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The function of male and female long-distance vocalizations in three mammalian taxa

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Juli 21, 2014

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Abstract

Recent research has demonstrated that female birdsong is present in the majority of songbird species worldwide. In addition, the results indicated that female birdsong was already present in the common ancestor of modern songbirds. These results are rather unexpected as it was generally believed that birdsong has evolved especially in male songbirds by ways of sexual selection. Similarly to research on birdsong, research on long-distance vocalizations in mammals often focuses on males. However, within many mammalian species these vocalizations are used by females as well. This study provides an overview of the production of long-distance vocalizations by males and females in three mammalian taxa: simian primates (*Simiiformes*), ungulates (*Perissodactyla* and *Cetartiodactyla*) and bats (*Chiroptera*). Additionally, an attempt was made to determine the function of these long-distance vocalizations. Five functional hypotheses of long-distance vocalizations have been proposed: 1) defence hypothesis; 2) alarm hypothesis; 3) spatial coherence hypothesis; 4) intragroup competition hypothesis and 5) finding a mate hypothesis. Data on long-distance vocalizations in the three mammalian taxa were gathered from literature. Factors indicative for a call's function, like call stimulus, consequence, and characteristics of the signaller, were included in the data acquisition. The results reveal that long-distance vocalizations were present in 63 species of simians, 26 species of ungulates and eight species of bats. These vocalizations were most often produced by individuals of both sexes within a species or exclusively by males. Females rarely produced long-distance vocalizations when males within the same species did not. All proposed functions were found in at least one of the researched taxa. The fact that long-distance vocalizations are present in both males and females and that these vocalizations serve distinct functions, suggests that long-distance vocalizations have evolved under different environmental and social conditions. Above all, similarly to birdsong, long-distance calls may have been present in ancestral primates, ungulates and bats.

Verdragende roepen zijn divers in zowel mannelijke als vrouwelijke zoogdieren

Mannelijke vogels staan bekend om hun opmerkelijke zang. Echter, sinds kort blijkt dat vrouwelijke zangvogels ook zingen. Bovendien heeft onderzoek uitgewezen dat vrouwelijke zang al aanwezig was in de gemeenschappelijke voorouder van de hedendaagse zangvogels. Eerder waren vooral mannelijke vogels het middelpunt van de aandacht in onderzoek naar vogelzang, waardoor vogelzang gezien werd als een eigenschap van voornamelijk mannelijke zangvogels.

Deze vondst heeft aanzet gegeven tot onderzoek naar vergelijkbare vocalisaties in zoogdieren, de zogenaamde 'langeafstandsroepen'. Het voornaamste voordeel van deze roepen is dat ze grote afstanden kunnen overbruggen en fysieke barrières kunnen omzeilen. In sommige soorten zijn deze roepen zelfs tot op enkele kilometers afstand hoorbaar. Evenals het onderzoek op het gebied van vogels, is onderzoek naar deze vocalisaties met name gericht op mannelijke individuen. Echter, langeafstandsroepen worden in verschillende zoogdieren door zowel individuen van het mannelijke als het vrouwelijke geslacht geproduceerd. Door middel van literatuuronderzoek is vastgesteld dat dit inderdaad geldt voor apen, hoefdieren en vleermuizen.

Langeafstandsroepen in deze zoogdieren worden gebruikt om allerlei informatie over de roeper, zoals de identiteit, lichaamsconditie en locatie, of over factoren in de omgeving, zoals de aanwezigheid van predatoren of voedsel, over grote afstanden te communiceren. In apen, hoefdieren en vleermuizen kunnen langeafstandsroepen onder andere gebruikt worden door individuen om soortgenoten te waarschuwen voor gevaar of om contact te houden ondanks ruimtelijke scheiding. Daarnaast kunnen langeafstandsroepen gebruikt worden om elkaars krachten in te schatten of om indruk te maken op een potentiële partner.

Omdat langeafstandsroepen aanwezig zijn in vrouwelijke en mannelijke individuen in apen, hoefdieren en vleermuizen en deze verscheidene functies hebben, zijn deze roepen waarschijnlijk geëvolueerd onder verschillende omstandigheden. Dit zou verder kunnen betekenen dat langeafstandsroepen, net als vogelzang in zangvogels, al aanwezig waren in de voorouders van deze zoogdieren.

1. Introduction

Recently, it has been revealed that in the majority of songbird species worldwide, females sing. Above all, phylogenetic analyses demonstrated that female birdsong was present in the common ancestor of modern songbirds (Odom et al. 2014). This finding throws a completely different light on the topic of birdsong as it contradicts the general belief that birdsong has mostly evolved in male birds through sexual selection. Consequently, many questions are raised in relation to the evolution of (female) birdsong and its function.

Similarly to research on birdsong, research on long-distance vocalizations (also named 'loud calls') in mammals mainly focuses on males (e.g. primates:. Wich and Nunn 2002; deer: Cap et al. 2008). However, in various species of mammals both sexes use long-distance vocalizations (e.g. spotted hyenas (*Crocuta crocuta*: East and Hofer 1991a; East and Hofer 1991b), African elephants (*Loxodonta africana:* Soltis 2010), roe deer, (*Capreolus capreolus*: Reby et al. 1999); howler monkeys (*Alouatta* spp.: e.g. Whitehead 1989; Holzmann et al. 2012)). In some species female loud calls are even far more common than male loud calls (e.g. greater spear-nosed bat (*Pyllostomus hastatus*: Wilkinson and Boughman 1998); silvery gibbon (*Hylobates moloch*: Geissmann and Nijmann 2006)).

Many different aspects of loud calls in mammals have been studied, including proximate mechanisms, call recognition, evolution and function. Most of the research done on the topic, however, is species specific and incomplete regarding to function.

The goal of this literature review, therefore, is to determine what role males and females play in the production of long-distance vocalizations in mammals. Additionally, the function of these vocalizations will be investigated. This study will focus on three large mammalian taxa, namely simian primates (or simians: *Simiiformes*), ungulates (*Perissodactyla* and *Cetartiodactyla*) and bats (*Chiroptera*). Species within all three taxa are in general highly social and have a comparable slow life history.

It is expected that long-distance vocalizations occur in both male and female mammals and that these may convey different kinds of information about the signaller and its environment. Consequently, it is assumed that these calls serve various functions which have evolved under different environmental and social conditions.

In order to test these expectations, possible information content of long-distance vocalizations will be listed. Thereafter, hypotheses concerning possible functions of long-distance vocalizations will be proposed and predictions about the signaller's sex and the environmental and social context of long-distance vocalizations in mammals will be made. Subsequently, loud calls of male and female simians, ungulates and bats described in literature will be examined. The function of these long-distance vocalizations will be suggested based on the predictions made beforehand. This will provide an overview of long-distance vocalization use in male and female simians, ungulates and bats, and possible functions of long-distance calls in these taxa. Finally, the outcome of the results and their implications for future research will be discussed.

2. Long-distance vocalizations

In most studies, long-distance vocalizations are defined as calls that have an audibility range that exceeds the diameter of the signaller's home range. However, in my opinion loud vocalizations do not need to be directed exclusively at receivers outside the signaller's home range. Individuals may use long-distance vocalizations to communicate with conspecifics within their home range as well, for instance to keep contact when visibility is low. Furthermore, 'loudness' may be a tool to inform receivers at close range of the signaller's quality or rank. In this study therefore, long-distance vocalizations are defined as vocalizations that have an audibility range of at least a hundred meters or more, measured in the natural habitat of the species.

During transmission, vocalizations degrade in both intensity and acoustic properties as a result energy loss (termed attenuation), absorption and scattering of sound waves caused by atmospheric and physical barriers (Wiley and Richards 1978). The degree in which a sound is degraded and so the distance it travels is determined by its intensity, frequency (also known as 'pitch') and various environmental factors. Generally, sounds with a relative high intensity travel further than low intensity sounds. But this may depend on the frequency of the sounds, since high-frequency sounds suffer higher degradation rates than low-frequency sounds. Because of this, low-frequency sounds are likely more suitable as long-distance vocalizations than high-frequency vocalizations. Additionally, the travel distance of both low- and high-frequency vocalizations depends on environmental factors like humidity and vegetation density as this influences the degree of degradation (Wiley and Richards 1978).

The frequency range of sound production in mammals largely depends on the size of the vocal tract, which consists of the pharyngeal, oral and nasal cavities. The frequency of the sound produced decreases with increasing vocal tract size, which is in turn positively related to skull and body size (Fitch 1997). Based on vocal tract and body size, relatively large mammals are able to produce lower frequency sounds than relatively small mammals. However, the frequency range of sound production also depends on the anatomy of the vocal apparatus, the so-called larynx. Many mammals have special adapted larynxes or additional structures that allow them to produce sounds lower or higher in frequency than expected based on their body size. Some of these adaptations in simians, ungulates and bats will be discussed in the next paragraph.

3. Studied taxa

3.1 Simian primates
The order of *Simiiformes* consists of the *Platyrrhini* (New World monkeys) and the *Catarrhini*. The latter includes the Old World monkeys (*Cercopithecidae*), gibbons (*Hylobatidae*) and apes (*Hominidae*) (Petter 2011). Simian primates have some of the most striking and diverse long-distance vocalizations, which have been widely described in literature (Mitani and Stuht 1998; Wich and Nunn 2002; Delgado 2006).

