm responses produced by these animal species. Updated from Schel (2009).

4 Recent Field Experiments with Black-fronted Titi Monkeys

Recent work on the anti-predator behaviour and alarm calling in one species of titi monkeys *Callicebus nigrifrons* has provided further insights into the nature of functionally referential and combinatorial properties

of primate vocal behaviour. Titi monkeys have long been known to possess complex vocal behaviour (Moynihan, 1966; Robinson, 1979), with some evidence for meaningful call sequences (Robinson, 1979), as discussed before. In the predation context, there have been reports of the occurrence of predation-related vocalisations, including mobbing calls (de Luna et al.,

2010; Cisneros-Heredia et al., 2005; Sampaio and Ferrari, 2005; see Table 1). However, to our knowledge, there has been no systematic description of the call repertoire and behavioural responses in predatory events in these monkeys, making it difficult to assess how their complex vocal system is employed in the predation context.

To address this, we carried out studies with five habituated groups of black-fronted titi monkeys, *C. nigrifrons*, living in a private reserve ('Caraça' 20°50'S, 43°29'W) in Minas Gerais, Brazil. The reserve is home to a number of potential primate predators, including several species of raptors and mammalian carnivores. Dangerous raptors include the crowned eagle *Harpyhaliaetus coronatus*, black-chested buzzard-eagle *Geranoaetus melanoleucus*, black hawk-eagle *Spizaetus tyrannus*, and several species of falcons (e.g. *Accipiter* sp.) and owls (Vasconcelos and Melo Junior, 2001; Vasconcelos, 2001). The area is also inhabited by several mammalian carnivores, including tayras *Eira barbara* and different species of cats; ocelots *Leopardus pardalis*, oncillas *Leopardus tigrinus*, jaguarondi *Herpailurus yagouaroundi*, pumas *Puma concolor* and possibly jaguars *Panthera onca*.

4.1 Natural observations

During approximately 730h of observations, we recorded a large number ($n=287$) of anti-predator re-

sponses during natural encounters with potential predators (Cäsar et al., 2012a). In response to raptors, which included crowned eagles, black-chested buzzard-eagles, black hawk-eagles, caracaras, vultures and several species of hawks, usually one individual produced a high-pitched quiet A-call ('chirp'). The caller usually remained alone before moving to a protected location (Table 3). There were differences in the number of calls produced to raptors, which appeared to be linked with the raptors' behaviour. Monkeys usually gave one call in response to flying and multiple calls to perched raptors. In response to terrestrial disturbances (spotted cat, deer and unidentified events on the ground) one individual produced a high-pitched B-call ('cheep'), which usually attracted other group members to the site and who then also called whilst showing specific alert behaviour and sometimes prolonged mobbing (Table 3; Cäsar et al., 2012a). A third call C ('squeak') was less common and was given in different contexts, which suggested that it did not relate to very specific external events. All three calls were predator-related calls and were mainly produced at the beginning of what sometimes turned into lengthy vocal responses, consisting of other acoustically very different calls, such as loud and low-pitched calls that were particularly common in later parts of a vocal response, especially whilst mobbing terrestrial predators.

Table 3 First call (high-pitched quiet call) produced during encounters with potential predators, associated behaviours and contexts (predatory and non-predatory)

| First call | Caller's behaviour | Listener's behaviour | Context |
|------------|---|---|---|
| A | Observing the stimulus, freezing or rapid flight away from the stimulus (usually descending) and towards a protected place. | Scanning the canopy/sky. Freezing or rapid flight away from the stimulus (usually descending) and towards a protected place. | In response to: 1) raptors, 2) unidentified sudden flying birds, 3) capuchins approaching or moving on the canopy and 4) other unidentified threats on the canopy ^{*1} . |
| B | Looking to the stimulus, and doing some visual displays [Arch postures, Pilo-erection (i.e. raising of the hair all over the body, limbs, and tail) ^{*2} , Tail lashing (swinging the whole tail from side to side) ^{*2} and Head swaying (moving from right to left)] at times. Rapid erratic movement towards and away from focal object. Intense visual fixation on mobbed object. | Looking towards the caller and/or scanning the forest ground or lower canopy. Approaching, calling and sometimes doing visual displays and mobbing ^{*3} (harassing the predator cooperatively) together. | In response to: 1) a potential predator (spotted cat and tayra), 2) a non-predator animal (adult deer), 3) other unidentified animals on the ground. Also, 4) when the observer was blocking their way from habituated groups or 5) in response to humans from unhabituated groups and 6) when descending or foraging close to the ground and 7) during some intergroup encounters. |

^{*1}Call A in response to capuchins only happened in sequences with other call types. ^{*2} From Moynihan 1966. ^{*3} Mobbing was observed in response to predators (spotted cat and tayra), but not in response to a deer, although they were agitated in both situations.

