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Pitheciid vocal communication: what can we say about what they are saying?

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ABSTRACT

The variation in ecological traits in pitheciids allow investigation of vocal communication across a range of social and acoustic circumstances. In this review, we present a summary of the history of pitheciid vocal studies, and review i) the status of current knowledge of pitheciid vocal repertoire sizes, ii) how much we understand about the context of different acoustic signals, and iii) how can we potentially use our knowledge of vocalizations in animal welfare practices. The repertoires described for titi monkeys and sakis have the expected sizes for these genera, considering their relatively small social group sizes. However, uacari groups can contain over 100 individuals, and a larger vocal repertoire than the ones described would be expected, which could be a consequence of the fission-fusion social system where the large group divides into smaller subgroups. Nevertheless, vocal repertoires exist for only about 12% of the pitheciid species and nothing is known, for example, concerning call ontogeny. We hope that this study will act as a reference point for researchers interested in investigating vocal behaviour in pitheciids, thus, optimising both funding focus and, researcher's time and effort. Also, we hope to help defining methodologies and strategies for the conservation and management of pitheciid monkeys.

Keywords: Vocal Repertoires; Meaning Attributed Calls; Alarm Calls; Conservation Methods; Playback Survey; Welfare Practices.

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INTRODUCTION

For animals living in densely vegetated habitats, the use of vocal communication has advantages as vocal signals can propagate over longer distances than visual signals. Thus, vocalizations in such habitats can optimize communication, balancing costs and benefits to both sender and receiver. Several information elements can be encoded in a single acoustic signal, ranging from species to body size, caller distance, gender, age, predation threats and the animal's inner state (Bradbury and Verrencamp 2011; Ey and Ficher et al. 2009; Wheeler and Fischer 2015).

It has been suggested that information encoded in vocalizations can help to maintain group structure, cohesion and survival, and may reveal patterns in habitat use and social organization between primate species (e.g. Brown and Waser 1988; Fitchel and Manser 2010; Maciej et al. 2013; Fischer and Price 2016). Since vocal communication is a biological process and requires adaptations from both caller and receiver, evolution had played a key role in structuring of the currently operating forms (Bradbury and Verrencamp 2011; Kroodsma and Miller 1996). Furthermore, vocal communication strongly shapes animal behaviours, influencing anti-predation strategies, mating and even such food gathering systems as cooperative foraging (Ey and Ficher et al. 2009; Semple and Higham 2013).

All living Pitheciidae are social and arboreal. The family comprises the subfamilies Callicebinae, where the titi monkey genus, *Callicebus*, was recently split into the genera *Callicebus*, *Cheracebus*, and *Plecturocebus* species [Byrne et al. 2016]), and the Pitheciinae (*Pithecia, Chiropotes* and *Cacajao*) (Groves 2001; 2005). There are currently 34 titi monkeys species, 16 *Pithecia* species (sakis), five *Chiropotes* species (cuxius) and six *Cacajao* taxa (uacaris) described (Byrne et al. 2016; Vermeer and Tello-Alvararado 2015, Marsh 2014; Dalponte et al. 2014; Silva-Junior et al. 2013). Pitheciids show considerable variation in social traits and range sizes – for example, while all titi monkeys and many sakis form small groups in small territories, groups of uacaris and cuxius in some areas can be very large and range over extensive areas (Barnett et al. 2005; Bowler et al. 2012; Defler 2003; Dixson and Anderson 2001; Fontaine 1981; Norconk 2006, 2007; Pinto 2008; Silva and Ferrari 2009; Souza-Alves and Ferrari 2010; Veiga 2006). This variation in social traits and range sizes in pitheciids allows investigations of the vocal communication in this primate family that cover a wide range of social and acoustic circumstances. The use of vocalizations for communication is important for pitheciid primates due to the restricted visibility of their structurally complex and dense natural habitats (Bezerra et al. 2011a,b).

Here we present a history of pitheciid vocal studies, and consider the following questions: 1) What is the current state of knowledge of the vocal repertoire sizes of pitheciid primates? 2) How much do we understand about the context and functional significance of different signals? and 3) How can we use the current knowledge to animal welfare, especially for captive animals? The answers provided are based on a review of the literature that aims to synthesize published information on the vocal communication of pitheciids. In our online literature search, we used the terms “(genus) bioacoustics”, “(genus) vocal communication”, “pitheciid communication”, “(genus) vocal repertoires”, “(genus) calls”, “(genus) vocalization” to search for