Primates have evolved special adaptations to produce long-distance vocalizations. Various monkeys and all apes for instance have a throat sac, which is an air inflatable cavity that is connected to the vocal tract near the larynx (Fitch 2000; Hewitt et al. 2002; De Boer 2008). Depending on the species, throat sacs are located ventrally or dorsally, and open within or above the larynx (Hewitt et al. 2002). Different theories exist regarding the contribution of these structures to long-distance vocalization in primates, which may depend on the type of throat sac. First of all, throat sacs are thought to amplify vocalizations, acting as a cavity resonator, allowing the production of loud vocalizations. This hypothesis is supported by the fact that the intensity of the long-distance vocalization in male Brazza's monkeys (*Cercopithecus neglectus*) is lowered when the air sac is punctured. Furthermore, the size of throat sacs seems correlated to the production of loud calls. Males belonging to the subfamily *Cercopithecinae* that produce loud calls for instance, have larger air sacs than the females that produce sounds with a lower intensity (Hewitt et al. 2002). Secondly, throat sacs may lower the pitch of vocalizations, which may be beneficial for long-distance communication (Hewitt et al. 2002). Thirdly, they may allow primates to produce calls or call sequences of longer duration, by lengthening the period of exhalation during vocalizations (MacLarnon and Hewitt 1999). Finally, throats sacs may enable primates to call at a faster rate than without throat sacs. In this case, the throat sac functions as a reservoir that can be

replenished at intervals that do not necessarily correspond with calling rate, hereby preventing hyperventilation (Hewitt et al. 2002).

In contrast to the hypotheses above, some authors deny a vocal function of throat sacs, as several primates that lack these throat sacs, like the smaller gibbons, are still able to produce long-distance vocalizations. Alternative functional hypotheses proposed that throat sacs are necessary for thorax strengthening in brachiators, or play a role in visual social displays. Additionally, throat sacs have been thought to be used during high physical effort, enabling re-breathing of air, so that the breathing of fresh air does not have to be repeated that often. These hypotheses have all been dismissed, however (Hewitt et al. 2002).

In contrast to some monkeys and all apes, humans lack throat sacs. Research suggests that at some point in the evolution of humans, throat sacs have become lost. The reason for this loss is still not clear. Assuming that throat sacs contribute to the production of loud vocalizations, humans may have had no longer need for throat sacs as quiet speech became more important than loud vocalizations. Furthermore, throat sacs may be advantageous in controlling constant exhalation, but may lack the capacity to control highly variable exhalation rates as is necessary in human speech (MacLarnon and Hewitt et al. 1999; Fitch 2000; Hewitt et al. 2002).

Primates have a second laryngeal adaptation to produce loud vocalizations, namely 'vocal membranes' (Mergell et al. 1999). These are membranous structures that form an extension of the vocal chords. These structures ensure that sound can be produced at lower 'subglottal pressures', which normally limit the intensity with which a vocalization can be given. By lowering the subglottal pressures, less energy is needed to produce loud vocalizations (Mergell et al. 1999). So, vocal membranes enable primates to produce loud vocalizations using less energy, or to produce louder vocalizations than would normally be possible. Vocal membranes are found in most of the New World monkeys, some of the Old World monkeys and in the apes (Mergell et al. 1999).

Besides the lack of a throat sac and vocal membranes, the vocal organ of humans differs from that of primates in that humans have a descended larynx. This means that the larynx of humans is positioned lower in the throat compared to the larynx of other primates. Because of this change in position, humans are able to move the tongue in all directions within the vocal tract. This way, humans can vary vocal tract shape, creating different filters or formants through which the sound travels when it is produced by the larynx. The use of different formants enables humans to use different vowels, and thus is very important in human speech (Fitch 2000).

3.2 Ungulates

Ungulates consist of the odd-toed ungulates (*Perissodactyla*), even-toed ungulates and cetaceans. The latter two have been combined into the order *Cetartiodactyla* (Montgelard et al. 1997). Cetaceans however, will not be included in this research.

Like simians, species within ungulates and bats are known to use long-distance vocalizations. Well-known species of ungulates that use long distance calls are deer (e.g. red deer (*Cervus elaphus*: Cap et al. 2008) and elephants (e.g. African elephant (*Loxodonta africana*: Soltis 2010). Similar to primates, some ungulates have specialized vocal apparatuses. Reindeer for instance have comparable throat sacs to primates (Frey et al. 2007). Additionally, males of the goitred gazelle (*Gazella subgutterosa*) and red and fallow deer, like male humans, have a mobile larynx which is retracted downwards during vocalization, hereby elongating the vocal tract (Fitch and Reby 2001; Reby and McComb 2003; Frey et al. 2011). In the saiga (*Saiga tatarica*), an antelope, the vocal tract is enlarged by expanding their nasal cavity while vocalizing (Frey et al. 2007). The enlargement or elongation of the vocal tract by throat sacs, mobile larynxes or flexible nasal cavities, enable these ungulates to produce vocalizations that are louder and lower in frequency than they could have produced without these adaptations (Fitch and Reby 2001; Reby and McComb 2003a; Frey et al. 2007a; Frey et al. 2007b; Frey et al. 2011).

3.3 Bats

The order of *Chiroptera* is dividable in two large suborders: the *Megachiroptera* (megabats) and

Microchiroptera (microbats) (Kerth 2008; Airas 2013). The ultrasound vocalizations of microbats, i.e. vocalizations that have a frequency of over 20 kHz, are best known for their use in echolocation, which enables bats to find their way and forage on flying insects in the dark. However, ultrasound vocalizations may furthermore have a communicative function, as conspecifics can possibly tune in on echolocation pulses of other bats (Jones and Siemers 2011). Besides echolocation pulses, microbats use ultrasound vocalizations during social interactions (e.g. Chaverri et al. 2010).

On first sight, ultrasound vocalizations would seem unsuitable for long-distance communication as high frequencies have a relatively high degradation rate (Wiley and Richards 1978). However, apart from their extremely high frequency, these vocalizations are also extremely loud (>120 dB: Surlykke and Kalko 2008), which theoretically makes them detectable over distances of 16 to more than 200 metres (Jones and Siemers 2011). On the contrary, megabats (*Megachiroptera*) do not use ultrasound vocalization to echolocate. Instead they use their eyesight and smell to locate fruit or nectar and use relatively low frequency sounds to communicate with conspecifics (Kerth 2008; Airas 2013).

Microbats produce ultrasound vocalizations within their larynx. The two main differences between the larynx of microbats and of other mammals are the relatively large size of the larynx and its additional structures, namely vocal membranes, as were seen in primates. Like in primates, vocal membranes allow bats to produce loud vocalizations at lower energy costs by enabling the production of sound at lower subglottal pressures. The effect of vocal membranes on the subglottal pressure is more effective at high frequencies, allowing bats to produce not only very loud, but also very high pitched sounds, which would otherwise cost too much energy (Mergell et al. 1999).

Like microbats, megabats may have special laryngeal adaptations to produce loud vocalizations. A species of megabats which gives a good illustration of this is the hammer-headed bat (*Hypsignathus monstrosus*). This bat is able to produce long-distance vocalizations because of its relatively large larynx, that fills half of its body cavity, its enlarged nasal cavity and two throat sacs (Bradbury 1977).

4. Information content of long-distance vocalizations

The function of long-distance vocalizations depends on the nature of the transmitted information, which is, besides the environmental and social context, an important factor in determining the function of long-distance vocalizations. Therefore the different types of information that may be encoded in long-distance vocalizations of mammals are described: 1) identity of the signaller; 2) characteristics of the signaller; 3) location of the signaller; 4) predatory threat; and 5) food resource.

4.1 Identity of the signaller
Various studies have demonstrated that long-distance vocalizations in mammalian species can contain individual or group specific acoustic features, which indicates the possibility that individuals of these species are able to use long-distance vocalizations to discriminate between individuals or social groups (e.g. tigers (*Panthera tigris:* Ji and Johnson 2013), sperm whales (*Physeter macrocephalus:* Antunes et al. 2011); wolves (*Canis lupus:* Zaccaroni et al. 2012)). Further testing of individual and group recognition by playback experiments have confirmed the capability of discrimination between different individuals or groups in a wide range of mammalian species (e.g. African elephants: McComb et al. 2000), Artic foxes (*Alopex lagopus*: Frommolt et al. 2003), chimpanzees (*Pan troglodytes*: Herbinger et al. 2009); giant otters (*Pteronura brasiliensis*: Mumm et al. 2014)). However, it is often unclear whether these individuals are merely able to differentiate between familiar and unfamiliar individuals or groups, or truly recognize specific individuals or groups. The latter requires call production, perception, template matching and behavioural response to be individual specific (Tibbetts et al. 2008).

