Vocal communication of wild western gorillas (*Gorilla gorilla*)

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Abstract of the Dissertation

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The communication system of a species is the fundamental basis upon which animal social relationships are built and contributes to a species' social organization. Among group-living anthropoid primates that inhabit forested environments, vocal signals are likely to be one of the most important communication channels because reduced visibility limits the use of visual communication. Accordingly, many primates have different vocalizations that convey meaningful information to conspecifics about caller behavior, external objects or events and cues used in recognizing individuals. Thus, in order to better understand the social and ecological factors that have shaped a species' vocal communication system, we must identify the species' repertoire of vocalizations, the behavioral contexts in which they are produced and the functions they serve, as well as the information encoded in their acoustic structure, such as individual distinctiveness, and how it varies across different calls.

This dissertation investigates the vocal behavior of wild western gorillas (*Gorilla gorilla*), in particular the use and function of calls used during within-group communication. I address three main questions regarding their vocal behavior: 1) How do changes in ecological and social factors affect the species' vocal repertoire and usage of their vocalizations? 2) What is the role of western gorilla long-distance calls in maintaining group cohesion? 3) What is the adaptive function of individual vocal cues in the western gorillas' vocal repertoire? To address these questions, I collected behavioral data on wild western gorillas and acoustic recordings of their calls at the Mondika Research Center (Central African Republic and Republic of Congo). The results indicate that 1) the vocal repertoire of western gorillas is largely similar to that of mountain gorillas (*Gorilla beringei*) although the two species differ to some degree in call usage and context. For example, most calls used by western gorillas are associated with specific behavioral contexts. Second, group composition and spatial spread determined the type of calls each age-sex class uses as well as the behavioral context in which they are given. Third, dispersed group members in western gorillas use long-distance calls in within-group communication to regain spatial proximity. And finally, all calls displayed acoustic variation and individual distinctiveness, suggesting that individual vocal cues might have evolved to facilitate the functions of all vocal signals used during within-group vocal communication, including those used at both close and at greater distances.

Taken together, these results indicate that the vocal behavior of western gorillas has been shaped by several ecological and social factors. Group composition may have influenced the repertoire of each age-sex class, the limited visibility of their environments may have selected for more calls used in specific contexts to facilitate within-group communication, and the greater group spread, compared to that of mountain gorillas, might have selected for using long-distance calls within the group when individuals are separated. Their call types display considerable inter- and intra-individual acoustic variability, suggesting that each of their calls might encode more information than just identity cues. Since all calls were individually distinct, this study suggests that the distance at which communication occurs and the social context in which calls are given might have selected for individual cues in gorilla vocal signals. Finally, providing the first data on western gorilla vocal behavior, this study enlarges the comparative data on ape vocal communication, which is indispensable for the development of theories on the evolution of human language.

“Probably no animal has fired the imagination of man to the same extent as has the gorilla. Over a hundred years have passed since the discovery in 1847 of this giant ape in the forest of West Africa, yet the gorilla has remained a creature of mystery.”

George B. Schaller

To my parents,
Manuela and Maurizio.

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I will never forget the faces of my parents, Manuela and Maurizio, when I told them that I wanted to spend one year in the tropical rainforest observing and collecting data on wild western gorillas for my undergraduate thesis. They suddenly became speechless and I could see their mixed feelings of concern and happiness. The dangers entailed in spending time in the wilderness of Congo spurred worries in them. Yet they were also happy to see my determination about what I wanted to do. They have been the major supporters of this dream since the beginning, and I will always be indebted to them.

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In 2003 I spent one year in the forest at Mondika Research Center. In the months Diane was at the field site, I learned how to collect, check, and store behavioral data, and more importantly how to not be scared of a 200 kg angry, screaming, and charging male gorilla.

Furthermore, Diane transmitted her enthusiasm for discovery and the enjoyment of spending a day in the forest in contact with these amazing animals (even if in the swamp!). This initiatory experience was one of the most interesting, challenging, and awe-inspiring of my entire life. The forest, the gorillas, Diane, and the Baihaka trackers taught me so much about life and myself that I find hard to find words to thank them.

After this incredible initial experience, I was convinced that I needed to go back to Mondika as soon as possible. This dream became a reality when Diane asked me if I was interested in entering Graduate School. Since then, Diane has been my academic advisor and taught me how to be a researcher, providing me with the skills to critically approach a research question and prepare manuscripts. She also constantly believed in me, even when I was not sure of myself. I cannot imagine accomplishing my dissertation without her mentoring and support.

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CHAPTER ONE

Introduction

According to socio-ecological theory, the social system of a species is a complex function of ecological and social constraints (Crook and Gartlan 1966; Terborgh and Janson 1986), which represents the outcome of individual strategies of survival and reproduction (Hinde 1976). Individuals may lead a solitary life or associate with other individuals from a period of a few days up to one that spans their entire life. In the case of group-living animals, body size, competition, predation pressure and reproductive strategy will favor groups of a particular composition and size (Dunbar 1980; van Schaik 1989). Both group-living and solitary animals have developed ways to communicate with their conspecifics. In solitary species, the communication functions in territory defense, intra-sexual competition, and/or mate attraction (Hauser 1996). Since solitary individuals are usually fairly distant from each other, communication generally occurs through olfactory and/or acoustic signals. When animals live in groups, visual, auditory, tactile and olfactory signals are used for social communication in a large set of circumstances (Zimmermann 1992; Hauser 1996; Fleagle 1999). Among group-living anthropoid primates that inhabit forested environments, vocal signals are likely to be the most important communication channel because reduced visibility limits the use of visual communication (Aylor 1971; Robinson 1981; Boinski and Campbell 1996; Uster and Zuberbühler 2001; Zuberbühler 2006).

Primates need to communicate with conspecifics from their own group, from other groups, and solitary individuals in order to acquire vital social and ecological information and to form those social relationships that return the greatest benefit. Inter-group communication usually occurs over long distances, and thus these vocal signals are adapted to travel long distances in the environment (e.g., Brown 1989; Cowlishaw 1992; Mitani and Stuht 1998; Schneider et al. 2008). Intra-group vocal communication may occurs over a range of distances, since group members may need to communicate at close range (e.g., while resting together), yet they also may need to communicate over long distances when the group is dispersed (e.g., while traveling or feeding). When adjusting to such differing circumstances, animals need to use different types of vocalizations (long and close distance range), or they may need to modify the acoustic features of a vocalization depending on the distance to other group members (Masataka and Symmes 1986; Mendes and Ades 2004; Brumm and Slater 2006; Sugiura 2007). The distance between the caller and the receiver affects the acoustic features of vocalizations because signals transmitted over long distances are subject to higher levels of attenuation, degradation and distortion (Morton 1975; Waser and Waser 1977; Wiley and Richards 1978). To overcome the environmental constraints of sound propagation, animals have developed several strategies such as lowering or increasing the fundamental frequency to avoid frequencies occupied by a high level of background noise (e.g., lowering: Palombit 1992; Sugiura et al. 2006; e.g., increasing: Egnor and Hauser 2006); vocalizing at specific times of the day when background noise is lower (Horwich 1976; Marler and Tenaza 1977; Sekulic 1982; Garcia-Rutledge and Narins 2001; Egnor et al. 2007); and increasing the number and/or duration of vocal signals (reviewed in Brumm and Slabbekoorn 2005). Calls that are used in within-group communication show acoustic properties that, in some cases, do not transmit well through the environment

(Waser and Waser 1977). Thus, there is a direct relationship between the acoustic proprieties of primate calls and the function for which they are used. Primate vocal signals may be divided into two gross categories, long and close calls, according to the distance at which the signals are typically transmitted (Mitani and Stuht 1998). They may encode several kinds of information depending upon the social and/or ecological function they serve in the organization of group-living primates.