information on acoustic communication in pitheciids. These terms could be either in the tittle or main of text of the study. To our knowledge no papers on titi monkey vocalizations have yet published using the new nomenclature of Byrne et al. (2016), but for convenience we will use the phrase "titi monkeys" when referring to *Callicebus*, *Cheracebus* and *Plecturocebus* collectively in this paper. Also, for convenience, we will be referring to *Cacajao* as "uacaris", *Pithecia* as "sakis", and *Chiropotes* as "cuxius". We searched the following databases: Google Scholar, Web of Science, PrimatLit, PubMed and Periódicos CAPES. We also considered books that are not available online and articles that were not available in electronic format. In the Google Scholar database, all articles included in the first 20 Google pages (up to 200) were inspected for information on pitheciid acoustic communication. We included only studies that focused on pitheciids, and excluded those that only mentioned any of the pitheciid species as part of their discussion or introduction. In the current review, we only focused on vocal communication and excluded non-vocal acoustic signals, such as noises made by shaking or breaking branches. We hope this study will serve as a reference for researchers aiming to identify gaps in the knowledge of vocal behaviour in this primate group and define effective methodologies (e.g. playback and automated call surveys in isolated areas) and strategies for the conservation (e.g. Sobroza et al. 2017) of pitheciid monkeys. Many pitheciid species face threats to their survival (IUCN 2017). However, studies on both threatened and non-threatened species are needed to help prevent the latter also attaining threatened status. For both threatened and non-threatened pitheciid species, focusing research on knowledge gaps may help optimize funding, researchers' effort and time, and contribute most effectively to the conservation of these primates.

Note: the text follows Ferrari et al. (2014) in using *Cacajao ouakary* for black-headed taxa south and west of the Rio Negro and *Cacajao melanocephalus* for those to the north and east of this river. We also follow Silva-Junior et al. (2013), Marsh (2014) and Byrne et al. (2016) for the taxonomy of cuxius, sakis and titi monkeys, respectively.

What is the current knowledge of the vocal repertoires sizes of pitheciid primates?

A total of 78 studies were related to vocal communication in the genera titi, sakis, cuxius and uacaris (Electronic Supplementary Material 1). Researchers have encountered a variety of difficulties when investigating pitheciids in the wild, many related to the challenging nature of their natural habitats, expensive fieldwork logistics, and an often protracted habituation process (e.g. Souza-Alves and Ferrari 2010; Pinto et al. 2013). Despite these issues, there have been significant advances in our knowledge of these monkeys in recent years (e.g. Veiga et al. 2013; Barnet et al. 2016). The studies on pitheciid vocal communication began in the 1960's with titi monkeys, but most studies have been conducted in the last two decades. Over this period, equipment became steadily more portable and efficient, making it easier to conduct recordings of wild primates (Bezerra et al. 2011a,b).

The size of the vocal repertoire varies from 9-12 call types in uacari species (*C. ouakary*: Bezerra et al. 2010a; *C. calvus*: Fontaine 1981), 12-13 call types in saki species (vocal repertoires described for *P. pithecia*: Buchanan et al. 1981; Henline

2007; and *P. irrorata*: Adams and Erhart 2009) and 6-13 call types in titi monkey species (vocal repertoires described for three species: *Plecturocebus moloch* (formerly *Callicebus moloch*: Moynihan 1966; Robinson 1979; *Cheracebus torquatus* (formerly *Callicebus torquatus*): Kinzey et al. 1977; *Callicebus nigrifrons*: Cäsar 2011; Cäsar et al. 2012a). There are no quantitative analyses of full vocal repertoires of cuxius, though van Roosmalen et al. (1981) provide onomatopoeic descriptions of three calls for *Chiropotes satanas*. In total some 12% of pitheciid taxa have had their vocal repertoires described.

How much do we understand about the context of different signals?

Call features

Call structure (e.g., duration and frequency) can often reveal information about the caller (Bradbury and Vehrencamp 2011). This is true in pitheciines: in uacari species, for example, such structure provide clues about the behavioural context and identity of the caller (Fontaine 1981; Bezerra et al. 2010a,b). For *Cacajao ouakary*, the structure of the tchó call (Figure 1) varies between individuals, indicating a potential for individual identification and monitoring in the wild (Bezerra et al. 2010a). Additionally, the structure of this call varied according to the behavioural context under which it was produced (i.e. foraging, traveling or agonistic interactions). When uttered in agonistic situations, tchó calls were on average shorter in duration and had higher frequencies than when emitted under foraging and travelling contexts (Bezerra et al. 2010b). It should be harder to locate a caller when it emits shorter calls than when it produces longer calls (Skowronski and Fenton 2009), as short high pitch signals are more easily dispersed in closed habitats when compared to longer lower pitch signals (Ey and Fischer 2009). Thus, in such circumstances, *C. ouakary* could be trying to avoid being located and engage in costly agonistic physical contacts, but still transmit information, by emitting shorter and higher pitch tchó calls in agonistic contexts. In terms of fighting strategy models (Bradbury and Vehrencamp 2011), this could be a tactic to help in conflict resolution with the lowest possible risk to the signaller. Predator avoidance is also a possibility as the species is known to be taken by harpy eagles (Barnett et al. 2011), a species known to use auditory as well as visual cues when locating prey (Gil-da-Costa 2007). Differences in call structure associated to different behavioural contexts could also be due to variations in the animal's inner state (Hewson 2004; Linhart et al. 2015). There is some evidence that tchó calls may be adapted for effective propagation in flooded forests, suggesting that the call could be related to group/territorial defence (Bezerra et al. 2010b; 2012). Similarly, some saki calls may be involved in both territorial defence and in providing information on a signaller's location (e.g. Di Fiore et al. 2007; Fernandez-Duque et al. 2013). Further studies are required to ascertain the meaning of the uacari and saki calls based on their structure and the signal receiver's perspective.