4.2 Characteristics of the signaller
Besides identity, long-distance vocalizations may inform others of the signaller's physical characteristics by honest signalling. According to the honest signal hypothesis, vocalizations can give a true indication of the

signaller's physical state or condition as the acoustic features of vocalizations are bound by factors like body mass and size. Honest signalling by vocalizations allows animals to assess each other's physical quality without the necessity of physical contact. This enables animals to selectively choose with which individuals they will interact, for instance in terms of fighting or mating. In this way individuals can save time, energy and unnecessary injuries (Alcock 2013). Experiments have demonstrated that vocalizations in mammals may indeed give an honest indication of body size, and hereby competitive ability (primates: Fitch 1997, Pfefferle and Fischer 2006, Erb et al. 2013; deer: Reby and McComb 2003). As mentioned before, body size can be determined by the pitch of the vocalization and vocal tract size of the signaller. Although some mammalian species are able to exaggerate their body size because of special adaptations that increase vocal tract size, like a throat sac or descended larynx, acoustic features indicative for body size still change with increasing body size, informing conspecifics of the signaller's body size relative to their own (Reby and McComb 2003; Harris et al. 2006).

Additionally, in calls which are costly to produce, call rate and duration can give an honest indication of the signaller's physical condition and stamina (Kitchen et al. 2003; Vannoni and McElligott 2009; Erb et al. 2013). Furthermore, long-distance vocalizations can inform receivers of the signaller's age, i.e. juvenile or adult, as vocal cord length and vocal tract length increase with body size (Reby and McComb 2003; Ey et al. 2007; Erb et al. 2013; Sharpe et al. 2013). Consequently, in species in which age is related to social rank, vocalizations can be indicative of rank (Sharpe et al. 2013).

Due to physical and behavioural differences between sexes in most species, acoustic features of vocalizations may differ between the sexes within a species. Loud calls may thus give away the signaller's sex (e.g. baboons (*Papio* spp.: Rendall et al. 2004).

Finally, in some species of mammals long-distance vocalizations are performed in duets or choruses, which means that pairs or groups call simultaneously and in a coordinated manner (e.g. black-crested gibbons (*Nomascus concolor*: Fan et al. 2009); chimpanzees (Fedurek et al. 2013)). Besides identity, these duets or choruses may signal the bond between the individuals (Cowlishaw 1992). Furthermore, in species in which group conflicts are common, long-distance vocalizations uttered in group bouts, can inform individuals of other groups of group number and thus strength. Experiments with group living black howler monkeys (*Allouatta pigra*) demonstrated that individuals can assess whether opponents outnumber them or not based on the calls of the intruders. When they do, the territory holders avoid confrontation (Kitchen 2004). Comparable results were found in a study on numerical assessment based on roars in lions (*Panthera leo*). The results showed that during an inter-pride conflict females adapt their decision to approach and recruit pride members to the size of the opposing group (McComb et al. 1994).

4.3 Location of the signaller
To determine the location of a signaller, a receiver needs to deduce two things from a vocalization: the direction from which it is delivered and the distance it has travelled. During the transmission, however, atmospheric and physical barriers cause scattering and degradation of vocalizations, complicating the assessment of the signaller's direction and distance (Wiley and Richards 1978). Nevertheless, when certain acoustic features degrade in a predictable way, receivers may be able to use acoustic degradation to assess the distance to the signaller (Wiley and Richards 1978). Additionally, several experimental studies have demonstrated that mammals indeed are able to orientate themselves by long-distance vocalizations of conspecifics, estimating the direction and distance of the call (e.g. in African elephants: Leighty et al. 2008).

4.4 Predatory threat
In some mammalian species, vocalizations can inform receivers of the presence of a certain type of predator (e.g. Diana monkeys (*Cercopithecus diana*: Zuberbühler et al. 1997)). Furthermore, vocalizations can convey information about the urgency of the threat (e.g. mongoose (*Suricata suricatta:* Manser 2001)), the distance of the predator relative to the group (e.g. blue monkeys (*Cercopithecus mitis stuhlmani*: Murphy et al. 2013)) and the location of the predator (e.g. in tree or on ground: black-fronted titi monkey (*Callicebus nigrifrons:* Cäsar et al. 2013)). Gunnison's prairie dogs (*Cynomys gunnisoni*) can even incorporate the size, shape and colour of the

predator in their alarm calls (Slobodchikoff et al. 2009; Slobodchikoff et al. 2012).

4.5 Food resource
Finally, long-distance vocalizations can convey information about the location, quantity, quality, divisibility and accessibility of a food source. In most mammalian species this information is specified by changes in call rate rather than the acoustic structure of the call (Clay et al. 2012). Call rate may, however, convey information on the signaller's internal state of excitement elicited by the presence of food rather than specific information about the food source. This means that individuals may be attracted to food-associated calls of other individuals due to the apparent excitement of the signaller, or because the signaller truly conveys information about the presence of a food source. When a call is specifically used in the context of food, it is more likely that the call reflects information about a food source, instead of the signaller's excitement (Clay et al. 2012).

5. Hypotheses and predictions

It is expected that long-distance vocalizations are exhibited by both males and females since long-distance vocalizations are probably used for various purposes that are more or less equally important for males and females. However, as some expected functions of long-distance vocalizations that involve competition over mates are assumed to be of greater importance in males than females, long-distance vocalizations are likely more common in males. This expectation is supported by results of former research on long-distance vocalizations in primates (Wich and Nunn 2002). As function is probably of great consequence in making predictions about the role male and female signallers play in long-distance vocalizations, predictions concerning sex of signallers are more broadly discussed throughout the descriptions of the functional hypotheses.

Several functional hypotheses of long-distance vocalizations are proposed based on possible information contents described above: 1) the defence hypothesis; 2) the alarm hypothesis; 3) the spatial coherence hypothesis; 4) the intragroup competition hypothesis; and 5) the finding a mate hypothesis. These hypotheses and their predictions concerning the context in which the long-distance vocalization is used, the characteristics of the signaller and vocalization, and finally, the signaller's social environment are described (Table 1).

5.1 Defence hypothesis

5.1.a Territory defence
Territorial animals actively defend a certain area against intruders (Alcock 2013). These individuals, pairs or groups may use long-distance vocalizations to inform conspecifics of their presence in a certain area. These territorial long-distance vocalizations may simultaneously convey information on the signaller's physical condition and identity, as means of honest signalling. In this way, long-distance vocalizations of territory defenders may function in the deterrence of neighbours or strangers. Territorial calls performed in duets or choruses may function to strengthen the message by signalling group bond or group number. In case of the former, territorial calls may be especially directed towards single individuals in monogamous species.

Territorial calls most likely take place near the borders of the territory and are uttered spontaneously or in reaction to calls of neighbours or intruders. Accordingly, territorial calls may elicit counter calls from neighbours and strangers. Individuals may react more violently towards strangers or displaced neighbours than neighbours that reside in their usual area. Additionally, territorial calls may be more powerful when the unwelcome guests are near the centre of the territory than when near the edge; the so called centre-edge effect. Besides that, territorial calls may be more powerful in periods when food resources are scarce or during the mating season when mates are valuable (Hopkins 2013).

Whether territorial calls are produced by males or females, or both, probably depends on the extent to which males and females benefit and take part in territory defence within a society. Territorial calls may be used by both polygamous and monogamous species.

5.1.b Intergroup spacing

Long-distance calls may furthermore be used in non-territorial species, i.e. species in which individuals do not use an exclusive area and in which home range overlap is common (Mitani and Rodman 1979), to control intergroup or interindividual spacing. Interindividual spacing involves individuals that do not belong to the same social entity and will from now on be included in the term 'intergroup spacing'.

Long-distance vocalizations which are used for intergroup spacing may be produced spontaneously or in response to the sound or sight of extra-group individuals. These vocalizations will eventually result in mutual avoidance. Like territorial calls, spacing calls may contain information on the physical strength and identity of the signaller. Additionally, pairs or groups may join in duets and choruses to signal their presence in the area and strength in numbers or their pair/group bond to extra-group individuals. As in territorial calls, the calling may be more intense when food or mates are valuable.

The sex of the signaller probably depends on the need for space defence in males and females, and their participation in intergroup spacing. When space defence is motivated by mate defence, calling may be more often performed by males than females. When motivated by infant and resource defence, both sexes may equally take part in vocalizations that keep extra-group individuals at a distance. Like territorial calls, long-distance vocalizations for the purpose of intergroup spacing probably occur in both polygamous and monogamous species.

5.2 Alarm

Loud vocalisations may also be used in threatening situations, like the presence of predators or non-predatory disturbances. In a predatory context, alarm calling seems an unwise thing to do from the signaller's point of view as it raises its conspicuousness to the predator. However, warning unaware group members by alarm calling may benefit signallers by evoking anti-predator behaviour in group members, like cooperative defence (like mobbing behaviour), fleeing or hiding, hereby protecting (valuable) group members (Da Silva et al. 2002; Wheeler 2008).

As this implies that individuals merely benefit via others when alarm calling, alarm vocalizations are expected to be uttered exclusively in the presence of other individuals; the so-called audience-effect (e.g. Wich and Sterck 2003). Taking this into account, alarm vocalizations are expected to be present in social mammals that live in rather coherent, and supposedly family, groups.