As in speech, primate calls are multidimensional, representing many things at the same time (Cheney and Seyfarth 2007). Accordingly, many primates have different vocalizations that convey meaningful information to conspecifics about caller behavior, external objects, or events as well as provide cues for recognizing individuals (Seyfarth et al. 2005). Therefore, identifying the array of vocalizations used, the behavioral context in which they are produced, the functions they serve, and the information encoded in their acoustic structure, allows us to understand how socioecological factors have shaped the vocal communication system of each species.

This dissertation investigates the vocal behavior of wild western gorillas, particularly the use and function of calls used during within-group communication. I collected behavioral data and acoustic recordings of the vocalizations of a fully habituated western gorilla group in its natural environment, which allowed me to address a series of questions on the vocal behavior of this little known ape species. First, how similar are vocal repertoire and call usage in closely related species that inhabit different environments and vary in social and ecological factors? Second, what are the functions and mechanisms behind the use of long contact calls? Third, what are the functions of individually distinct vocal cues across the species' vocal repertoire?

Vocalizations and Social Systems in Hominoids

Apes (superfamily Hominoidea) display an array of different social organizations with wide variation in the degree of gregariousness, group size and composition. Orangutans (*Pongo* spp.) are solitary, gibbons and siamangs (family Hylobatidae) live in territorial pairs, chimpanzees and bonobos (*Pan* spp.) form fission-fusion societies composed of several males and females, and mountain gorillas live in cohesive polygynous groups in which all individuals travel, feed, and sleep together and are rarely less than 50 meters from all other group members (Strier 2011; Harcourt and Stewart 2001). Not surprisingly, ape communication systems reflect these differences and have evolved to cope with different social and ecological needs (Marler 1976). Gibbons have acoustic signals that travel farther than the extension of their territory, thereby seem to regulate inter-group spacing (Chivers and MacKinnon 1977; Raemaekers et al. 1984; Mitani 1985a; Raemaekers and Raemaekers 1985). Since gibbon groups often contain only two adult individuals, described as “not very talkative” (Brokelman pers. comm.), the requirement for complex intra-group vocal communication may be reduced. Technical constraints, however, have limited the study of close calls in gibbons to a few pioneering descriptive studies (Chivers 1974; Ellefson 1974) and more data are needed to confirm this possibility. Solitary orangutans primarily communicate vocally to locate mates and advertise their own location to competitors over long distances, and thus loud calls dominate their repertoire (Mitani 1985b). Chimpanzees and bonobos live in more socially complex environments, interacting with upwards of 100 other individuals of differing sex, rank and relatedness, often spread over long distances, with party composition changing frequently (Goodall 1986; Nishida 1990; Boesch and Boesch-Achermann 2000). Accordingly, their vocal communication system seems to be fairly complex, including long calls used to coordinate spacing of individuals (Marler 1976; Clark 1993) as well as a large number of close and long calls used in social contexts, such as when rejoining parties after an absence, acknowledging rank differences, or in communication between mothers in nursery groups (Marler 1969; Goodall 1986). Mountain gorillas live in groups with one dominant silverback male, several adult females and their offspring, and in 40% of groups, one or more additional lower-ranking adult males (Harcourt 1979a; Watts 1996). Since Karisoke mountain gorilla groups are cohesive and individuals spend most of their time in close proximity (Vedder 1984; Watts 1991), close calls make up the majority of the vocal repertoire, with long calls used only by males in inter-group communication, potentially to maintain the spacing between different groups and never used in within-group communication (Harcourt et al. 1993).

Gorilla Ecology, Social System and Vocal Communication

Mountain gorillas (*Gorilla beringei*) are among the most herbivorous of primates (Schaller 1963; Fossey and Harcourt 1977; Watts 1984; but see Rothman et al. 2007) and because their food is relatively abundant and evenly distributed, individuals face little feeding competition (Harcourt and Stewart 2007). One silverback male, dominant to all other individuals, represents the center of activities (Schaller 1963), and plays an important role in diffusing conflicts between females (Harcourt and Stewart 2007). Grooming, although rare, occurs most frequently between males and females, initiated primarily by the females (Schaller 1963; Harcourt and Stewart 2007). This suggests that the most important social relationship for each female is that with the group male, and that social relationships between non-kin females are relatively less important (Harcourt and Stewart 2007). It would thus be expected that vocal communication also reflect this pattern, exchanged more frequently between each female and the male rather than between females. Males have often been described as the major decision-makers about when and where to move (Watts 2000). Their displays, especially during the end of a resting bout, have been interpreted as visual information of the male's location, intention to move, and preferred traveling direction (Schaller 1963; Harcourt et al. 1986; Watts 2000). Group movement has been described as directed by the dominant male who may stay at the end of the moving group following females, adjusting his speed with theirs (Schaller 1963; Watts 2000). Thus, it may be that group cohesion is more dependent upon each female's coordination with the alpha male, rather than with nearest neighbors, as has been found in other taxa with differing social structure.

The vocal repertoire of Karisoke mountain gorillas has been well studied. Their vocal repertoire consists of: 1) long-distance calls, used by males but not females during inter-group encounters, and 2) a variety of close-distance calls, including grunts, grumbles, aggressive vocal signals, and others, used by all age-sex classes to varying degrees (Harcourt et al. 1993). During inter-group encounters, males exchange loud vocalizations and chest-beats, which are believed to play a functional role in male-male competition, allowing males and females to assess the relative quality and/or strength of competitors. The most common close calls are grunts and grumbles, which are emitted in many different contexts, most commonly (60%) in response to the vocalization of another gorilla (Harcourt et al. 1986). Adult males vocalize more frequently and have a larger repertoire than females (Fossey 1972; Marler 1976; Harcourt et al. 1993). One particular close call (the double grunt) has been investigated in detail in the past (Seyfarth et al. 1994; Stewart and Harcourt 1994; Harcourt and Stewart 1996) and has been suggested to serve many functions including: signaling the caller's intention to move, provoking responses from other group members, notifying others of the caller's intention to resume feeding, and generating consensus in order to coordinate travel departure (Seyfarth et al. 1994; Stewart and Harcourt 1994). However, to date, no study has tried to integrate the varying functions of gorilla calls into a broader understanding of how ecology and sociality have shaped their vocal communication, allowing groups to maintain cohesion and to communicate social needs, thereby permitting the functioning of stable groups through time. One way to achieve this goal is by examining the relationship between ecological variation and the vocal communication system in closely related species.