Call contexts

Saki species have, at least, three loud calls that could possibly be related to group coordination and defence of resources (Henline 2007). Uacari species have context- and age-specific calls as well as calls uttered in a range of different

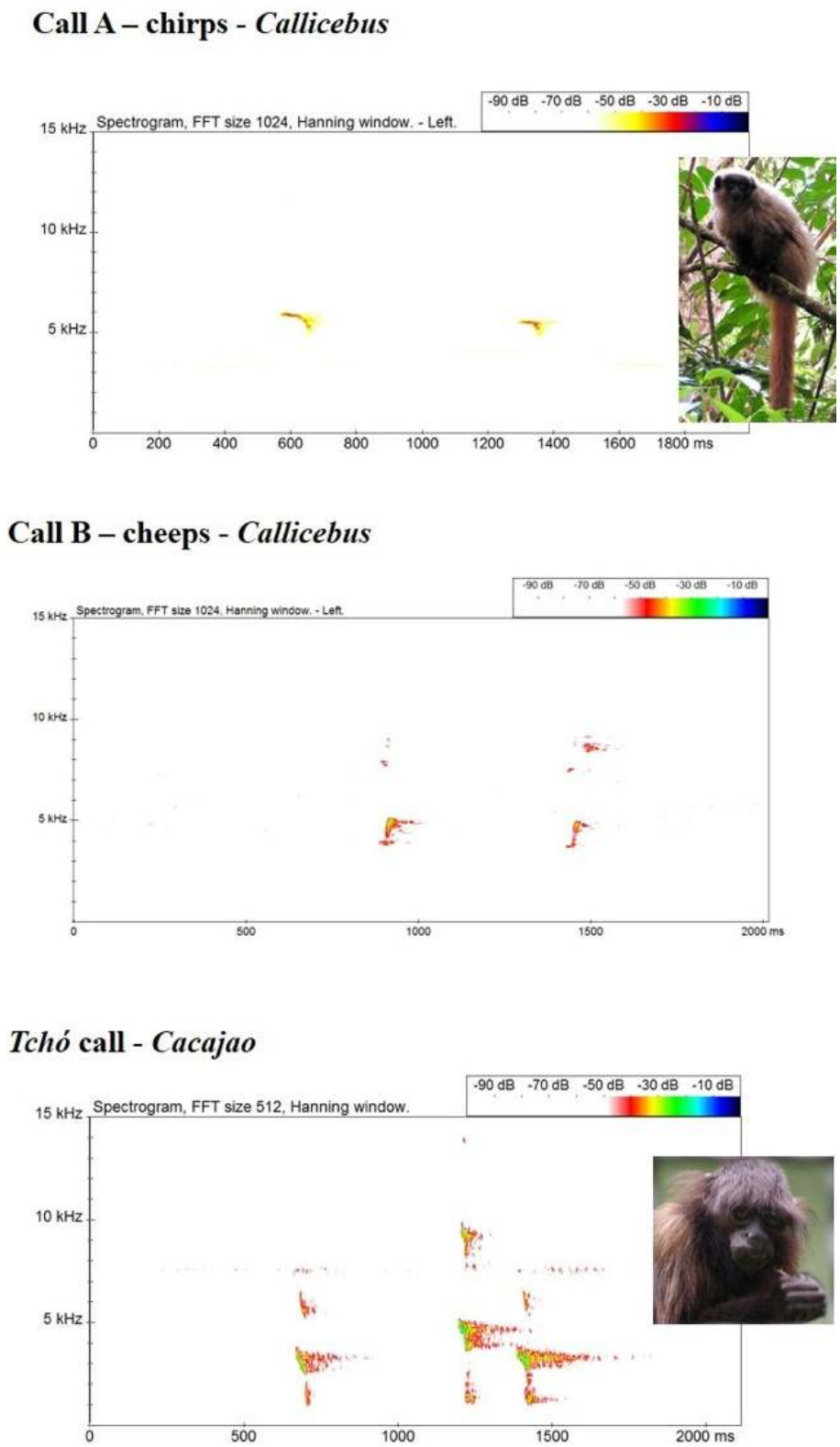

Figure 1. Spectrograms showing titi monkey and uacari calls. Call A - chirp: *Callicebus nigrifrons* alarm calls to raptors; Call B - cheeps: *titi monkey* alarm calls to terrestrial (*titi monkey* calls described in Cäsar et al. 2012a); Tchó call (also known as bi koh: e.g. Barnett 2010): *Cacajao ouakary* alarm call sequence (*Cacajao* call described in Bezerra et al. 2010a). The *Cacajao tchó* call is also used in other contexts and its physical structure changes slightly according to the context. Photos: titi monkey - Cäsar C.; uakary monkey - Bezerra B. Spectrograms made using Batsound 3.1.