However, research on the calling behaviour of tufted capuchin monkeys (*Cebus apella nigritus*) suggests that alarm calling may benefit signallers that are on their own as well by means of directing the call at the predator instead of conspecifics, informing the predator of its being detected. This may be especially effective in case of predators of which hunting success depends on the act of surprise (Wheeler 2008). So, even in solitary individuals, alarm vocalizations could function as anti-predatory behaviour.

When directed at conspecifics, information about the whereabouts of the predator and its characteristics may benefit both signallers and receivers. When alarm calls are solely directed at the predator on the contrary, the vocalizations will most likely contain almost no information as the calls are merely about making noise.

When males and females equally benefit from alarm vocalizations, alarm vocalizations are likely used by both sexes. When alarming behaviour depends on the presence of kin, usage of alarm vocalizations may be sex biased as the certainty of parenthood may differ between sexes (Burke Da Silva et al. 2002; Wheeler 2008).

It is very likely that several individuals within a group call simultaneously when alarmed. However this is probably not coordinated and thus there is no question of a chorus or duet.

5.3 Spatial coherence

The great benefit of communication by sound is its ability to overcome great distances and physical barriers (Kondo and Watanabe 2009). This advantage makes long-distance vocalizations particularly fit to advertise one's location or the location of a resource to conspecifics when separated over a considerable distance. This enables scattered individuals or subgroups to locate each other and if necessary, to gather. Societies that

temporally vary in spatial cohesion among group members and in party size and composition are known as fission-fusion dynamic societies (Aureli et al. 2008). These dynamic societies are caused by the spatial distribution of resources, like foraging or sleeping areas, or by spatiotemporal variation in social relationships (Aureli et al. 2008). Because the causes of spatial separation and aggregation vary, spatial coherence calls may be used in different situations and for different purposes: 1) coherence; 2) roosting and 3) feeding.

It is expected that all three types of spatial coherence vocalizations are given individually and so do not occur in duets or choruses.

5.3.a Coherence

The most obvious function of spatial coherence calls is the coordination of group and pair movements. Conveying information on the location and identity of the signaller, long-distance vocalizations enable individuals to perceive and locate each other (Fan 2009; Spehar and Di Fiore 2013).

Coherence calls may be started spontaneously or in reaction to calls of a group member or mate, followed by the movement of the involved individuals towards each other. Coherence calls are most likely used by individuals of both sexes.

5.3.b Roosting

Communal roosting provides safety in numbers and, in mammals that sleep in very tight groups like some bats, social thermoregulation (Chaverri 2010). Especially in species in which the roosting location changes regularly, long-distance vocalizations may be employed to inform group members of the location of a roosting place. Besides location, roosting calls may contain information on the identity of the individuals, enabling reunion of individuals that belong to the same social group (Furmankiewicz 2011).

The calls may be initiated by individuals that choose a roosting place and inform the others of the new location, or they may be initiated by individuals that are in search of a roosting place. In case of the latter it is crucial that the roosting calls are answered by individuals that are already at the roosting spot. When individuals of both sexes take part in communal roosting, it is expected that both males and females take part in the calling.

5.3.c Feeding

Long-distance calls may be used to inform group members of the existence of a food resource and gather them to the location of the resource. Besides location, long-distance calls may inform conspecifics about the characteristics of the food resource (see paragraph 4.5). Food calls, as I will call this type of long-distance calls from now on, are likely to be initiated upon the finding of a considerable amount of food that is sharable with a number of individuals. Furthermore, it is expected that there is an audience-effect, i.e. other individuals are within hearing distance of the signaller.

Individuals may gather conspecifics to a food source to cooperate with each other by sharing the food (Bitetti 2005). In this case calling may be directed at specific receivers, for instance close group members or kin (Schel et al. 2013). Furthermore, a large number of individuals feeding simultaneously at a feeding ground may create a dilution effect and/or higher vigilance. This will lower the predation risk of foraging individuals. Additionally, higher vigilance may increase foraging efficiency as more time can be spent on foraging instead of standing guard (Alcock 2013; Clay et al. 2012). Finally, feeding in a group may help defend the food resource against other groups (Alcock 2013).

Food calls may be produced by individuals of both sexes. However, when food calls are directed towards kin, usage of these vocalizations may be sex biased as the certainty of parenthood may differ between sexes. When long-distance food calls are used for anti-predatory or efficiency reasons, males and females probably equally benefit from cooperative feeding and so food calls are likely produced by both sexes.

5.4 Intragroup competition

In hierarchical societies, relationships are reflected by social rank. Long-distance vocalizations may be used by individuals in a hierarchical system to prevent contests or escalation of contests by communicating social rank

and competitive ability (Kitchen et al. 2003; Neumann et al. 2010). This type of long-distance call is most likely in large fission-fusion multi-male and/or multi-female groups in which individuals often need to assess each other's dominance status as the group is too large and flexible to form stable groups.

This type of long-distance vocalizations is most likely used during displays of dominance or aggression. The social rank of the signaller's opponent may influence its calling behaviour, ending its calling when countered by an individual with a higher rank, and increasing calling when of a similar rank (Kitchen et al. 2003). These calls may take place in choruses or duets, in which individuals call alternately.

When high competition for a certain resource takes place in only one of the sexes, the call is expected to be sex specific (Neumann et al. 2010).

5.5 Finding a mate

5.5.a Mate attraction

Mate attraction calls are emitted when individuals of one sex are in search of mating partners. This may either be when individuals are solitary, when individuals live in either multi-male or multi-female groups, or when individuals seek additional mating partners. This may occur in both mono- and polygamous species.

By the means of long-distance vocalizations, an individual without a partner and isolated from potential partners may advertise its presence and furthermore its identity and body condition to individuals of the opposite sex that are ready to mate. Mate attraction calls may be traced by a receiver or be answered. In case of the latter, mate attraction calls may result in a mutual approach and ultimately union. So, mate attraction calls may be used by individuals of both sexes or of one particular sex. Unpaired individuals are assumed to use or answer to mate attraction calls more often than paired individuals. As individuals that are in search of a mate probably do not cooperate with others to attain mates, mate attraction calls are expected to be given individually and not in duets or choruses.

5.5.b Courtship

Contrary to mate attraction calls, courtship calls are assumed to be used by individuals to impress a potential mate that is already in the signaller's presence. Regarding its function, courtship calls are expected to occur in association with courtship behaviour and copulations.

Elaborate courtship vocalizations may have evolved by sexual selection. In order to be sexual selected, a call has to meet several requirements. These include sexual dimorphism of the call and variation of the call between same-sex individuals. Furthermore, the receivers (which are of the choosing sex) have to be able to discriminate between call variants and express their preference (or avoidance) for certain variants. Additionally, difference in preference for variants must correlate with reproductive success (Snowdon 2004). Courtship calls may be present in multi-male and multi-female groups with a polygamous mating system, in which high competition for mates is present, or during pair bonding in monogamous pairs in which one mate proves itself after it has attracted a mate.

Opposed to mate attraction calls, courtship calls are associated with high mate competition between same-sex individuals. Courtship calls may, however, play some part in mate attraction, as courtship calls range far and draw the attention of potential mates. Like mate attraction calls, courtship calls likely contain information about the signaller's identity and physical condition. It is expected that courtship calls are used by one particular sex, namely males, as these are more likely to compete with other males for access to females (Alcock 2013). Although courtship calls may be uttered by several males at the time, for instance at special display areas in lek-breeding mammals, these are probably not coordinated and so do not form a duet or chorus.

Table 1. Functional hypotheses with predictions on vocalization level (information content, context and consequence), on level of the signaller (its sociality and sex) and on group level (only applies to group living species; group size, coherence, social organization and mating system). Abbreviations stand for: social (SC); solitary (SL); male (M); female (F); fission-fusion society (FF); multi-male and multi-female group (mM-mF).

Functional hypothesis	Long-distance vocalization			Signaller		Group				
	Information content	Context	Consequence	Sociality	Sex	Size	Coherence	Home range	Social organization	Mating system
Defence										
a. territory defence	- Identity - Physical condition	- Interaction neighbour(s) or intruders - Aggression/agonistic display - At borders territory - Spontaneously - Possibly in duet/chorus	- Avoidance by neighbours or intruders	- SC - SL - Territorial	M and/or F	no specific prediction	Intermediate – high	no specific prediction	no specific prediction	no specific prediction
b. intergroup spacing	- Identity - Physical condition	- Interaction between extra-group individuals - Aggression/agonistic display - Spontaneously - Possibly in duet/chorus	- Mutual avoidance	- SC - SL	M and/or F	no specific prediction	no specific prediction	no specific prediction	no specific prediction	no specific prediction
Alarm	- Characteristics or location predator - Urgency of danger	- Presence predator - Other disturbance	- Anti-predator behaviour	- SC - SL	M and/or F	Intermediate – high	Intermediate – high	no specific prediction	- Social (family) group	no specific prediction
Spatial coherence										
a. coherence	- Identity	- During social isolation - Interaction (distant) group members	- Response conspecific - Movement towards/alongside each other	- SC	M and/or F	no specific prediction	Low – intermediate	Intermediate – high	- FF - Social group	no specific prediction
c. roost	- Identity	- In advance of roosting	- Response group members - Communal roosting	- SC	M and/or F	no specific prediction	Low – intermediate	Intermediate – high	FF	no specific prediction

Table 1 continued.