Western gorillas (*Gorilla gorilla*) are closely related to mountain gorillas. The ecological conditions vary considerably between the two species, providing a natural experiment to examine how changes in group cohesion, daily travel distances, and social relationships impact vocal communication in closely related species. Western gorillas live in lowland forests and are more frugivorous than mountain gorillas (e.g., Doran-Sheehy et al. 2004; Rogers et al 2004; Doran-Sheehy et al. 2009; but see: Rothman et al. 2007). As a result their daily path length is roughly four times as long as that of mountain gorillas, and when feeding on fruit or traveling to swamps, western gorillas travel quickly over long distances in a highly directed fashion (Goldsmith 1999; Doran-Sheehy et al. 2004). Such long-distance travel poses communication challenges not faced by mountain gorillas. Additionally, at some sites, western gorilla home-range overlap with other groups is greater than that of mountain gorillas and encounters with other groups (or solitary males) occur four times more often than in mountain gorillas (Doran-Sheehy et al. 2004), potentially affecting the use of long calls. Additionally, it has long been hypothesized that group members forage less cohesively than mountain gorillas (Tutin 1996; Doran and McNeilage 2001; Bermejo 2004), and might form subgroups (Remis 1997), although to date no quantitative data on group spacing are available. However, if so, then distances between individuals will vary considerably throughout the day, which may necessitate more varied and extensive communication to maintain group cohesion and coordinate travel.

Communication and Group Cohesion

Gorilla groups, like those of other primates, are composed of individuals differing in age, sex, and reproductive state. As a result, at any given time, group individuals may differ in their metabolic requirements and competitive and reproductive strategies. If individuals act independently and according to their needs, reduced group cohesion could result. For example, lactating females have higher energetic demands and may need to feed longer or on different food items than other group members, leading to differences in activity budgets and travel decisions and resulting in their separation from other group members (Kummer 1968; Fischhoff et al. 2007). Individuals of lower rank may be excluded from food patches, causing them to forage separately from other group members (e.g., van Noordwijk and van Schaik 1987). These different requirements and motivations may cause fluctuating levels of cohesion within the group. For the group to maintain cohesion and move as a unit, individuals must vary in their use of communication (i.e., how far the call travels) to accommodate changes in distance relative to other group members. Recent evidence indicates that within-group communication plays an important role in regulating interactions involving conflicts of interest among group members (Silk et al. 2000).

Studies that focused on the mechanisms and strategies by which group-living animals maintain cohesion and coordinate movements are still scant. Most research has been conducted on arthropod (e.g., Dyer and Seeley 1994; Seeley and Buhrman 1999; Visscher and Seeley 2007), avian (e.g., Radford and Ridley 2008; Arnold and Wilkinson 2011; Bode et al. 2012;

Carter et al. 2012), and mammalian taxa (e.g., marine mammals: reviewed in Smolker 2000; carnivores: reviewed in Holekamp et al. 2000), with limited studies of nonhuman primates (Boinski and Garber 2000). So far, little research of this sort has been done among hominoids, despite its significance for reconstructions of the evolution of human sociality and communication systems.

In species with fission-fusion social systems, loud calls are often used to maintain connections between dispersed members of the same community (chimpanzees: Mitani and Nishida 1993; Guinea baboons: Byrne 1981; spider monkeys: Chapman and Weary 1990; Ramos-Fernandez 2005; bonobos: Hohmann and Fruth 1994). In more cohesive species, loud calls (i.e., lost or contact calls) have often been assumed to function as a means of rejoining dispersed/lost individuals with the rest of the group (Robinson 1982; Snowdon and Hodun 1985; Cheney et al. 1996; Di Bitetti 2001), although this has rarely been tested (but see: Cheney et al. 1996; Ramos-Fernandez 2005; Digweed et al. 2007). To investigate the function of vocal communication in regulating intra-group spacing and cohesion, it is important to recall that more than one call type may contribute to spacing mechanisms in different ways (Palombit 1992). Long calls may be used by isolated individuals to regain contact with the group while different close calls may attract group members to a food resource, maintain contact among individuals at short distances (in dense vegetation) and regulate intra-group spacing. Two acoustic features of primate vocalizations have been proposed as requisites for playing a role in maintaining general group cohesion: 1) individual variation, which allows listeners to distinguish between calls from familiar individuals and those emitted by non-familiar conspecifics (e.g., Snowdon et al. 1983; Wich et al. 2002), and 2) acoustic localizability, which allows listeners to locate the caller (Brown et al. 1978). These qualities are expected to be stronger in calls used when visual contact is limited (i.e., over long distances or in areas of low visibility) compared to calls used when other cues may contribute to the identification of the caller. Individual differences have been documented in the structure of contact vocalizations in a number of primate species (Macedonia 1986; Hauser 1991; Mitani et al. 1996; Rendall et al. 1998) and several studies have shown that listeners can discriminate the calls of different individuals, responding more strongly to those of particular individuals (Cheney and Seyfarth 1982; Rendall et al. 1996; Hammerschmidt and Fischer 1998; Fischer et al. 2000).

Acoustic Variability in Primate Vocal Signals

Technical advances in the study of animal vocal communication allowed to show how many species display higher acoustic variability in their vocal repertoires than previously thought (e.g., birds: Robisson et al. 1993; Evans and Evans 2007; Berg et al. 2011; bats: Boughman 1997; Arnold and Wilkinson 2011; Carter et al. 2012; ungulates: Reby et al. 2005; Vannoni and McElligott 2007; carnivores: Theis et al. 2007; Schehka and Zimmermann 2009; primates: Hauser 1991; Fischer et al. 2001; Fischer et al. 2002; Clay and Zuberbühler 2011; Leliveld et al. 2011). This challenges the idea of innate, fixed production of animal vocal systems and their limited flexibility, with any variation long considered involuntary and a consequence of morphological changes (Gautier and Gautier 1977). It is now recognized that vocal signals have the potential to carry different kinds of information, although it is less clear if these subtle acoustic differences are always meaningful for the animals. For instance, a vocal signal may transmit information regarding a stimulus such as the presence and type of a predator (e.g., Seyfarth et al. 1980; Wheeler 2008) or the quantity and quality of a food source (e.g., Hauser et al. 1993; Slocombe and Zuberbühler 2006), as well as the identity of the “caller”. In some species specific calls have been found to contain acoustic features associated with individual strength or agonistic ability (Steenbeek et al. 1999; Wich and Nunn 2002) and are thought to be honest indicators of male competitive ability (Kitchen et al. 2003; Fischer et al. 2004; Pfefferle and Fischer 2006; but see: Harris et al. 2006). Other studies have found that calls can provide information about the caller's internal state (Seyfarth and Cheney 2003; Lemasson et al. 2012). Most important, the acoustic properties of vocal signals vary across individuals within or between groups, which provides the potential to carry information about caller identity (Waser 1977; Macedonia 1986; Hauser 1991; Butynski et al. 1992; Cheney et al. 1996; Mitani et al. 1996; Rendall et al. 1996; Dallmann and Geissmann 2001), enabling individuals to distinguish calls of familiar individuals from those of unfamiliar individuals (e.g., Snowdon and Cleveland 1980; Weiss et al. 2001; Wich et al. 2002; but see: Teixidor and Byrne 1997; Maciej et al. 2013). Acoustic properties of calls have also been shown to vary between groups in several species, and have been interpreted to indicate group membership (e.g., Mitani et al. 1992; Mitani et al. 1999; Crockford et al. 2004; de la Torre and Snowdon 2009; Candiotti et al. 2012).