behavioural contexts (Fontaine *1*981; Bezerra et al. 2010a). Titi monkeys are reported to engage in duet calling (i.e., call sequences emitted by male and female pair-mates), which may function in resource and territorial defence (e.g. Caselli et al. 2014; Müller and Anzenberger 2002; Robinson 1981). Several calls described for titi monkeys are linked to predation risk, perhaps reflecting the high overall level of predation risk for the genus (e.g. Cisneros-Heredia et al. 2005; de Luna et al. 2010; Sampaio and Ferrari 2005; Electronic supplementary material 1).

Titi monkeys are known among primatologists for their apparently meaningful alarm calling (e.g. Cäsar and Zuberbuhler 2012; Cäsar et al. 2012a). Meaning-attributed signals transmit information about the events or objects of the environment considering the signal receiver's perspective/behavioural response (Wheeler and Fitcher 2015). Besides being produced in context-specific ways, these signals must elicit specific adaptive responses in listeners (e.g. Wheeler and Fitcher 2015). Titi monkeys produce three alarm call types in response to their main predators. Chirps (call A) are daily given in response to different raptors species; while cheeps (call B) are usually given in response to terrestrial predators. Playbacks of these two calls indicate that each elicits appropriate anti-predator behaviours (Cäsar et al. 2012b). The third call type, *squeak* (call C), is not very specific; it is usually given when there is some intention to move (Cäsar et al. 2012a), but it is unknown if this call elicits a predator-specific response. These calls are produced both singly and at the beginning of different alarm call sequences (Cäsar et al. 2012a; 2013). Other call types, typically loud and conspicuous, are also produced later in titi monkeys alarm calling sequences, especially in response to terrestrial predators (Cäsar and Zuberbühler 2012). However, the function and meaning of some of these calls and respective sequences has still to be tested. It is important to point out that studies made by Cäsar and collaborators focused on one titi monkey species in a fairly well-preserved area (i.e. relatively low anthropogenic pressure). Thus, further studies would be necessary on other titi species living in preserved and disturbed habitats to add to our understanding of how fragment size and structure, predator presence and absence, predator type and anthropogenic pressures, might influence the vocalizations produced by titi monkeys in general.

Alarm calls have also been reported for the other pitheciid genera (e.g., cuxius: Barnett el al. 2017, Martins et al. 2005; Silva and Ferrari 2009; van Roosmalen et al. 1981; sakis: Henline 2007; Rettig 1978; uacari: Barnett et al. 2011; Bezerra et al. 2010a,b; Fontaine 1981). However, no further studies have been conducted to verify the meaning attributed to these signals. Overall, most primates vocalize when threatened by a predator, and the study of these alarm signals has proved particularly valuable for examining the cognitive processes in non-human animals (Zuberbühler *2*006). As shown above for titi monkeys, there is evidence that pitheciids possess a complex alarm calling system. To attain greater understanding of the evolutionary aspects behind the variety and form of communication signals in this family, further focused studies are required.

Food/feeding associated calls have been reported for cuxius (van Roosmalen et al. 1981), uacaris (Barnett *2*010; Bezerra et al. 2010a) and titi monkeys (Cäsar and Zuberbühler *2*012). Further experimentation needs to be conducted to investigate, among

other considerations, whether these calls function to attract conspecifics to the food source (e.g. Di Bitetti *2*003; Dittus *1*984), or to announce food ownership and thus avoid conflicts between group members (e.g. Gros-Louis *2*004).

Call combinations

The use of combinations of calls has been observed in uacaris and titi monkeys (Bezerra et al. 2010b; Cäsar et al. 2012a; Robinson 1979), and there is recent strong evidence that call sequence may be meaningful (*Callicebus nigrifrons*: Cäsar et al. 2012b *2*013). Here, individuals produce uniquely composed alarm call sequences, consisting of two main call types, call A and B (Cäsar et al. 2013, Figure 2). These calls convey both information about the location and type of predator within the same utterance (Cäsar et al. 2013). In response to a feline predator, the locational information is conveyed by the first call of each sequence, while in responses to predatory raptors, the locational response is conveyed by the later parts of the sequence (Cäsar et al. 2013). Some of these sequences are meaningful to others, as conspecifics respond in specific ways, even in the absence of the referent - in this case a predator (Cäsar et al. 2012b).