4.2 Predator-specific alarm calling

To investigate the alarm calling behaviour of black-fronted titi monkeys more systematically we carried out a field experiment in which we presented different types of natural predator models, including one species of raptor, five species of typically terrestrial predators and one non-predatory control, a deer (Cäsar,

2011). Results were consistent with the previously reported natural observations. The basic pattern was that callers responded with the same high-pitched quiet calls when discovering a predator but call production was very predator-specific. A calls were given to the raptor models whereas B calls were given in response to terrestrial predators and the control (Fig. 1).

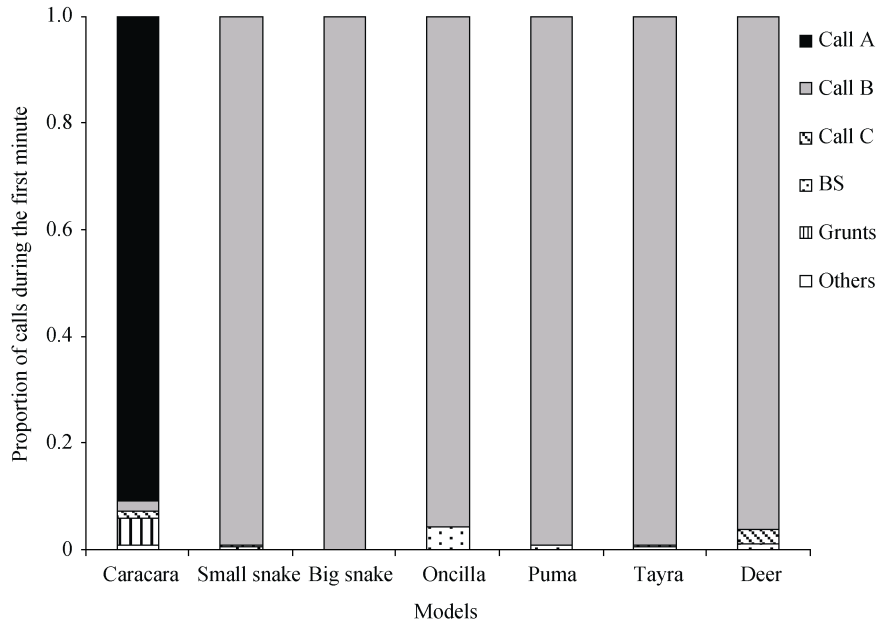


Fig. 1 Proportion of each call type produced during the first minute

Description of call types is presented on table 4.

In addition, monkeys' responses to terrestrial disturbances were dependent on the type of model they detected. Mobbing behaviour and the production of loud low-pitched calls were only recorded in response to the oncilla, puma and tayra models, but not to the deer or snake models. Although the first response to all disturbances on the ground was the production of at least one B call, later parts of the vocal responses varied in predator-specific ways, demonstrating that callers discriminated the threats or risks associated with the different models (Fig. 2, Table 4). The role of the low-pitched calls has remained unclear and will require further investigations.

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., 2009b; 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 began with these quiet calls. In later parts of their calling sequences, usually after having examined the terrestrial predators, titi monkeys then switched to different calls,