Individual Vocal Cues

Individually distinct vocalizations have been shown to occur in many different species and to be of crucial importance in many of the functions served by vocal signals (birds: Jouventin and Aubin 2002; deer: Vannoni and McElligott 2007; koalas: Charlton et al. 2011; hyenas: Theis et al. 2007; hyraxes: Koren and Geffen 2011; pandas: Charlton et al. 2009; primates: Waser 1977; Cheney and Seyfarth 1980; Snowdon and Cleveland 1980; Owren and Rendall 2003; Miller and Thomas 2012). As mentioned earlier, they allow for recognizing familiar versus unfamiliar individuals (Snowdon and Cleveland 1980; Weiss et al. 2001; Wich et al. 2002; Herbinger et al. 2009), as well as neighbors versus strangers (e.g., Tripovich et al. 2008; Feng et al. 2009; Mager et al. 2010; Kirschel et al. 2011; Digweed et al. 2012), and kin, especially parents and offspring, versus non-kin (Gouzoules and Gouzoules 1990; Pitcher et al. 2010; Briefer et al. 2012; Kessler et al. 2012). They allow individuals to monitor the behavior and social interactions of other group members (e.g., Cheney et al. 1995; Bergman et al. 2003; Crockford et al. 2007; Wittig et al. 2007) and are essential in maintaining cohesion among group members (e.g., Cheney et al. 1996; Janik and Slater 1998; Leighty et al. 2008).

Four non-mutually exclusive hypotheses have been proposed to explain the evolution of individually distinct vocal signals and their variation across a species' vocal repertoire. These explanations are based on 1) the distance at which calls are given (or exchanged), 2) the social or 3) spatial context in which calls are produced, and 4) the direct effects to the nervous system they can elicit in receivers. As early as the 1960s, Marler (1967) formulated the distance communication hypothesis, in which he proposed that calls given or exchanged over long distance should be more distinct than those given at close distances, since no other cues could be simultaneously used to enable listeners to recognize the identity of the caller. Three decades later, the social function hypothesis proposed by Snowdon & Elowson (1997) hypothesized that close calls used in intragroup social interactions such as affiliative or threat calls (given toward a specific target) should be more individually distinct than louder (long) calls directed to a more generalized audience (e.g. the entire group). In 1998 Janik & Slater (1998) postulated that call types used to trigger group cohesion would be better suited to encode individual characteristics than those calls used in other social contexts (i.e., cohesion hypothesis). Finally, Owren and colleagues (Owren et al. 1997; Owren and Rendall 2001) proposed the structure-affective processing hypothesis to explain the asymmetries of identity signaling in baboons and redefine the mechanisms underlying animal vocal communication. They suggested replacing the "emphasis on linguistic and informational constructs/metaphors" with an "emphasis on influence" on listeners' behaviors and nervous systems (Rendall et al. 2009). They proposed that vocal signals may influence listeners in two major ways: (a) directly, through specific acoustic features commonly present in distress calls and alarm calls (sharp onset, high amplitude noise, repeated energy pulses or fluctuations of frequency or amplitude), which induce a "cascade of behavioral and physiological changes in listeners that involve the immediate cessation of ongoing activity and abrupt shifts in attention toward, and in movement away from, the stimulus" (Rendall et al. 2009: 1802-3), and (b) indirectly, eliciting a conditioned response in listeners from past experience (other calls). Accordingly, calls to which animals respond based on their past experiences may have been strongly selected for individual signaling whereas screams and alarm calls have not because they serve a narrower range of functions, which explains their very peculiar acoustic structures eliciting similar behavioral and physiological reactions in most taxa.

Subsequent research on red-capped mangabey (*Cercocebus torquatus*) and female Campbell's monkeys (*Cercopithecus campbelli*) have found that all call types were individually distinct, including contact, threat, loud, and alarm calls, although close calls given during social/affiliative contexts were most individually distinct (Lemasson and Hausberger 2011; Bouchet et al. 2012). In contrast, in solitary species or species where individuals are more widely separated, such as chimpanzees and mouse lemurs, long calls used when individuals are not in visual contact were more individually distinct than close calls (Mitani et al. 1996; Leliveld et al. 2011).

Few studies, and none on apes, are available that examine the adaptive function of individual variation and call distinctiveness across an entire species' repertoire (but see: mouse lemurs: Leliveld et al. 2011; red-capped mangabeys: Bouchet et al. 2012; Campbell's monkeys: Lemasson and Hausberger 2011). It remains unclear whether acoustic variation and individual distinctiveness vary throughout the repertoire in graded vocal systems characteristic of apes.

Study Site and Subjects

This study was conducted at the Mondika Research Center (50 km^2), which is located on the border between the Central African Republic (Dzanga-Ndoki National Park) and the Republic of Congo (021 21085900 N, 0161 160 46500 E) (Fig. 1.1.). The study area includes several habitat types, with different degrees of visibility: mixed tropical lowland forest (closed and open), mono-dominant *Gilbertiodendron dewevrei* (Caesalpiniaceae) forest (open), and swamp forest (closed and open). Data was collected in May-July 2007 and April 2009-May 2010 on one group of wild western gorillas and the male of a second group. All individuals were easily recognizable by their facial and body characteristics. The habituation of the first group began in 2001 and at the time my research started the entire group was already fully habituated (Doran-Sheehy et al. 2007). The group consisted of one silverback (adult) male, four to five adult females and their offspring. Group composition changed slightly through time. In 2007 the group included one male, four adult females and one juvenile female. At the end of 2008, one adult female died and a juvenile female dispersed from the group. During the same year two females immigrated into the group. Although one of the newly migrated females was quickly habituated to the presence of human observers, the second one remained shy for most of the data collection period, and I could not include her as a study subject. In 2008, the habituation of a second group of gorillas began, and in 2009-2010 I could follow the silverback (adult male) of this group to collect additional data. The second group consisted on one adult male, six females, one juvenile male, and six infants of varying age. However, most of the group members were not habituated and they commonly hid from human observers.

Overview of Thesis Chapters

In this section, I summarize the major objectives of each thesis chapter. Extensive background on previous studies and related theories/hypotheses is provided in the chapters themselves. While I am the primary author, thesis chapters Two, Three and Four will be submitted for publication to peer-review journals with coauthors, who contributed in the design of the study and/or the interpretation of the results. I therefore use the pronoun "I" in the following section but I will use "we" in each research chapter.

In Chapter Two, I provide the first quantitative description of the vocal repertoire of wild western gorillas, including a description of call types, calling rates, and the context of use. Using discriminant function analysis I test how well calls can be categorized by their acoustic structure. Then using behavioral data, I determine the contexts of western gorilla calls and whether they were given primarily in a single context. I investigate the occurrence of context-specific calls, analyzing their proportion in the vocal repertoire and daily vocal output (frequency). I compare my results to previously published data on mountain gorillas to determine how differences in ecological and social factors are associated with the species' vocal repertoire and usage of vocal signals.

Chapter Three addresses the function and mechanisms of western gorilla long calls used in within-group communication. I test whether calls function as long contact calls, and specifically if they are used to regain proximity when group members are separated. If they serve such a purpose, calls are expected to be individually distinct, given when individuals are separated, solicit a response from other group members, and, after calling, the distance among group members should be reduced. I investigate the mechanisms behind the use of these calls, assessing the spatial contexts of repliers and the responsibility of reunion. Finally, I compare the function of the western gorilla long call with the analogous call in mountain gorillas to determine the degree of flexibility in the production and usage of long calls in gorillas.