	Cues	Context	Call type	Sex					
d. food	- Characteristics food resource	- Upon the finding of a relatively large amount of food - During foraging - Audience effect	- SC	M and/or F	no specific prediction	Intermediate	no specific prediction	- FF - Social (family) groups	no specific prediction
Intragroup competition	- Age - Identity - Rank	- During intragroup conflicts - Dominance display	- SC	M and/or F	Intermediate – high	Intermediate – high	no specific prediction	- mM-mF - Social group with dominance hierarchy	no specific prediction
		- Vocalization of higher ranking individual causes avoidance in lower ranking individual - Vocalizations more intense in individuals of equal rank - No escalation of conflict							
Finding a mate **a. mate attraction**	- Identity - Physical condition - Sex	- Isolation from potential mates - During mating season	- SC - SL - Unpaired	M and/or F	no specific prediction	Low (between sexes)	Intermediate – high	- FF - all M and/or all F groups	no specific prediction
		- Approach or answer potential mate - Copulation							
b. courtship	- Identity - Physical condition - Sex	- Directed towards potential mate - Possibly physical display - During mating season	- SC - SL	M or F (most likely M)	Intermediate – high	no specific prediction	no specific prediction	- mM-mF - Social group with high mate competition	no specific prediction
		- Copulation							

6. Research methods

Literature research was done on male and female long-distance vocalizations in simians, ungulates and bats, as well as on the context in which they were used. Research included long-distance communication in adult males and females only. So, infant-mother long-distance interactions were excluded from the data.

Vocalizations were considered true long-distance vocalizations when they matched the definition of long-distance vocalizations used in this study described in paragraph 2. In case the audibility range was not explicitly mentioned in literature, the volume of the call was determined by certain terms used in the description of the call like 'loud', 'long distance', 'high amplitude', in combination with the information on the context in which the call was used. An example of a context which is indicative of audibility range is for instance that individuals used particular calls when they were separated from other group members by a hundred meters or more and that these calls elicited a reaction from group members.

Calls were considered distinct calls when they were used consistently in the same context(s). So, separate phrases of which calls consisted were not considered distinct calls, unless they could be used separately in a specific context as well. A distinctive call is still allowed to vary in structure between individuals and/or sexes as long as the differences in the call variants are subtle.

Table 2. Features of long-distance vocalizations and signallers that were taken into account during data acquisition.

	Measurements
Characteristics of long-distance vocalization	1. Audibility range 2. Information content 3. Sexual dimorphism
Call context	4. Spatial context 5. Temporal context 6. Behavioural context 7. Social context 8. Environmental context 9. No context (spontaneously) 10. Consequence of call
Characteristics of signaller	11. Sex 12. Sociality
Social structure within species	13. Group size 14. Group coherence 15. Home range 16. Mating system 17. Social organization

Several factors that are indicative for a call's function according to the predictions were included in the data acquisition (Table 2). For each long-distance call within a species, characteristics of long-distance vocalizations were noted down, including audibility range, information content and sexual dimorphism. Furthermore, the context of long-distance vocalizations was taken into account. Long-distance calls can be elicited by different stimuli that belong to five different types of contexts: 1) spatial; 2) temporal; 3) behavioural; 4) social; and 5) environmental. The spatial context indicates whether long-distance calls are used at a specific location, for instance at territory borders. The temporal context concerns the time or season at which a call is always or often given, like dawn or the mating season. The behavioural context describes which behaviour of the signaller accompanies the long-distance vocalization just before, during or shortly after the call is uttered. Some examples of these behaviours are agonistic display, travelling and flight behaviour. The social context describes the social interactions between the signaller and conspecifics that take place shortly before or during

the calling. Finally, the environmental context includes environmental events that took place shortly before the calling. This includes the presence of predators, falling trees and food. It was also possible that long-distance calls were uttered spontaneously, i.e. no particular stimulus preceded the long-distance call. The final measurement concerning context is the consequence of the long-distance vocalization on the behaviour of the signaller and receiver(s). Last of all, the sex and sociality of the signaller and the social structure within the species were included in the measurements.

By means of these measurements, one or, in case the call was used in different contexts, several of the nine proposed functions were assigned to each call based on the hypotheses and predictions made. When the measurements were not sufficient to make a prediction about the function of the call, the function was labelled 'unknown'. In case both males and females were known to use a certain call, but it was rarely observed in females, the function was assigned only to males and vice versa, as the context of the call was possibly only observed in the sex in which the call was most common.

In some studies, calls were already termed for their function, for instance 'contact calls' or 'mate attraction calls'. These functions were only assigned to the calls when the contexts of the calls indeed corresponded with the predictions made in the published study. Exceptions to this rule were long-distance calls that were already named 'alarm call'. Due to the easy recognizable function of alarm calls, long-distance vocalizations termed 'alarm call' were considered to function as one, even when no further information about context was available.

7. Results

7.1 Simian primates
Within the simian primates, 63 species across seven different families were found that use long-distance calls (Table 3 and Appendix A). Within these species a total number of 122 distinct long-distance calls were described, ranging from one to nine calls per species (1.9 on average). Over half of all long-distance calls were used by both sexes (54.1 %). Exclusive use of particular long-distance calls was far more common in males than in females (32.8 % against 2.5 %). In 10.7 % of the cases, the signaller's sex was unknown (Figure 1).

Table 3. The number of species within different families of simian primates, ungulates and bats that use long-distance vocalizations.

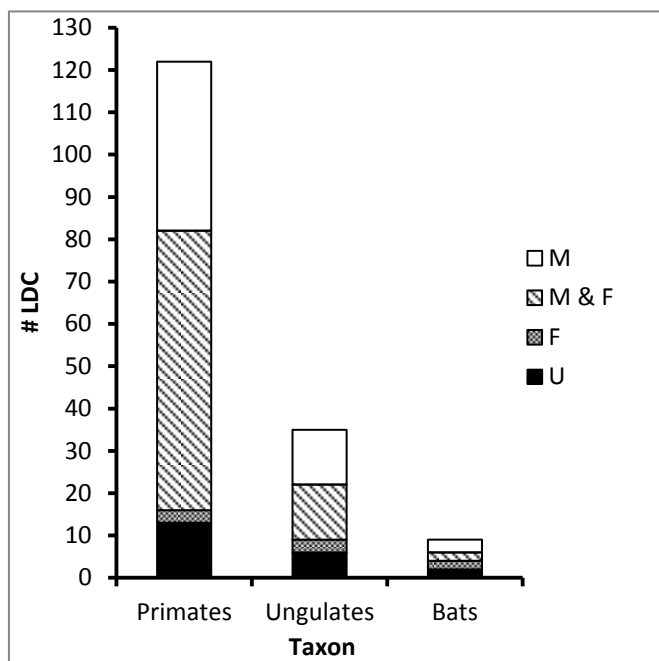|	*Family*	No. of species
Simian primates	*Atelidae*	8
	Callitrichidae	6
	Cebidae	1
	Cercopithecidae	26
	Hominidae	5
	Hylobatidae	12
	Pitheciidae	5
Ungulates	*Bovidae*	7
	Cervidae	11
	Elephantidae	2
	Equidae	5
	Procaviidae	1
Bats	*Megadermatidae*	1
	Phyllostomidae	3
	Pteropodidae	2
	Vespertilionidae	2

Figure 1. The number of long-distance calls (LDC) used by males (M), both males and females (M & F), females (F) or individuals of unknown sex (U) in simian primates, ungulates and bats.

A total number of 131 functions were assigned to 89 calls, ranging from one to four functions per call (1.5 on average). Of 33 long-distance calls (20.1 %) no prediction could be made concerning the function. All proposed functions of long-distance vocalizations were found in simians, except for courtship. The most common function in simians is alarm (29.3 %), followed by coherence (16.5 %), territory defence (12.8 %) and intergroup spacing (11.0 %) (Figure 2a).

In some cases long-distance vocalizations seemed to have functions which were different than those predicted. In most of these cases, long-distance vocalizations were used during short-distance interactions, in which the calls were used during greeting, copulation or affiliative interactions. Furthermore, in the proboscis monkey (*Nasalis larvatus*), males seemed to use a particular call to calm group members during group confusion.

No type of long-distance call was exclusively present in individuals of a specific sex. But all types of long-distance vocalizations, except roosting calls, were exclusively produced by males in some species. Cases in which certain long-distance calls were used exclusively by females were only found in contexts of intergroup spacing, alarm and coherence. However, in all of these cases males of the same species had structurally different long-distance vocalizations that served the same function. Additionally, when individuals of both sexes within a species used the same calls in context of territorial defence or intergroup spacing, these calls were often more common in males than in females. Alarm vocalizations were often more common in females than in males of the same species.

7.2 Ungulates

In total, 26 species across five families of ungulates were found to use long-distance calls (Table 3 and Appendix A). Almost half of these species belongs to the family of the *Cervidae*. Within these 26 species a total number of 35 long-distance calls were found, ranging from one to three calls per species (1.3 on average). Exclusive calling by males was as common as calling by both sexes (both 37.1 %). Only three long-distance calls were exclusively used by females (8.6%). In 17.1 % of the cases the signaller's sex was unknown (Figure 1).