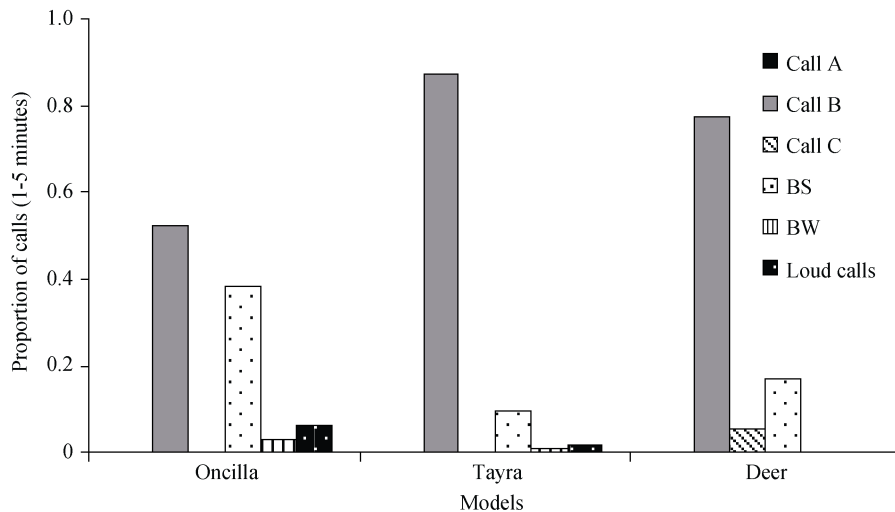


Fig. 2 Proportion of calls produced within the first five minutes after detecting two species of predators (oncilla, tayra) and a control non-predator model (deer)

typically loud and conspicuous calls. It is possible that these calls are directed to the predator, or that they function as recruitment signals for mobbing behaviour (Cäsar, 2011). Digweed et al. (2005) argued that capuchin alarm calls functioned to recruit others to a mobbing party, and the same mechanism may be at work in the titi monkeys. The use of different call variants may be important to inform others about the degree of threat. In the older literature on mobbing behaviour one

prominent functional explanation has to do with facilitating predator recognition in naïve offspring (Curio, 1978, reviewed in Wheeler, 2008).

It has been argued that high-pitched quiet calls have evolved to avoid detection by the predator when trying to alerting others (Marler, 1955; Campbell and Snowdon, 2007). Based on these observations, it seems plausible to conclude that the titi monkeys' first alarm calls primarily function to inform conspecifics about the

Table 4 Calls produced by *Callicebus nigrifrons* during natural and experimental encounters with predators at Caraça (from Cäsar, 2011)

| Call | Description | Context at Caraça |
|--|---|--|
| <i>Simple high-pitched quiet calls</i> | | |
| Call A (chirp) | A quiet high-pitched, with an 'arch'-shaped down-sweep modulated call. Frequency around 5 or 6 kHz and duration around 0.04 seconds | In response to raptors, some unidentified flying birds, and in sequences to other predators in the canopy |
| Call B (cheep) | A relatively quiet high-pitched 'S'-shaped, or upsweep, modulated call. Frequency range from 2.5 to 8 kHz and duration from 0.01 to 0.05. | In response to threats on the ground (deer and an unidentified spotted cat) and all stuffed predators (tayra, oncilla, puma, snakes) and a stuffed baby deer. In non-predatory contexts, especially when descending or foraging close to the ground. |
| Call C (squeak) (squeak: Moynihan, 1966; Robinson, 1979) | A high-pitched, mostly unmodulated call. Extreme calls C were very short and rather soft. The pitch of the fundamental frequency ranged from 4 to 8 kHz and the duration from 0.01 to 0.09 seconds. Intergrade with other high-pitched calls, mainly whistles and trills, which are not described here due to their low occurrence in this study. | In predatory contexts, but 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. |
| <i>Simple low-pitched calls</i> | | |
| Call G ('grunt'-like) (grunts: Moynihan, 1966; Robinson, 1979) | They were noisier, typically unvoiced, low-pitched call with some variation in the number of harmonics. Grunts were monosyllabic and very rare in Cäsar's sample. | Only produced by two groups: one in response to a stuffed perched raptor and another in response to an uncoiled big snake, however, in the last case, part of the group was moving towards a neighbouring group. |
| Call M ('moan'-like) (moans: Moynihan, 1966; Robinson, 1979) | These were low-pitched, usually long and monosyllabic. | Only produced in response to stuffed oncillas and tayra and in one event in response to capuchins. |
| <i>Composite medium-pitched calls</i> | | |
| Call AS ('chirrup' and 'chucks': Moynihan, 1966; 'chirrup': Robinson, 1979) | A compound call with two syllables, a high-pitched A immediately followed by a low-pitched suffix, which makes it louder and more conspicuous than a pure A. | Mainly in response to two eagles flying and perching around one group. |
| Call BS ('chirrup' and 'chucks': Moynihan, 1966; 'chirrup': Robinson, 1979) | A compound call with two syllables, a high-pitched B immediately followed by a low-pitched suffix, which makes it louder and more conspicuous than a pure B. | Produced in response to all stuffed models on the ground, with the exception of snakes. |
| Call BW ('chirrup' and 'chucks': Moynihan, 1966; 'chirrup': Robinson, 1979) | 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, 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. | Only produced on the sequences in response to oncilla, tayra and puma. |
| <i>Composite low-pitched loud calls</i> | | |
| Honk ('resonating notes': Moynihan, 1966; 'honks': Robinson, 1979) | Honks were usually compound with two, low-pitched, syllables 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. |
| Resonating calls ('resonating notes': Moynihan, 1966; 'pants and 'bellows': Robinson, 1979) | 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 by 3 syllables, which appear to correspond to the 4 'components' (including a pause) of loud calls described by Robinson 1979. | They were only produced in response to oncilla (in the canopy and on the ground) and tayra. |
| Pumps ('pumping notes': Moynihan, 1966; 'pumps': Robinson, 1979) | Pumps were usually compound with two similar, low-pitched, syllables and only occurred in series and/or sequences, intergrading specially with other loud, low-pitched calls. | They were only produced in response to oncilla (in the canopy and on the ground) and tayra, and in one event when two eagles pursued them. |