In Chapter Four, I investigate the function of individual distinctiveness across the vocal repertoire of western gorillas. I assess the acoustic variability within and between individuals of eight calls commonly uttered by adult females, and, using a multivariate approach, I determine how well each call can be assigned to the correct caller and whether some calls are more distinct than others. Since two major hypotheses (i.e., the distance communication hypothesis and the social context hypothesis) gained equal support in explaining the variation of acoustic variability and individual distinctiveness in primates' vocalizations, I test which of them better explains the pattern observed in the western gorilla vocal repertoire.

In the final chapter, I provide a summary and synthesis of the major results from this research in the context of previous research on primate vocalizations. Finally, I discuss some limitations of the present study, and consider future research directions, including the assessment of the functions served by commonly used calls and food associated calls, the presence of acoustic call subtypes and the implementation of playback experiments in the study of western gorilla vocal behavior.

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Tables and Figures

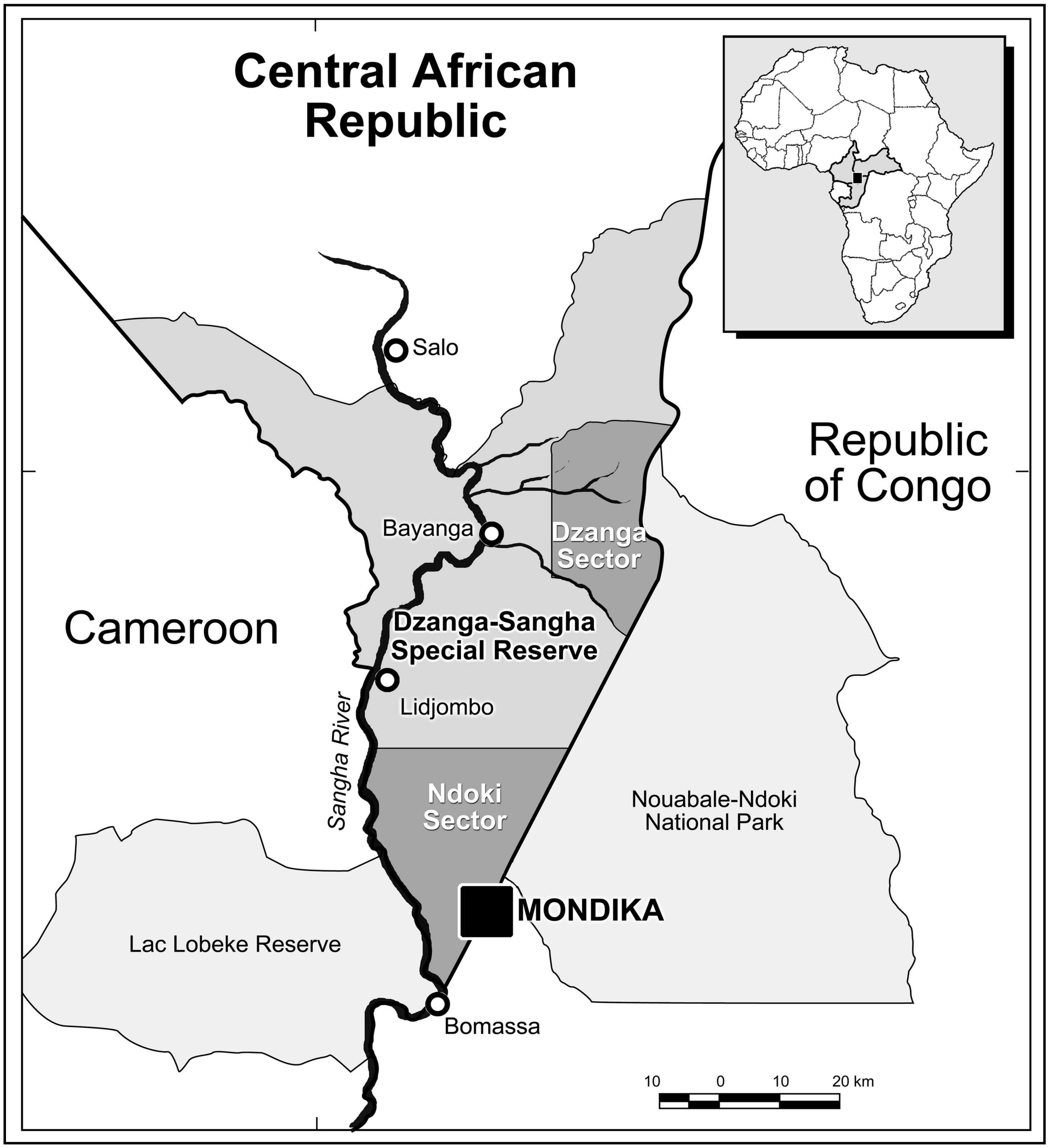

Fig. 1.1. Location of Mondika Research Center (from Mehlman and Doran 2002).

CHAPTER TWO

Western Gorilla Vocal Repertoire and Contextual Use of Vocalizations[1]

Abstract

Despite considerable interest in the vocal communication of non-human primates and its possible relevance to theories of language evolution, we know surprisingly little about how vocal communication varies between closely related species inhabiting differing environments. This study provides the first quantitative description of the vocal repertoire, calling rates, and call usage in wild western gorillas, and it compares it to the previous work on mountain gorilla vocal behavior. During 1,572 hours of focal follows (n = 533), we collected behavioral data on and recorded vocalizations (n = 2,163) of eight individuals in one group at Mondika Research Center (Republic of Congo). We supplemented these data with opportunistic recordings of an additional adult male in a second group. We used discriminant function analysis to test how well calls can be categorized by their acoustic structure, and used behavioral data to determine the typical usage of western gorilla call types. The vocal repertoire consisted of 17 call types. Twelve of seventeen call types were given primarily in a single context. However, these context-specific call types accounted for a relatively small proportion of the overall calling rate. Our results were similar to previous studies of mountain gorillas in that grunts and grumbles were used most frequently and that the silverback male vocalized more frequently than other group members.

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[1] Chapter submitted for publication to Ethology with D.M. Doran-Sheehy, Department of Anthropology, Stony Brook University, and K. Hammerschmidt, Cognitive Ethology, German Primate Center as co-authors.

However, compared to mountain gorillas, western gorillas used an additional call type (sex-whinny), used a second call type (hoot series) in a completely different context and by all age/sex classes, and used many more call types in a more context-specific fashion. Therefore, although vocal production is highly constrained by morphology and phylogeny, under differing social and ecological conditions the use and function of calls can differ even between two closely related species such as western and mountain gorillas.

Introduction

Communication is what separates or brings and maintains individuals together, creating and regulating social relationships that are critical for fitness and survival (Lucas and Freeberg 2010). While communication is multimodal (including visual, auditory, tactile, and olfactory modalities; reference), vocal signals are probably the most important communication channel for species such as nonhuman primates inhabiting forested environments, where visual cues may be limited (e.g., Altmann 1967; Robinson 1981; Boinski and Campbell 1996; Uster and Zuberbühler 2001). The study of the complete vocal repertoire, including the comprehensive analysis of the behavioral context of vocalizations, is a necessary step for investigating the vocal communication of any species. Additionally, it allows comparison across species of call structure, meaning, and function (e.g. Morton 1977; Mitani 1996; Owings and Morton 1998; Owren and Bachorowski 2003) as well as of repertoire complexity and flexibility (McCowan et al. 2002; Fedurek and Slocombe 2011; Gustison et al. 2012).