Call playbacks

Playback has proven successful in eliciting vocal responses in sakis (Di Fiore et al. 2007; Fernandez-Duque et al. 2013), uacaris and titi monkeys (e.g. Cäsar, unpublished data; Chagas and Ferrari *2*010; Dacier et al. 2011; Jerusalinsky *2*013; Marques et al. 2013; Melo and Mendes *2*000, Printes et al. 2011; Souza-Alves and Ferrari *2*010). *Cacajao ouakary* responded more strongly to calls from neighbouring groups than from its own group (Bezerra et al. 2010b). This suggests that a certain level of territorial defence does exist for the species, despite the low levels of agonistic interactions observed (i.e. less than 1% of their activity budget Barnett 2010; Bezerra 2010; Bezerra et al. 2011a,b), and the large inter-individual distances and extensive daily ranges recorded (Barnett *2*010; Barnett and Shaw *2*014; Bezerra *2*010; Bezerra et al. 2011). In *Pithecia aequatorialis*, playback experiments provided preliminary evidence that males respond more strongly to a potential intruder than do females (Di Fiore et al. 2007; Fernandez-Duque et al. 2013), suggesting that male *P. aequatorialis* may have a role in group defence. The calls could possibly be used to avoid costly agonistic interactions in both uacaris and sakis. As shown above, call playback in titi monkey species has revealed the potential function and meaning of their alarm calls (Cäsar et al. 2013).

Call playback has already been used successfully for distribution surveys of several titi monkey species, including *Callicebus coimbrai* (Aldrich et al. 2008; Chagas and Ferrari *2*010; Jerusalinsky *2*013; Jerusalinsky et al. 2006; Souza-Alves and Ferrari *2*010), *Plecturocebus discolor* (formerly *Callicebus discolor*) (Dacier et al. 2011), *Callicebus barbarabrownae* (Marques et al. 2013; Printes et al. 2011), *Plecturocebus modestus* (formerly *Callicebus modestus*) (Martinez and Wallace *2*016), *Callicebus nigrifrons* (Gestich et al. 2017), and *Plecturocebus olallae* (formerly *Callicebus olallae*) (Martinez and Wallace *2*016). In all cases, the technique was found to increase the likelihood of encountering the target animals. For example, in a comprehensive study of the geographic distribution of *C. coimbrai*, over 71% of reports (in 49 forest fragments of varying