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. It is also remarkable how similar the titi monkeys' quiet alarm calls are in their general acoustic structures (Cäsar et al., 2012a, b). A main finding was that these minor variations in shape have major effects on listeners (see below), suggesting that these subtle acoustic differences convey major differences in meaning. This raises the possibility that other primates' quiet calls may also function in similar ways, such as in tamarins, marmosets and other small primates that are highly vulnerable to predation (Moynihan, 1967; Moynihan, 1970; Ferrari, 2009).

4.3 The meaning of titi monkeys alarm calls

In our research on titi monkeys, we focused on two of the high-pitched quiet calls regularly given to predators, by carrying out a series of playback experiments using call series recorded in response to a perched raptor (caracara) and two terrestrial predator mammals (oncilla and tayra; Cäsar et al., 2012b). Our general finding was that listeners' responses were highly predator-specific in that they looked significantly longer upwards when hearing raptor-related than terrestrial predator-related calls, and significantly longer towards the caller when hearing terrestrial predator-related compared to raptor-related calls. As pragmatic cues were excluded due to the experimental design, we con-

cluded that discrimination must have been based on the calls' acoustic features alone (Cäsar et al., 2012b).

Interestingly, these findings held even if we used playback stimuli of calls produced by conspecifics that were not part of the focal animals' family group. Nevertheless, we found preliminary evidence suggesting that listeners can discriminate between group members and non-group members (Cäsar et al., 2012b; Cäsar, unpublished data). In two separate trials, two adult males responded more quickly and strongly to B calls produced by group members than non-group members, suggesting that this call also conveys information about individual identity (Cäsar, unpublished data). Individuality can be important to recognise unreliable callers, especially if there is a tendency for individuals to use calls 'deceptively', as suggested for tufted capuchin monkeys experiencing feeding competition (Wheeler, 2009), or if some individuals call in response to innocuous stimuli (Hare and Atkins, 2001; Cheney and Seyfarth, 1988).

4.4 Reference in titi monkey alarm calls?

Our natural observations and experiments showed that the two main alarm calls produced by black-fronted titi monkeys, A and B calls, showed varying degrees of context-specificity. A calls were highly specific, elicited almost exclusively by raptors located in the canopy, while B calls were given to terrestrial predatory and non-predatory events (see Fig. 3 and Tables 3 and 4),