Despite considerable interest in the vocal communication of non-human primates and its possible relevance to theories of language evolution (Pinker and Bloom 1990; Zuberbühler 2003; Cheney and Seyfarth 2005; Seyfarth et al. 2010), we know surprisingly little about vocal communication in great apes, humans' closest living relatives (Slocombe et al. 2011). Early studies described and classified the vocal signals of chimpanzees (Reynolds and Reynolds 1965; van Lawick-Goodall 1968; Marler 1969), bonobos (de Waal 1988; Bermejo and Omedes 1999) and mountain gorillas (Schaller 1963) as part of their natural history. Interspecific comparisons of the vocal repertoires of African apes documented that they produce acoustically homologous calls, which may be broadly categorized into four gross acoustic groups, including grunts, hoots, screams, and barks (Marler 1969; Mitani 1996). However species differ in call rate and function, which appear to be linked to differences in group cohesion and social structure across species (Marler 1976; Marler and Tenaza 1977; Mitani 1996). For instance, mountain gorillas live in cohesive groups and vocalize frequently (8 times per hour), mostly using short-range grunts (Harcourt et al. 1993). In comparison, chimpanzees exhibit fission-fusion social dynamics, and vocalize half as frequently (4 times per hour), mostly using long-range pant-hoots (Clark and Wrangham 1993; Mitani 1996). Intraspecific comparison of vocal repertoires has also documented age/sex class and individual differences in both repertoire and vocal behavior (Fossey 1972; Harcourt et al. 1993; Mitani 1993; Hohmann and Fruth 1994). In both chimpanzees and gorillas, males are the highest-ranking individuals and have been reported to produce the largest vocal repertoire and to call more often than any other individual (reviewed in: Mitani 1996). In contrast, females and infants are more vulnerable to predators and infanticide, and it has been suggested that this is associated with less frequent calls and more fearful signals to seek protection and allies (Fossey 1972). In addition, as in other primates (i.e., weaning calls), apes produce calls in infancy (Fossey 1972; Goodall 1986) that they do not produce as adults.

Among African apes, western gorillas (*Gorilla gorilla*) remain largely unstudied and, as a consequence, their vocal repertoire is still unknown. Here we present data on the full repertoire, with the goal of assessing which calls are limited to specific contexts to explore the role they play in the vocal repertoire and vocal behavior of western gorillas. The first aim of this study is to categorize and quantitatively describe wild western gorilla vocalizations. Given the morphological and phylogenetic constraints inherent in vocal production (reviewed in: Hammerschmidt and Fischer 2008; Seyfarth et al. 2010), we predict that the vocal repertoire of western gorillas is very similar to that of the closely related mountain gorilla, and expect to identify the same 16 major vocalizations described for mountain gorillas (Schaller 1963; Fossey 1972; Harcourt et al. 1993; summarized in Table 2.1). However, clear differences in ecological and social factors exist between the two gorilla species, which might affect their communication systems and consequently their vocal behavior, as shown also in other primate species (Snowdon and Hodun 1981; Waser and Brown 1986; Oda 1996; Sugiura et al. 2006; Ey et al. 2009). For instance, mountain gorillas live in montane forests, and travel short distances while feeding on abundant herbs (Schaller 1963; Vedder 1984; Watts 2000; but see: Rothman et al. 2007). In contrast, western gorillas inhabit tropical lowland forests, and tend to travel greater daily distances, due to their diet including much more fruit (Goldsmith 1999; Doran-Sheehy et al. 2004). Most importantly, for the current study, these differences in diet and ranging appear to be associated with differences in group cohesion. In mountain gorilla groups, all individuals are usually found within a 50 m radius of one another (Vedder 1984; Watts 1991b). In contrast, western gorillas group members may forage on resources separated by several hundred meters (Tutin 1996; Doran and McNeilage 2001; Bermejo 2004). However, a systematic investigation of inter-individual distances has not been published for western gorillas. Previous comparisons between mountain gorillas and chimpanzees suggest that differences in cohesion are reflected in both the absolute and relative frequency in the use of long-range calls (Goodall 1986; Clark 1993; Harcourt et al. 1993; Mitani 1996). Thus, while close calls (e.g., grunts, grumbles, hums, copulation calls, whinnies, or aggressive calls) represent the bulk of mountain gorilla vocal output (Harcourt et al. 1993; Stewart and Harcourt 1994; Mitani 1996), western gorillas might rely also on long-range calls for within-group communication, due to reduced group cohesion.

In addition, due to the presumed reduction in visual cues in tropical forests (Morton 1975; Robinson 1981; Uster and Zuberbühler 2001; Zuberbühler 2006), context-specific calls might be more common in western gorillas to facilitate within-group communication and coordination (e.g., Boinski 1991; Boinski 1993). Consequently, our second aim is to assess the behavioral contexts of western gorilla vocalizations, and to compare them to those of mountain gorillas. Because it has been proposed that signals that are strongly associated to particular contexts have evolved in circumstances with strong selective pressure (Hauser 1996), we predict that western gorillas use them in mating, agonistic (within- and between-groups), and potentially threatening contexts (Hauser 1996). Finally, we assess the proportion of these calls within the complete repertoire and their occurrence in the vocal behavior of wild western gorillas (i.e., call rates). We discuss our results in light of current knowledge about mountain gorilla vocal behavior, to determine whether differences in call production and/or usage exist between the two species and, if so, whether they are explained by differences in gorilla socio-ecology.

Methods

Study Site and Study Subjects

Behavioral data and vocal recordings were collected over a 19-month period (June–August 2007; March 2009–June 2010) from a single, well-habituated group of wild western gorillas at the Mondika Research Center (02° 21′ 859″N; 016° 16′ 465″E), Central African Republic and Republic of Congo (Doran-Sheehy et al. 2004; Doran-Sheehy et al. 2007). During most of the study, the group included the same adult silverback male, four adult females, and two older infants (4.5 and 5 years old in 2009). In addition, three individuals were present for briefer periods of the study: two adult females, one present in 2007 but not in 2009 (death), the other in 2009-10 but not in 2007 (immigration) and finally a juvenile female of 6–7 years in age during 2007 but not in 2009-10 (natal dispersal). From November 2009 to May 2010 data were also collected for one silverback male, one adult female, and one infant of a second less habituated group.

Data Collection

Two teams, each containing two researchers (led by RS), collected simultaneous 2-hour focal animal samples (Altmann 1974) of the habituated silverback and one of the four group's adult females or, less frequently, juveniles or infants. Attempts were made to rotate sampling evenly among the females, and, because rates of vocalization may vary with time of day (e.g., Tenaza and Tilson 1977; Sekulic 1982; Egnor et al. 2007), to sample individuals equally across four time periods (7:00–9:30; 9:30–12:00; 12:00–14:30; 14:30–17:00). Total sampling of the habituated group included 533 focal follows, for a total of 1,572 hours (Table 2.2). This dataset includes 170 male follows (764 h), 319 female follows (695 h), including and average of 80 ± 6 follows and 173.8 ± 14.5 h per female, 12 juvenile follows (54 h), and 32 infant follows (59 h) (Table 2.2). The male in the less habituated group was observed for 54 hours during 17 focal follows of 2-4 hours each. However, we used only the recordings of his calls for the acoustic analysis, and did not use the behavioral data collected, because previous studies demonstrated that habituation level influences vocal behavior (Fossey 1972; Harcourt et al. 1986; Harcourt et al. 1993).