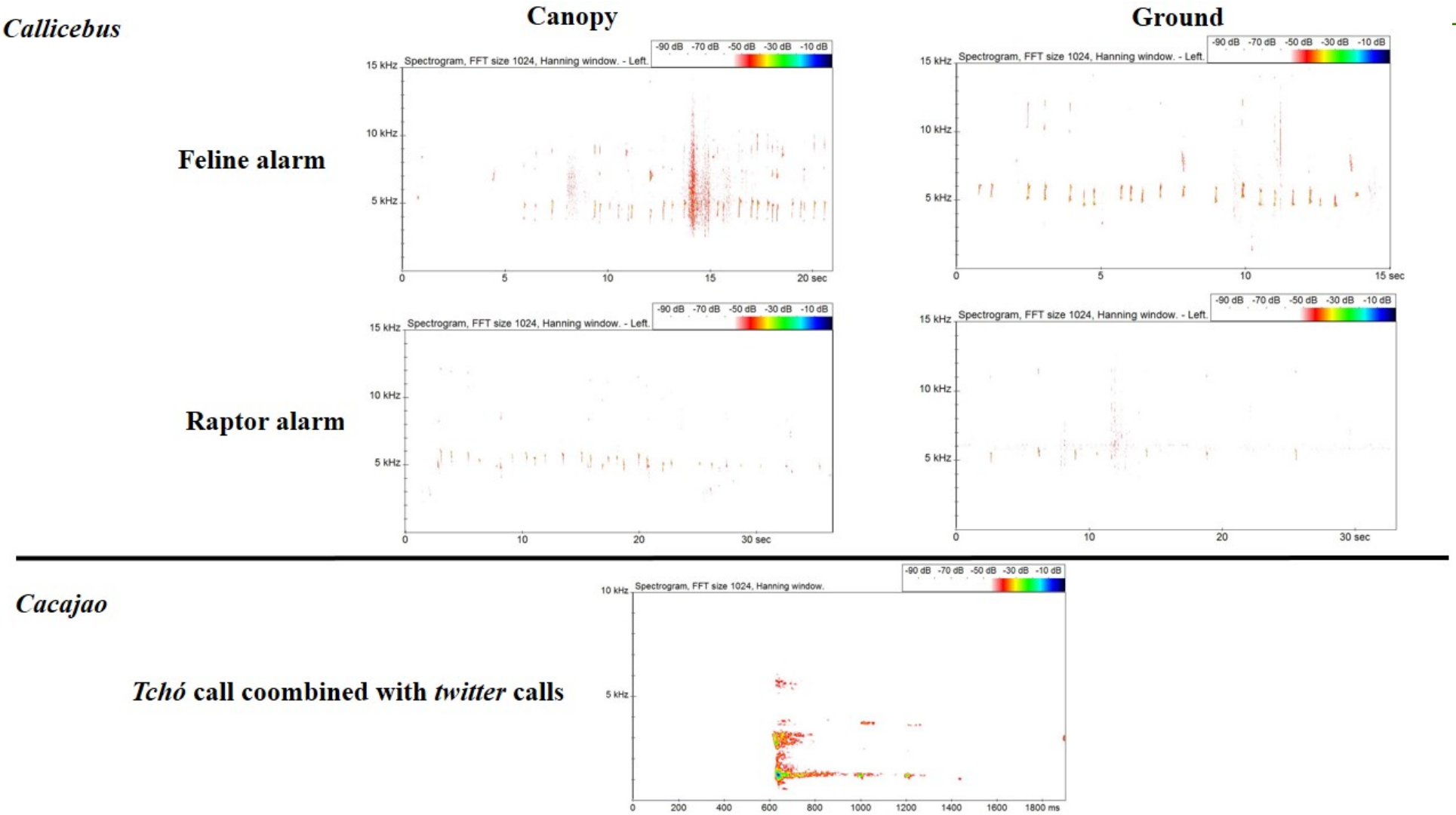

Figure 2. Call combinations in titi monkey and *Cacajao*. Top: spectrograms showing meaningful call sequences of *Callicebus nigrifrons* (call sequences described in Cäsar et al. 2013). The interval between the calls of the sequence changes according to the type and the position of the predator. Bottom: call combination from *Cacajao ouakary* (call combination described in Bezerra et al. 2010a). Further studies are still needed to confirm the meaning of *Cacajao* call combinations.

size) resulted from the detection of spontaneous vocalizations and vocal responses to call playbacks by this and other titi monkey species (Jerusalinsky *2*013). This study used territorial duet calls from *Callicebus personatus* and obtained responses from *C. coimbrai* and *C. barbarabrownae*, showing that congeneric call playbacks can be also effective for species surveys. These species are very closely related and were once considered to be a single species (see Byrne et al. 2016 for a summary of past taxonomic arrangements).

How can we use the current knowledge for animal welfare?

Since calls can be used as indicators of behavioural patterns (e.g. Bezerra et al. 2010a; Caselli et al. 2014; Henline 2007), and appear useful for monitoring social communication and dynamics (McCowan and Rommeck *2*006), vocalizations could potentially be integrated into standard animal welfare assessment for some pitheciid species. By comparing the similarities of the vocal repertoires of captive populations with those used by wild conspecifics, zookeepers and laboratory managers could provide the necessary stimuli to expand the vocal repertoire (and perhaps enrich the environment) of captive animals. This could be made possible for *Cacajao ouakary* (Bezerra et al. 2010a), *Pithecia irrorata* (Adams and Erhart 2009), *Pithecia pithecia* (Henline 2007), and some titi monkeys (Electronic Supplementary Material 1). The study and description of vocal repertoires of wild pitheciids for this purpose should be encouraged.

It is not only the expansion of the vocal repertoire in captive animals which should be used in animal welfare practices, however, as we should also consider monitoring specific calls. In captive capuchin monkeys, for instance, the frequent use of terrestrial predator alarms seems to be associated with higher levels of stress hormones and poorly enriched environments (Jacobsen et al. 2010). Monitoring alarm calls in captive pitheciids could be an interesting initial study. Such calls could be easily quantified for titi monkey species due to their well-defined and evident alarm calls (Cäsar et al. 2012b *2*013, Fig 2). In uacari species, the lack of evident described predator-specific alarm calls (Mourtè and Barnett *2*014) would make it harder for such quantifications. Nevertheless, they have multi-context calls that present subtle variations in agonistic/alarming situations (i.e. the tchó call), becoming shorter and higher pitched (Bezerra et al. 2010a). Thus, considering the structure of multi-context calls in pitheciids would be an alternative route to monitor alarming situations. The latter would require non-invasive passive recorders and automated analyses software such as that produced by Wildlife Acoustics Inc. (http://www.wildlifeacoustics.com). Such arrays could be potential tools for such a monitoring system in captive settings.