Overall 32 functions were assigned to 26 different calls, ranging from one to two functions per call (1.2 on average). In case of nine long-distance calls (22 %) the function was unknown. The majority of long-distance calls in ungulates served as alarm calls (34.1 %). The second most common function was intergroup spacing (17.1 %), followed by coherence (12.2 %), territory defence (9.8 %), intragroup composition (2.4 %) and mate attraction (2.4 %). No calls within ungulates were found that functioned as roosting, feeding or courtship calls (Figure 2b). Besides its function in territory defence, the long-distance call in males of the Somali wild ass (*Equus africanus somaliensis*) was used during greeting and pre- and post copulatory behaviour.
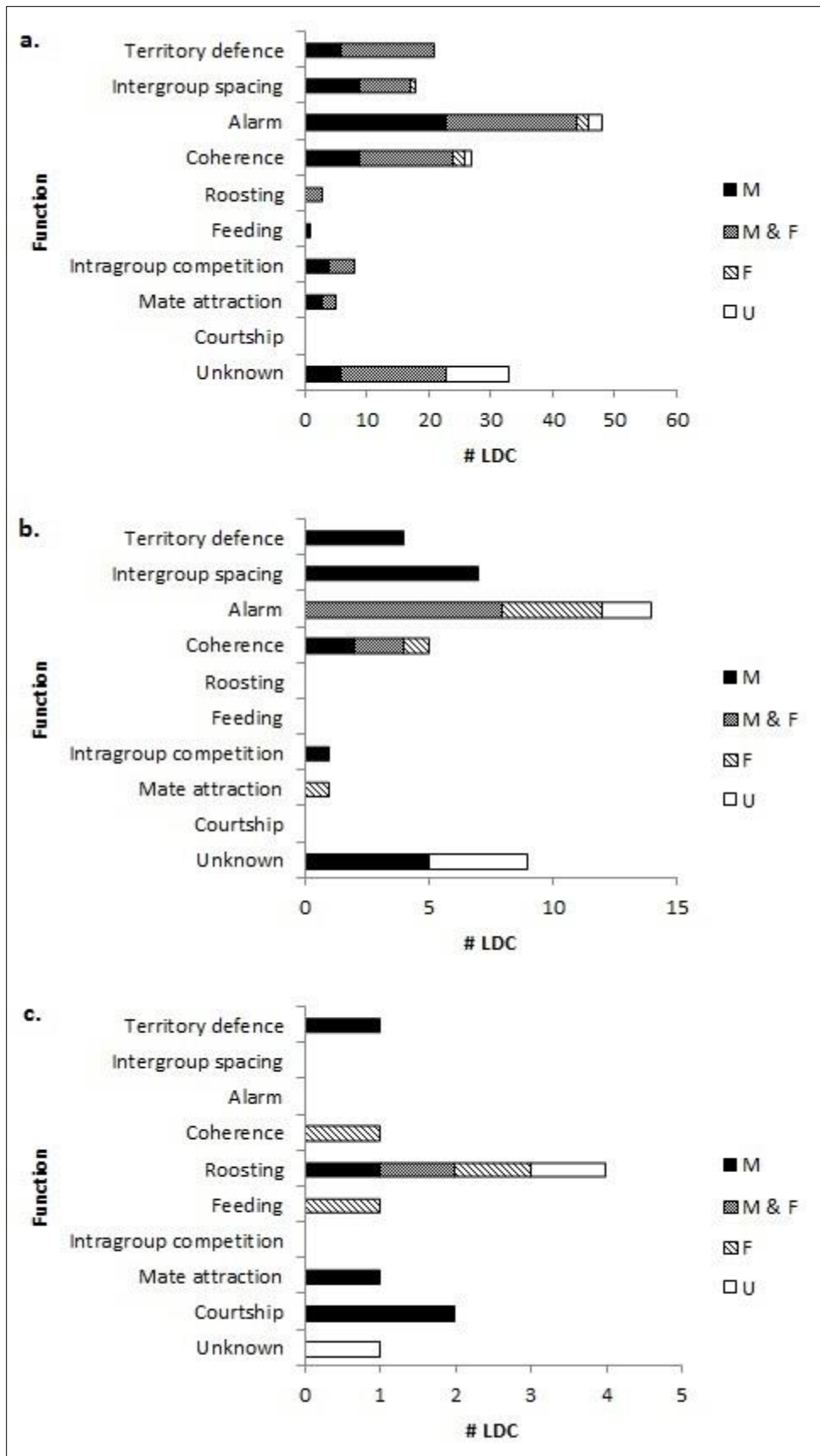
Figure 2. The number of long-distance calls (LDC) that were used by males (M), both males and females (M & F), females (F) or individuals of unknown sex (U) during different contexts, in a) simians; b) ungulates; c) bats.

Territory defence, intergroup spacing, and intragroup competition calls were merely used by male ungulates. Mate attraction calls occurred only once in ungulates, namely in African elephants, and were exclusively present in females. Alarm calls were used either by both sexes or exclusively by females. When used by both sexes, the alarm call was often more commonly used by females than by males.

7.3 Bats

Only eight species of bats, belonging to four different families, were found that use long-distance calls (Table 3 and Appendix A). Within these species, nine long-distance calls were described. Use of long-distance vocalizations by one or both sexes was nearly equal. In two cases the sex of the signaller was unknown (Figure 1). In most species only one distinct long-distance call was present; in only one species two different long-distance calls were present.

The majority of calls seemed to have only one specific function; two calls had two different functions (on average 1.3 functions per call). In case of one call no function could be assigned. Long-distance vocalizations were used by bats for all proposed functions, except for intergroup spacing and alarm. Roosting calls were the most common (33.3%), followed by courtship calls (16.7 %). The remaining functions each only occurred once (Figure 2c). Roost calls were used by all sex classes. To the contrary, calls used in the context of territory defence, intragroup competition, mate attraction and courtship were merely used by male bats. Calls used exclusively by females were used in the context of coherence, roosting and feeding.

7.4 Simians, ungulates and bats compared

The number of species within each taxa found to use long-distance vocalizations differs greatly. According to the literature available, the number of simian species that use long-distance vocalizations is far higher than the number of ungulate and bat species that use long-distance vocalizations. Furthermore the number of long-distance vocalizations per species is higher in simians.

In all three taxa long-distance calls were used by either both sexes or exclusively by one specific sex. Long-distance vocalizations in ungulates and bats seemed more sex specific than long-distance vocalizations in simians, as a higher proportion of long-distance vocalizations were exclusively used by one particular sex (Figure 3). Territory defence and intragroup competition calls in ungulates and bats for instance were merely used by males. However, in simians these call types were often used by both sexes.

The average number of functions per long-distance call did not differ greatly between the three taxa. However, the maximum number of functions per long-distance call in simians was four, in contrast to the maximum of two functions per long-distance call in ungulates and bats.
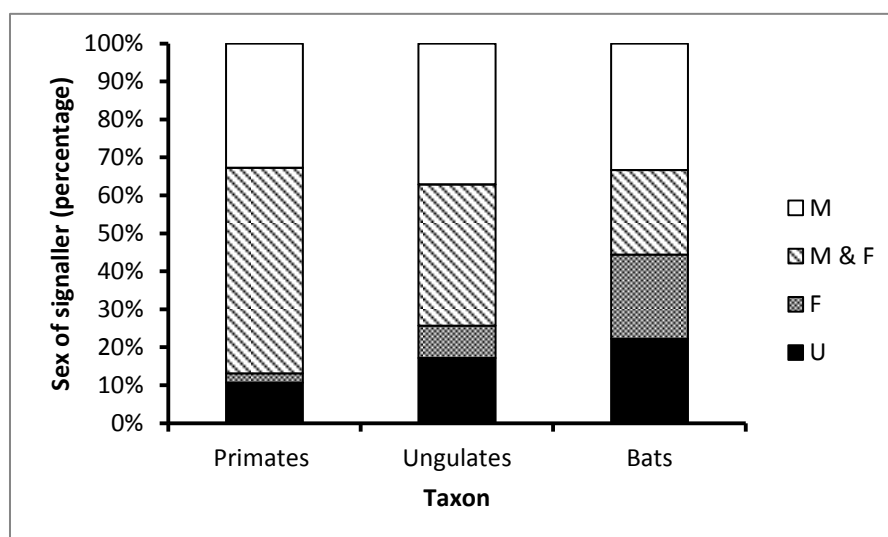

Figure 3. Percentage of long-distance calls in simians (n=122), ungulates (n=35) and bats (n=9) that is produced by males (M), both males and females (M & F), females (F) and individuals of unknown sex (U).