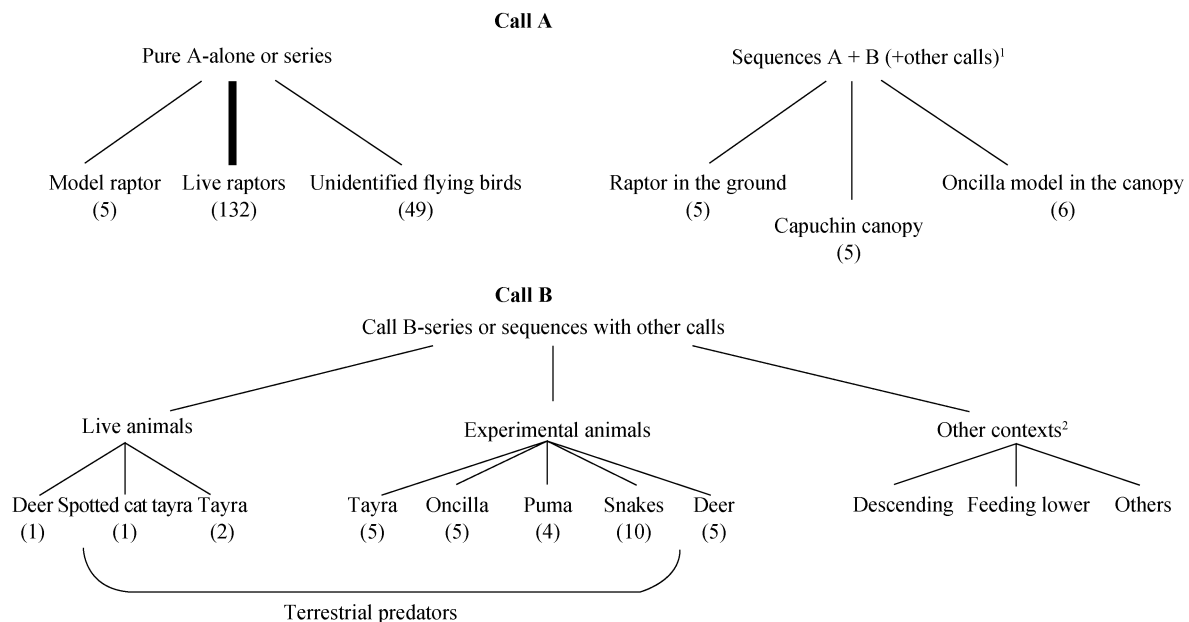


Fig. 3 The natural and experimental contexts in which Calls A, A+B and B occurred

The number of events for each context is presented in brackets. Lines represent all contexts in which the calls are produced, bold line represents the most common event recorded. ¹Number and order of calls were context specific (based on Cäsar et al., 2012; Cäsar 2011). ²Common non-predatory contexts in which call B is produced (not quantified); others include observer blocking monkeys passage and unhabituated groups in response to humans.

similar to what has been reported for other New World monkeys (Fichtel et al., 2005; Digweed et al., 2005; Kirchhof and Hammerschmidt, 2006), some Old World monkeys (Arnold and Zuberbühler, 2006a; Ouattara et al., 2009b) and some prosimians (Fichtel and Kappeler, 2002). In response to playbacks of series of A calls, 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, indicating 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 that normally elicited the calls. Also, given the impaired visibility within a tropical forest, the chances of a terrestrial disturbance being near the caller are very high, so that looking towards the caller is a good strategy to identify the cause of B calls. 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, usually on the ground, which first needs to be identified. In the case of A calls, there is evidence that the signal functions in a contextually narrower way, referring only to predators located within the canopy. In the case of B calls, results need to be interpreted more cautiously. There is some evidence for context-specific acoustic differences (Căsar, 2011), but it is currently unknown whether listeners perceive them. To B calls produced to predatory *oncillas* and *tayras*, the listeners' main response was to look towards the speaker, but it is still unclear how listeners react to B calls produced in non-predatory contexts. Interestingly, the titi monkeys' first response to disturbances on the ground was always the production of a B call, while the later parts of call sequences often contained additional call types.

Overall, the titi monkeys alarm calling behaviour reveals no fundamental difference from the patterns already reported in Old World monkeys. This type of predator-specific alarm calling behaviour, in other words, appears to be phylogenetically old, with an early origin within the primate lineage, although there is also evidence for an independent evolution of these features in several lineages (including birds: Gyger et al., 1987; suricates: Manser, 2001; and prairie dogs: Slobodchikoff et al., 1991). What is needed is research on acoustic variation within the different call types and how this affects the receivers' perception and assessment of a threat and on how receivers take context into account

when responding to an utterance. It is also interesting that comparable findings have not been reported in any of the great apes, suggesting that the behaviour either has been lost during evolution, possibly due to the relative protection afforded by large body size, or that the relevant studies have yet to be conducted. Great ape vocal behaviour is relatively understudied, a fact that currently prevents strong conclusions.