Trends in Pitheciidae vocal communication studies

Research on pitheciid vocalizations has revealed information on repertoire size, call structure, context and propagation, as well as meaning-attributed signals. Although there are difficulties when investigating pitheciid vocal communication in the wild, the increasing number of publications indicates an expanding interest and effort by researchers to investigate these elusive and highly threatened primates. As might be expected from the relatively widespread

geographic distribution and large number of titi monkey species (Silva Júnior et al. 2013; see, however, Marsh 2014 for number of saki species), approximately 64% of the tallied studies focused on these primates (Electronic Supplementary Material 1). Titi monkey populations are distributed throughout the Amazon area, as well as northeast and southeast Brazil (Silva Junior et al. 2013). Reasonable road networks in the non-Amazonian areas of Brazil facilitate access to many titi monkey populations and field sites. This situation contrasts with uacari, cuxius and sakis populations, which are concentrated in the highly inaccessible Amazon basin, where poor infrastructure means there is usually a need for boat expeditions to locate study populations, resulting in greater logistic and financial challenges (Pinto et al. 2013).

Despite the advances in the knowledge of pitheciid vocal communication, information on the majority of the species is still lacking. For instance, we have vocal repertoires for only about 12% of the 61 pitheciid species, and most of the knowledge currently available on meaning of calls (i.e. context-specific signals that provoke a response that is context independent - Wheeler and Fitcher 2015) comes from titi species. Future efforts should also investigate vocalizations of other members of the pitheciid clade. Studies of captive animals could also add to our understanding of vocal communication in this group. Despite the limitations posed by studies of captive animals (e.g. confined, often-unnatural conditions), captive studies provide logistically viable approaches to studying the vocal behaviour of animals that are challenging to study in the wild. For uacaris and sakis particularly, studies of semi-captive animals would be extremely valuable in this context, as they could provide larger group sizes (or at least natural sub-group sizes) from which to obtain a valid range of the call types emitted by these monkeys.

The vocal repertoires described for titi monkeys and sakis have the expected sizes for these genera, considering their relatively small social group sizes (McComb and Semple *2*005). However, uacari groups can contain over 100 individuals (Barnett 2010; Barnett et al. 2005; Bowler et al. 2012; Defler 2003), and a larger vocal repertoire would then be expected given that, in primate lineages, vocal repertoire size generally increases with increasing group size (McComb and Semple 2005). Also, vocal repertoire size in non-human primates seems to be directly related social bonding reflected in time dedicated to grooming in their activity budget (McComb and Semple *2*005). The three groups of *C. ouakary* investigated by Bezerra et al. (2011) showed a fission-fusion social system. The "subgroups" observed in this study were relatively small (maximum counts were: 5, 15, and 26 individuals) when compared to full group sizes previously reported for uacaris (including uacari groups inhabiting the same study site – Barnett *2*010; Barnett et al. 2005). For pitheciid primates with a fission-fusion social system, it seems that it is not the full group size, but the subgroup size and structure (the latter based on Kappeler and van Schaik *2*002) that is likely to drive vocal repertoire size. This would be in line with the theory of a social-vocal coevolution of communicative abilities proposed for primate species by Bouchet et al. (2013). Also, very little time appears to be dedicated to social grooming by the groups of *C. ouakary* investigated by Bezerra and collaborators (i.e., ~1% of their activity budget, Barnett *2*010, Bezerra et al *2*011), and this may play a role in the relatively small vocal repertoire size. The trend "group

size directly related to small vocal repertoire" can be observed in pitheciids if we consider the few studies that attempted full repertoire descriptions. Nevertheless, an increase in studies of pitheciid vocal behaviour should allow a better understanding of their vocal abilities and how evolution has shaped their social structure, behaviour and communication. Investigation of social calls between individuals as they groom and mate, between mother and offspring, or between offspring as they play, would also be interesting topics for investigation. Studies on such calls are known in several primate species (Arbid et al. 2008), but are still lacking in pitheciids. Such studies could provide not only context-specific information about the calls, but also insights into call ontogeny in pitheciids.

While the number of call types certainly contributes to vocal complexity, it is not only factor involved (Bouchet et al. 2013; Kershenbaum *2*014; Krams et al. 2012). Call combination, for instance, may also play a big role in this. The combination of calls (which individually can themselves have defined meanings) into meaningful sequences increases the variety of messages that can be generated (e.g. Arnold and Zuberbühler *2*006; Cleveland and Snowdon *1*982; Marler et al. 1992; Mitani and Marler *1*989; Robinson *1*984; Robinson *1*979; Zuberbühler *2*002). The production of meaningful call sequences has been reported in *Callicebus nigrifrons* (Cäsar et al. 2012b *2*013), in other New World monkeys including cotton-top tamarin (e.g., *Saguinus oedipus*: Cleveland and Snowdon *1*982), and weeper capuchins (*Cebus olivaceus*: Robinson *1*984), and in Old World primates, including putty-nosed monkeys *(Cercopithecus nictitans*: Arnold and Zuberbühler *2*006), Diana monkeys (*Cercopithecus diana*: Candiotti et al. 2012; Zuberbühler *2*002), Campbell's monkeys (*Cercopithecus campbelli* campbelli: Ouattara et al. 2009), guereza colobus (*Colobus guereza*; Schel and Zuberbühler *2*012), white-handed gibbons (*Hylobates lar*; Clarke et al. 2006), and chimpanzees (*Pan troglodytes*: Crockford and Boesch *2*005; and *P. paniscus*: Clay and Zuberbühler *2*009).