Each focal sampling hour was divided into six 5-minute periods of continuous sampling (0–4; 10–14; 20–24; 30–34; 40–44; 50–54; (Martin and Bateson 1993) alternated with six 5-minute periods of scan sampling (data used for a separate study). During continuous sampling, we noted all focal animal vocalizations, coding each as one of 17 call types, distinguishable by ear and corresponding to the 16 described previously for mountain gorillas (Schaller 1963; Fossey 1972; Harcourt et al. 1993; Table 2.1) plus a call type (sex-whinny) used by western gorillas but not described in mountain gorillas. When the observer could not identify the call, it was still recorded but as "miscellaneous" call type. For each vocalization, we recorded one of 14 mutually exclusive contexts, which were modified after contexts identified previously for mountain gorillas (Table 2.1). These contexts included: 1) within-group aggression; 2) alarm/alertness; 3) within-group display; 4) extra-group display; mother-infant nursing-interaction (when the focal individual was the infant), which was divided into two contexts 5) nipple contact and 6) nipple conflict; 7) foraging; 8) play; 9) resting; 10) pre-mating courtship behavior; 11) sex; 12) travel-pause; 13) traveling; and 14) other behaviors (see Appendix 1 for a detailed description of contexts). We also recorded focal animal activity at 1-minute instantaneous sampling intervals, using the same ethogram to provide a baseline measure of activity. At the beginning of the study, we computed inter-observer reliability between the two team leaders in the identification of the 17 call types and 14 behavioral contexts by means of Cohen' kappa. Data were included in the analysis only after consistency between observers was confirmed ($\kappa \geq 0.90$).

During continuous focal animal sampling periods, one team (led by RS) made digital recordings of all focal vocalizations (at a distance of <10 meters), using a portable Professional Solid State Recorder Marantz PMD671 and a Sennheiser MKH 416 short shotgun microphone, with a modular suspension (shock mount) and protected by a foam windshield (MZW415ANT). To increase the sample of rare vocalizations (i.e., hoot series, screams, and barks) used in the acoustic analysis, we also recorded 167 calls opportunistically, from females 5 and 6 in the habituated group, and male 2, female 7 and infant 3 in the less habituated group (Table 2.2).

Acoustic Analysis

Digital recordings were made in mono at a sampling frequency of 48 kHz, and saved as PCM format. We converted the sampling frequency of calls to one of three frequencies (22,050 Hz, 11,025 Hz, or 4,000 Hz), depending on the call frequency range, using the software Avisoft SASLab Pro 5 (R. Specht, Berlin, Germany). We used a frequency resolution of 1,024 points for the fast Fourier transform analysis, and worked with the Hamming window. Spectrograms were generated using acoustic software Avisoft. Of the 11,738 calls recorded, 2,163 were selected (Table 2.2) for further acoustic analysis based on the quality of spectrographs (i.e., low call-background noise ratio).

Gorilla vocalizations are typically composed of one or more call segments, each of which may be used once or more than once. For example, a bark is composed of a single segment (a loud, harsh sound) that could be given once (“bark”) or several times (“bark, bark, bark”). A copulation grunt is also composed of a single segment (a soft, guttural call), although it is always emitted in long sequences of more than 80 repeats (“huh, huh, huh…”). A double grunt is a soft vocalization that is composed of two distinct segments, which may be given once (“uhm-humh”) or several times (“uhm-humh, uhm-humh, uhm-humh”). We considered the minimum number of unique call segments that characterize a particular vocalization as the unit for acoustic analysis regardless of how often they are repeated (following Bezerra et al. 2010). Thus, in the three examples described above, the unit of acoustic analysis would be a single bark (bark), a single copulation grunt (huh) and a single two-syllabled double grunt (“uhm-humh”).

We used a custom software program (LMA 2011), developed by Kurt Hammerschmidt, to calculate a suite of acoustic parameters (Schrader and Hammerschmidt 1997) using the general result tool. We excluded acoustic characteristics that were highly influenced by external factors, such as habitat structure and recording conditions (i.e., call start and end parameters: Maciej et al. 2011). We then selected 28 acoustic characteristics related to time, frequency, dominant frequency bands measurements (DFB), global modulation, relative amplitude characteristics, and tonality (see Appendix 2), for use in the statistical analyses of vocalizations.

Statistical Analysis – Call Classification

We conducted acoustic analysis on 14 of the 17 call types (Table 2.3), excluding three call types (chuckles, roars, and barks) because of limited (n < 6) sample size or quality of acoustic recordings. We tested whether the call types were acoustically distinct by performing Discriminant Function Analysis (DFA; Klecka 1980) of 28 acoustic parameters (Appendix 2), using a stepwise procedure (with F-value thresholds set for acceptance or rejection of independent variables at F = 3.84 and F = 2.71) and a cross-validation Discriminant Function

Analysis, using leave-one-out cross validation procedure (Fischer et al. 2001; Wich et al. 2003; Barros et al. 2011). We present the results from both the DFA and cross-validated DFA, because the similarity of the results indicates that the profiles derived from calls are stable (Barros et al. 2011). We identified which acoustic parameters were significant in distinguishing call types, by running linear mixed models (LMMs; West et al. 2006) of each parameter that was significantly correlated ($r > 0.5$) to the functions generated by DFA. Within this analysis, we tested for differences across call types, while controlling for random effects (i.e., repeated and unequal sampling of individuals), as necessary. To adjust for multiple analyses, we used the Hochberg correction (Hochberg 1988).

When calls were misclassified we examined whether they were likely to be assigned to call types with similar acoustic structure. For this, we code each call type as one of nine broad acoustic categories (grunts, grumbles, singing, whinnies, whimpers, laughs, screams, barks, and hoots) on the basis of shared similarities in the spectrograms, following Beeman's (1998) acoustic classification of animal vocalizations, which were modified from the four principal acoustic groups identified in apes (i.e., grunts, screams, barks, and hoots). Number of call types within a call category ranged from 1 to 4 (see Appendix 3 for detailed description of both call types and acoustic categories).

Behavioral Data Analysis

From the focal data, we assigned 99.09% of calls (n = 11,053) to one of 17 call types that we could identify by ear and spectrographic analysis. We could not classify the remaining 0.9% of calls, because they were not heard clearly or were included in sequences of multiple call types (i.e., miscellaneous call type). Although the latter is a potentially intriguing area of study, we did not consider it further.

As a first step towards assessing the potential function of call types, we examined the context in which the 11,053 focal calls were used, following Seyfarth et al. (1980). We classified a call type as context-specific if it was given in the same behavioral context more than 75% of the time. We then examined whether this was the primary call type for this context, classifying it as signal-specific if it accounted for more than 75% of all calls given during that context (Seyfarth et al. 1980). Call types that were signal- and/or context-specific were classified as "specific calls". Call types that were neither context- nor signal-specific were classified as a "general calls." We determined the daily rate of each call type for each individual from focal follows, averaging the daily rates across months, before averaging monthly averages across the 12 months to obtain the overall rates. We used a one-way ANOVA (Miller 1997) to test for individual differences in adult calling rates (1 male and 4 females). To assess the relative contribution of general versus specific calls, we coded each call type as either general or specific, and then summed the rate of each call type within each category.