4.5 Meaningful call combinations?

A number of naturalistic observations suggested that the alarm calling behaviour in titi monkeys goes beyond producing predator-specific call types. For example, although call A was reliably given in response to raptors perched in the canopy, we also observed this call as part of sequences to predatory capuchin monkeys and other predators, provided they were located within the canopy (Căsar et al., 2012a; Fig. 3). One interpretation was that the calls did not signal predator type but something about the location of the threat, a pattern also found in chickens (Evans et al., 1993; Evans and Marler, 1995). However, a second experiment, designed to systematically test monkeys' responses to models of a terrestrial and aerial predator on the ground and within the canopy, showed 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. Both number and order of calls were context-specific. 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 (Căsar, 2011).

In addition to spatial information, the sequential composition of call types A and B was related to the predator type encountered, a fact that is difficult to reconcile with only arousal-based models of primate alarm calling discussed earlier. Although black-fronted titi monkeys use their call sequences to encode information about a predator type and its location, it is currently unknown whether acoustic variation within individual calls is indicative of differences in the perceived level of threat. More specific studies will be required to explore this possibility. So far, however, results suggest that A and B call series are meaningful to them (Căsar et al., 2012b), in ways that fulfilled the criteria of functionally referential signals (Macedonia and Evans, 1993).

Overall, our results suggest that titi monkey call sequences follow a simple syntax, with both lexical and phonological features (*sensu* Marler, 1977). Both A and B calls can be given alone, but only A appears to have

its own independent meaning, when given alone (see Fig. 3). In contrast, when given as part of a sequence, A appears to refer to location. Despite the apparently lower context specificity of call B, it may be that listeners invariably perceive this as evidence for the presence of a terrestrial predator. Thus, individual calls and sequences appear to have their own individual meanings but obtain additional meanings when combined into other sequences.

Although there has been evidence in other primate species for syntactically organised call sequences (e.g. Robinson, 1979, 1984; Zuberbühler, 2002; Arnold and Zuberbühler, 2006a, b; Clarke et al., 2006; Schel et al., 2010), the recent findings in black-fronted titi monkeys go beyond the current theory by suggesting that sequences refer to various aspects of the environment simultaneously, that is, predator type and location. Similar claims have been made for Diana monkey alarm calls (Zuberbühler, 2000d), due to indications that some locational information is incorporated in these calls. Similarly, Schel et al. (2010), working with Guereza colobus monkeys, suggested that ‘snort’ calls preceding roaring sequences indicate that the event was taking place on the ground, suggesting that alarm call systems capable of incorporating spatial information may be more common than currently thought.

It is tempting to assume that meaningful sequential vocal behaviour is indicative of complex underlying cognitive abilities, but this hypothesis needs to be addressed by future research. At the same time, such findings have some implication for understanding the evolutionary pathways to human language but the details will eventually have to be specified (e.g. Lieberman, 2001; Gil da Costa et al., 2006). To this end, further research will be required to describe the full range of realised call combinations and their contextual meanings.

5 Conclusions

New World monkeys have been less well researched in terms of the production patterns and context-specificity of their alarm calls. Judging from the available evidence, however, it seems safe to conclude that these primates also possess specific alarm calls to raptors and terrestrial disturbances, suggesting that this is an ancestral feature in the primate lineage (Fichtel et al., 2005; Digweed et al., 2005; Kirchhof and Hammerschmidt, 2006; Wheeler, 2010; Cäsar et al., 2012a). Our recent observational and experimental studies with black-fronted titi monkeys further indicate that the communicative functions and meanings are not conveyed by sin-

gle calls but by sequences of call types, as is evident from the fact that alarm calls convey information about predator class and location (Cäsar et al., 2012a; Cäsar 2011). The acoustic features of the individual component calls differ from each other, which suggested that individual calls served as the main semantic vehicles of this combinatorial communication system. The black-fronted titi monkeys’ vocal system thus provides another example of zoo-syntax, in which acoustically fixed units are combined into higher order sequences that are meaningful to recipients. In addition, the system is functionally referential, by referring to different predator classes and their location (Cäsar et al., 2012b). Although the existing literature is biased towards studies of Old World monkeys, our recent studies with black-fronted titi monkeys indicate that functionally referential and combinatorial properties evolved in primate communication long before the advent of language.

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