In both simian and ungulate species, alarm long-distance calls were the most common. Furthermore, these two taxa have a comparable distribution of the different functions except that ungulates do not have roost and feeding loud calls, while these calls are present in some species of simians (Figure 4). Courtship calls were exclusively found in two species of bats.
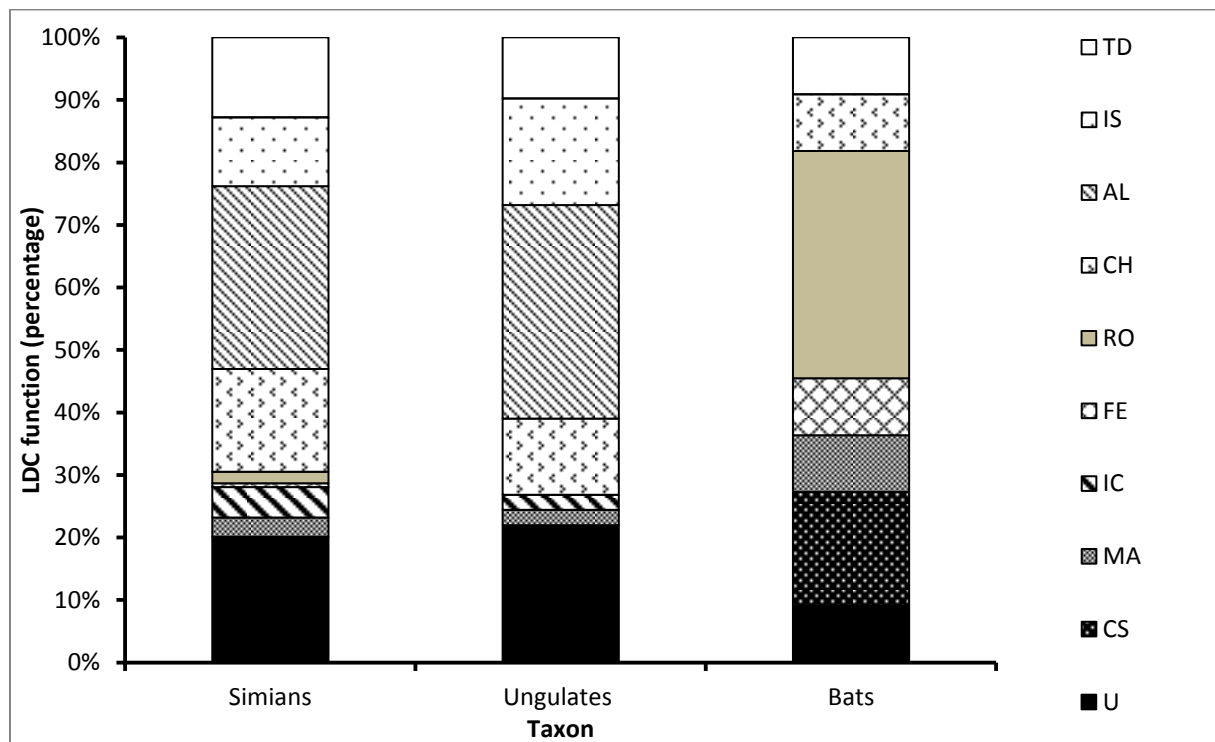

Figure 4. The percentage of long-distance calls in simians (n=122), ungulates (n=35) and bats (n=9) used in different contexts: territory defence (TD), intergroup spacing (IS), alarm (AL), coherence (CH), roosting (RO), feeding (FE), intragroup competition (IC), mate attraction (MA), courtship (CS) and unknown (U).

8. Discussion

The aim of the published study was to survey the presence of long-distance vocalizations in male and female simian primates, ungulates and bats. Additionally, an effort was made to determine the function of male and female vocalizations in these three mammalian taxa. The results demonstrate that both males and females in species of simians, ungulates and bats produce long-distance vocalizations. Within some species, individuals produced a number of different long-distance vocalizations. Within all three taxa, long-distance vocalizations were used in various contexts and for different purposes. These results are more extensively discussed below.

8.1 The presence of long-distance vocalizations in simians, ungulates and bats
Long-distance vocalizations seemed far more common in primates than in ungulates and bats. In fact, the occurrence of long-distance vocalizations in bats was relatively rare. However, there is no direct reason to suspect that long-distance vocalizations are indeed less common in ungulates and bats. Instead, this difference may be due to the relatively low amount of literature that was available on vocalizations in ungulates and bats compared to the amount of literature on vocalizations in primates, which was quite extensive. Additionally, in case of all three studied taxa, it was often impossible to assess the audibility range of a vocalization based on literature. This may have caused exclusion of calls from the data while these were in fact long-distance calls. Assessment of audibility range was especially difficult in echolocation vocalizations of bats. So, despite the fact that literature on echolocation pulses in bats was available and that there are indications for long-distance communication in bats by echolocation pulses (Wilkinson 1995; Gillam 2007; Jones and Siemers 2011), echolocation calls are not included in the data of this study. This may have greatly reduced the number of long-

distance vocalizations found in bats since the majority of bat species use echolocation vocalizations (Kerth 2008). Thus, throughout this discussion, it has to be kept in mind that the amount of data in ungulates and bats is small and that conclusions regarding long-distance vocalizations in these two taxa have to be treated with caution.

8.2 Sex of the signaller

Most long-distance vocalizations were performed by both sexes within a species. Long-distance vocalizations that were exclusively used by males within a species were more common than long-distance vocalizations used exclusively by females, which were actually quite rare. Within simians, females never produced long-distance vocalizations when males within the same species did not. Similar results were found in primates by Wich and Nunn (2002). In contrast, exclusive use of long-distance vocalizations by females was present in some species of ungulates and bats. A possible explanation for this will be discussed later on.

8.3 Function

Male and female long-distance vocalizations were used in different contexts. Indications for all functional hypotheses of long-distance vocalizations have been found across species of simians, ungulates and bats. However, in none of the three taxa all types of long-distance vocalizations were present.

The most common functions of long-distance vocalizations in simians and ungulates were alarm, territorial defence, intergroup spacing and coherence. Long-distance vocalizations in bats however, most often functioned as roosting calls. While alarm and intergroup spacing seemed common functions in long-distance vocalizations of simians and ungulates, these functions did not apply to the long-distance vocalizations that were found in bats. Long-distance calls used in the contexts of alarm and intergroup spacing in bats are possibly not yet described in literature or may indeed be absent. However, long-distance vocalizations are used for territory defence in at least one species, so the presence of long-distance vocalizations for intergroup spacing is not necessarily unlikely. Furthermore, alarm calls have been observed in at least three species of flying foxes (*Pteropus*). The audibility range of these calls is unclear, however (Nelson 1965; Wilkinson 1995).

Long-distance roost calls were present in only three species of simians and four species of bats, and were absent in ungulates. The absence of roosting calls in ungulates was not unexpected because ungulates do not have specific resting areas, in contrast to some primates and most bats.

Long-distance food calls only occurred once in primates and once in bats, and were absent in ungulates. Perhaps the costly production of long-distance vocalizations does not pay off in this context because individuals in search of food are already relatively near each other when foraging, so short-distance vocalizations may suffice. Indeed, food-associated calls that are used during short-distance communication have been reported in many species of primates (Clay et al. 2012).

Long-distance courtship calls were solely found in two species of megabats, namely Wahlberg's epauletted fruit bat (*Epomophorus wahlbergi*) and hammer-headed bats (*Hypsignathus monstrosus*). Although it was expected that courtship calls could be used in polygamous and monogamous species, both species were polygynous. The courtship calls were produced at a display area, or lek, where males gather and females visit the males. In both species, the calling is accompanied with beating wings and the Wahlberg's epaulleted fruit bat erects tufts of fur on its shoulder (Wickler and Seibt 1976; Bradbury 1977; Schoeman and Goodman 2012). Lek polygyny evolves in species when resources are scattered and females are widely distributed, so that males are unable to defend clumped resources to attract females or to defend groups of females (Alcock 2013). Lek polygyny also occurs in some ungulates, including fallow deer (*Dama dama*) and sika deer (*Cervus nippon*), which were both included in the data (Clutton-Brock et al. 1988; Clutton-Brock et al. 1993). The mating strategy of fallow deer differs between populations, however. In some populations, males defend groups of females and in others males defend mating territories that are visited by females (Clutton-Brock et al. 1988). The literature used during data acquisition on long-distance vocalizations in fallow deer, reported that fallow deer defended females and formed harems. Because of this, male loud calls in fallow deer were thought to be used for intergroup spacing. However, now that it is clear that fallow deer also take part in lek polygyny, male loud calls in this species may also function as courtship calls. Similarly, mating strategies of sika deer vary greatly

between populations. Mating strategies that have been observed in this species are female defence, resource-based territoriality and lek territoriality (Bartos et al. 1998). In this study, long-distance calls of male sika deer were assumed to be used for territory defence, based on the defence of resources. In case of lek territoriality, the calls of male sika deer may be used for territory defence and/or courtship.

Finally, the number of functions per long-distance call was equal in ungulates and bats, but slightly higher in simians. This might be a result of limited data. Furthermore, some long-distance vocalizations may have more functions than were actually assigned to them, simply because some functions did not become clear from literature. So, the question remains whether the degree of specificity in functionality in long-distance calls differs consistently between the three studied taxa or not, and what selection pressures cause these differences in functional specificity in (long-distance) vocalizations. Why do some species have several calls with specific functions, and others just one or two, which have multiple functions?