Evidence of meaningful acoustic signals in pitheciid primates has come from *Callicebus nigrifrons* alarm calls (Cäsar et al. 2012b*, 2*013). These signals have been observed in several other non-human primates in a variety of contexts, including food-associated calls (chimpanzees, *Pan troglodytes*; Slocombe and Zuberbühler *2*005 and tufted capuchin monkeys, *Sapajus apella nigritus*; Di Bitetti *2*003), social screams (rhesus macaques, *Macaca mulatta*; Gouzoules et al. 1984), and various studies on predator-specific alarm calls (e.g. vervet monkeys, *Chlorocebus aethiops*, Seyfarth et al. 1980; Diana monkeys, *Cercopithecus diana*, Zuberbühler et al. 1997; Campbell's monkeys, *Cercopithecus campbelli*, Zuberbühler *2*001; moustached tamarins, *Saguinus mystax*, Kirchhof and Hammerschmidt *2*006; tufted capuchin monkeys, *Sapajus apella nigritus*, Wheeler *2*010).

Call playback is not only useful to investigate meaning of pitheciid calls, but also to conduct distribution surveys, which are extremely important for conservation of field sites and the species that inhabit them. Given that primate calls are generally species-specific and readily assignable to the vocalizing species (Bradbury and Vehrencamp *2*011), they can be used in field surveys both by recording and identifying vocalizations, and also via monitoring responses to call playbacks that assist with attracting or locating animals and estimating

population abundance (e.g. Bezerra et al. 2010b; Gestich et al. 2016; Plumptre et al. 2013; Chagas and Ferrari *2*010). Even though playback of calls from congeneric species may elicit a vocal response in pitheciid primates (Jerusalinsky *2*013), recording of acoustic responses and analysis of their physical structure may help assigning calls to species. Pitheciid monkeys have shown marked vocal responses to call playbacks, thus, we believe this technique should be considered for field use whenever rapid assessments of a species' presence are needed, but visual contact is difficult to obtain and maintain. A standard call playback survey protocol should be adopted, so that comparative information can be obtained from simple field-site assessments. The 'lure counts' method as described in Plumptre et al. (2013), where by the researcher actively attracts the animals by doing call playbacks and estimate animal distances to sound source by using a detection function model previously established, could be used as a standard protocol.

CONCLUSIONS

In summary, the information available on the vocal communication systems of pitheciid species is still very limited, and is reduced even further when the recent taxonomic revisions of sakis (Marsh 2014) and titi monkeys (Byrne et al. 2016) are considered. Basic information on vocal repertoires and acoustic communication are still lacking for most pitheciid species (Bezerra et al. 2013). This lack of information is a major obstacle to testing proposals concerning the evolution of pitheciid communication, and for potentially locating threatened species in habitats in which they are difficult to detect visually. Existing data on pitheciid vocal repertoires could be used for immediate conservation and welfare practices. Vocalizations can, potentially, represent a rapid, simple and non-invasive method of assessing the level of stress/wellbeing of the animals via the identification and monitoring of stress-associated calls. Three mains ways could be explored in pitheciids to promote welfare in captive animals: 1) the use of environmental enrichment to expand the vocal repertoire, providing the necessary behavioural stimuli for such expansion; 2) monitoring of specific calls, such as alarm-related signals, that may indicate stress and poorly enriched enclosures, and 3) monitoring of multi-context calls structure which may also indicate stress-related situations.

Advances would doubtless be made if researchers were to share high quality sound files of pitheciid vocalizations. This would facilitate species identification and consequently call playbacks could be more widely used to aid locating pitheciid species in the wild. The creation of an internet-based, freely available pitheciid vocal library would be ideal for that purpose. It should include high quality non-compressed sound files (i.e., WAV format) covering a wide range of specified behavioural contexts representative of as many pitheciid species and individuals as possible. Such sound library could be available, for example, at the Pitheciine Action Group (PAG) website. We will attempt the creation of such sound library and hope to launch it on PAG website in early 2018. Also, an alternative route would be to integrate our pitheciid sound library to an existing one such as the Macaulay Library (http://macaulaylibrary.org) and the Primate Information Network (http://pin.primate.wisc.edu).

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Electronic supplementary material 1 - List of studies related to vocal communication in Pitheciids.

Cacajao studies

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