An additional function of long-distance vocalizations has been suggested in literature, but was not included in the analysis of the data. According to some authors, duets or choruses may strengthen pair or group bonds (e.g. Fan et al. 2009; Harding 2012; Fedurek et al. 2013). However, considering the loudness of long-distance vocalizations, bonding seems not to be the primary function of long-distance vocalizations. Instead, better relationships may be a by-product of cooperative resource or mate defence by advertising group number and pair/group bond towards extra-group individuals by long-distance vocalizations.

8.4 Functional use of male and female long-distance vocalizations
As expected, most types of long-distance calls could be used by individuals of both sexes or of a particular sex within a species. Only courtship calls were expected to be sex specific. This was confirmed, as these were merely produced by males in both cases. Long-distance vocalizations in ungulates and bats however, seemed more sex specific, i.e. more long-distance vocalizations are exclusively used by individuals of one sex within a species, than in simians. In case of ungulates, this apparent sexual specificity might be caused by the fact that most species included belonged to the family of the *Cervidae* and *Bovidae*. All of these species, except one, had mate defence polygyny, which was most often established by forming harems. It has been found that ruminants, including species of *Cervidae* and *Bovidae*, with harem mating systems have a higher level of sexual dimorphism than ruminants that are territorial polygynous or that are monogamous (Weckerly 1998). This relatively high level of sexual dimorphism may cause sexual differences in vocal behaviour. If more species of ungulates with mating systems other than harem polygyny had been included, like species of *Equidae*, this sexual specificity might not have been that obvious. In case of bats, the amount of available data is too small to form a conclusion about the contribution of males and females to the production of long-distance vocalizations.

8.5 Further findings
During data acquisition, I came across some noteworthy aspects of long-distance vocalizations. First of all, within all three taxa both low-frequency calls (e.g. Guatemalan black howler monkey (*Alouatta pigra*; around 700 Hz: Kitchen 2004), fallow deer (35 Hz: Reby et al. 1998), African elephant (< 20 Hz: Soltis 2010)) and high-frequency calls (e.g. common marmoset (*Callithrix jacchus*; around 20 kHz: Bezerra and Souto 2008), heart-nosed bat (*Cardioderma cor* ; 12 kHz: Vaughan 1976), wapiti (*Cervus canadensis*; up to 2 kHz: Feighny et al. 2006)) were used to communicate over long distances. The use of high frequency long-distance calls is rather surprising considering the high attenuation rate of high frequency sounds (Wiley and Richards 1978). However, research on the high-frequency loud calls of the pygmy marmoset (*Cebuella pygmea*; over 8 kHz: Snowdon and Hodun 1981) shows that high-frequency calls may be advantageous as the frequencies of ambient noise are lower than those of the call. In this way, sounds in the environment do not interfere with the vocal communication within pygmy marmosets (Snowdon and Hodun 1981). Furthermore, these high frequency calls seem inaudible for raptors, which are the main predators of pygmy marmosets. So, high frequency loud calls may be an adaptation against predatory eavesdroppers, preventing detection by predators (Snowdon and Hudon 1981). Additionally, the costs of a reduced audibility range may be of less consequence to the pygmy marmoset as its home range is only a hundred meters in diameter. So, its vocalizations do not need to travel

further than a hundred meters to communicate with its group members within its home range. Indeed, the audibility range of loud calls in pygmy marmosets is just a hundred meters (Snowdon and Hudon 1981).

Secondly, some long-distance vocalizations were used during short-distance communication involving greeting, copulatory behaviour and affiliative behaviour. This was unexpected as high intensity calls do not seem to have an advantage over low intensity calls in these interactions, opposed to vocalizations that are used in short-distance interactions like courtship or competition. However, when the costs of producing these vocalizations during short-distance interactions are minimal, this behaviour is not selected against.

8.6 Conclusion

The most important finding is that both males and females within species of simians, ungulates and bats produce long-distance vocalizations. This and the distinct functions of long-distance vocalizations in these taxa, suggest that these vocalizations have evolved under various environmental and social conditions. It would be interesting to investigate whether similar results are found in other mammalian taxa that use long-distance vocalizations, like cetaceans (but see Appendix C), carnivores, pinnipeds and rodents.

Moreover, it may be possible that long-distance vocalizations, like song in songbirds, were already present in ancestral primates, ungulates and bats. The relatively high amount of literature on primate long-distance vocalizations could be used to reconstruct the ancestral state of these vocalizations in primates. This may provide insights in the evolutionary process of long-distance vocalizations in primates and mammals in general.

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Appendix A

List of species of simians, ungulates and bats with long-distance vocalizations that were included in the data.

Simians	Ungulates	Bats
Alouatta caraya	Aepyceros melampus	Antrozous pallidus
Alouatta guariba (clamitans)	Alces alces	Cardioderma cor
Alouatta palliata	Axis axis	Dermanura watsoni
Alouatta pigra	Bison bison	Ectophylla alba
Alouatta seniculus	Capreolus capreolus	Epomophorus wahlbergi
Ateles belzebuth	Cervus albirostris	Hypsignathus monstrosus
Ateles geoffroyi	Cervus canadensis (rooseveltii)	Nyctalus noctula
Brachyteles hypoxanthus	Cervus elaphus	Phyllostomus hastatus
Cacajao melanocephalus	Cervus nippon	
Callicebus cupreus	Dama dama	
Callicebus nigrifrons	Elephas maximus (maximus)	
Callicebus personatus	Equus africanus (somaliensis)	
Callimico goeldii	Equus ferus (przewalskii)	
Callithrix jacchus	Equus grevyi	
Cebus capucinus	Equus kiang (holdereri)	
Cercocebus albigena	Equus quagga (boehmi)	
Cercocebus aterrimus	Gazella subgutturosa	
Cercocebus galeritus	Loxodonta africana	
Cercocebus torquatus atys	Muntiacus muntjak	
Cercopithecus campbelli	Muntiacus reevesi	
Cercopithecus diana	Oreotragus oreotragus	
Cercopithecus mitis (stuhlmanni)	Ovibos moschatus	
Cercopithecus neglectus	Procapra gutturosa	
Colobus badius	Procavia capensis	
Colobus guereza	Rangifer tarandus	
Colobus polykomos	Saiga tatarica	
Colobus vellerosus		
Gorilla gorilla		
Gorilla beringei beringei		
Hoolock hoolock		
Hylobates agilis		
Hylobates klossi		
Hylobates lar (entelloides)		
Hylobates moloch		
Hylobates muelleri		
Hylobates pileatus		
Leontopithecus rosalia		
Macaca maura		
Macaca nigra		
Macaca silenus		
Macaca tonkeana		
Nasalis larvatus		
Nomascus concolor (jingdongensis)		
Nomascus sp. Cf. nasutus		

Nomascus gabriellae

Nomascus leucogenys

Pan paniscus

Pan troglodytes (schweinfurthii and verus)

Papio cynocephalus (ursinus)

Papio hamadryas (ursinus)

Papio papio

Pithecia pithecia

Pongo pygmaeus (wurmbii)

Presbytis comata

Presbytis johnii

Presbytis potenziani

Presbytis thomasi

Procolobus verus

Saguinus fuscicollis

Saguinus imperator

Simias concolor

Symphalangus syndactylus

Appendix B

List of references that were used for data acquisition on long-distance vocalizations in simians, ungulates and bats.

Simians

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Appendix C

Initially, the aim of this study was to research the use of long-distance vocalizations in cetaceans as well. However, many cetaceans had a relatively large and complex repertoire, making it hard to distinguish distinct vocalizations or vocalization sequences. Furthermore, many aspects of their vocalizations, like audibility range or the sex by which it was produced, and aspects of their social life were unknown, making it impossible to make predictions about the presence and function of long-distance vocalizations in cetaceans. However, for some species the use of vocalizations for long-distance communication is known, for instance for fin whales (*Balaenoptera physalus*: Croll et al. 2002). Moreover, I found that long-distance vocalizations may be present in some other species of cetaceans (Table 1).

Table 1. Species of cetaceans that potentially produce long-distance vocalizations.

Balaena mysticetus

Balaenoptera acutorostrata

Balaenoptera borealis

Balaenoptera musculus

Balaenoptera physalus

Cephalorhynchus hectori

Delphinapterus leucas

Delphinus delphis

Delphinus spp.

Globicephala macrorhynchus

Globicephala melas

Grampus griseus

Inia geoffrensis

Lagenorhynchus albirostis

Lagenorhynchus obliquidens

Lagenorhynchus obscurus

Megaptera novaeangliae

Monodon monoceros

Orcinus orca

Peponocephala electra

Physeter macrocephalus

Pseudorca crassidens

Sotalia fluviatilis

Sotalia guianensis

Sousa chinensis

Sousa teuszii

Stenella coeruleoalba

Stenella longirostris

Tursiops aduncus

Tursiops truncatus

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Croll, D. A., Clark, C. W., Acevedo, A., Tershy, B., Flores, S., Gedamke, J., & Urban, J. (2002). Bioacoustics: Only male fin whales sing loud songs. *Nature*,*417*(6891), 809-809.