Results

Vocal Repertoire Based on Acoustic Characteristics and Usage

In the field, we distinguished 17 call types based on acoustic characteristics and their contextual use (Table 2.3). These include the 16 call types reported previously for mountain gorillas (Table 2.1) and one additional call type, the sex-whinny. Call types, named following the nomenclature used for mountain gorillas, are described in Table 2.3 (further description is provided in Appendix 3). The spectrograms are presented in Fig. 2.1. The 17 call types include both close-range (i.e. soft, low amplitude) and long-range (i.e. loud) calls, the latter used for within- and extra-group communication (Table 2.3). Close-range calls include single, double, cough, copulation grunts (Table 2.3; Fig. 2.1.A), grumbles, hums (Fig. 2.1.B), singing (Fig. 2.1.C), two types of horse-like sounds or whinnies (Fig. 2.1.D), whimpers (Fig. 2.1.F), and chuckles. Long-range calls comprise adult screams, high frequency infant cries (Fig. 2.1.G), barks, roars, and two hooting calls, with sequences of 15 ± 7 (n = 89; range = 3-44) tonal segments, distinguished by whether they were followed or not by chest beats (Fig. 2.1.E.1 and 2).

Age/sex classes seem to differ in the number of calls in their vocal repertoire (Table 2.3). As in mountain gorillas, the silverback male had the widest repertoire, using 12 call types, including five used exclusively by him (whinny, sex-whinny, hoot-chest beat, roar, and bark; Table 2.3). Adult females used nine call types, including one call (scream) used uniquely by adult and juvenile females (Table 2.3). Immature gorillas, including both infants and juveniles, used nine call types (Table 2.3), three of which (sing, cry and whimper) were not used by adults.

Structural Examination of Vocal Repertoire (DFA)

Discriminant function analysis (DFA) significantly distinguished among the 14 call types tested. Correct assignments were made significantly more often than expected by chance (7.14%), with a classification accuracy of 63% and 62% for DFA and cross-validated DFA analyses, respectively (*Wilks' λ* = 0.001; χ^2 = 14,149.1, $p < 0.001$). DFA generated seven canonical discriminate functions that explained more than 2% of the variance. The first three functions explained 84% of variance and were the only functions that had eigenvalues >1 (eigenvalues: F1 = 8.1; F2 = 3.2; F3 = 1.6). Function 1 was primarily correlated with frequencies and pitch parameters (i.e., df1mean, dfa1mean, dfa2mean, fp1mean, and pfmean; description of parameters in Appendix 2), and accounted for 53% of the variance. Function 2 was correlated with call duration and accounted for 21% of the variance. Function 3 was correlated with the maximum value of the first frequency in the call with more energy (df1max; see Appendix 2), and explained 10% of variance. The seven acoustic parameters used to generate the DFA were all significant when tested using LMMs and after controlling for multiple analyses. The percentage of calls assigned correctly to each call type (Table 2.4) by cross-validated DFA was 66% on average, ranging from 39% for copulation grunts to 89% for singing (DFA: 40 to 89%). All calls, except copulation grunts, grumbles, and hums, achieved ≥ 55% correct classification (Table 2.4). Mean values of most significant acoustic parameters for all call types are shown in Table 2.5.

When calls were misclassified, they were almost always assigned within the same broad call category (Table 2.4; Fig. 2.2). For example, 38% of single grunts and 61% of copulation grunts were misclassified, but most of these calls (single grunt: 20%; copulation grunt: 48%) were classified as other grunts (Table 2.4).

Context and Signal Specificity

Twelve out of 17 call types (71%) were context-specific, including cough-grunts (during aggression), copulation grunts (during mating), humming and singing (during foraging), sex-whinnies (during male courtship), infant whimpers (attempting nipple contact), infant cries (when nipple contact was rejected), screams (during escalated aggression), barks (when alarmed), and chuckles (during play; Table 2.6). Additionally the hoot-chest beats and roars were considered context-specific because they always occurred in a single context (hoot-chest beats:

during within- and between-group displays; roars: when the silverback charged humans during the habituation process). However, because roars were only heard during ad libitum sampling of unhabituated gorillas this call is not included in Table 2.6. All context-specific calls were given in a single context more than 97% of the time, except for hums, which were given in a context-specific way 91% of the time (Table 2.6).

Eight context-specific call types were also signal-specific (Table 2.7), including cough-grunts, copulation grunts, sex-whinnies, hoot-chest beats, whimpers, cries, screams, and play chuckles. The other context-specific call types (barks/roars, humming, and singing) were given in a single context (alarm in the former and feeding in the latter), but were not the only call types given during a specific activity. Thus, a total of eight call types (i.e., cough-grunts, copulation grunts, sex-whinnies, hoot-chest beats, whimpers, cries, screams, and chuckles) showed both signal- and context-specificity. Five call types (single grunt, double grunt, grumble, and non-sex whinnies) were neither context-specific (Table 2.6) nor signal-specific (Table 2.7), and were considered "general calls" (Table 2.3).

Most of call types used exclusively by a single age/sex class (87.5%) were context and/or signal specific. Context-specific call types used uniquely by the male appear to function in group defense (hoot-chest beat, bark, and roar) and courtship (sex whinny). Context-specific calls used only by females occurred during escalated within-group aggression (scream), and by infants in response to distress related to weaning (whimper, cry).

Occurrence of Specific and General Calls

On average, adult western gorillas vocalized at a rate of 8.9 ± 6.3 calls per hour (n = 5 individuals, range 18.7–3.0 calls per hour), although call rates varied among individuals

($\text{ANOVA}_{\text{adult}}$ $F = 92.27$; df = 4; $p < 0.001$). The mean overall calling rate of the male (18.6 ± 3.1 calls/h) was roughly triple that of the mean rate of females (6.5 ± 4.2 calls/h) or immatures (7.3 ± 4.3 calls/hour) (Fig. 2.3). The calling rate for specific calls (i.e., the sum of call rates of all context- and/or signal-specific call types) was similar between the male (2.5 calls/hour) and female (1.8 ± 1.4 calls/hour), whereas immatures had the highest specific call rate (4.1 ± 0.8 calls/hour). For the six-year-old juvenile, this rate resulted from relatively frequent humming, singing, and grumbling, whereas for infants, the common call types were primarily related to play and weaning (i.e., weaning/nipple contact) (Table 2.3). The male's calling rate for general calls (16.1 calls/hour) was much higher than either that of the females (4.7 ± 2.8 calls/hour) or immatures (2.67 ± 1.1 calls/hour), and therefore accounted for the difference in overall calling rate. The male's higher general call rate was primarily the result of his more frequent use of double grunts, which were given 10.42 calls/hour, and therefore more than 10 times the rate of other age sex classes (Table 2.3).

Although specific calls (signal- and or context-specific) account for a large part of the vocal repertoire (12 out of 17; 71%), they contribute relatively little to the overall daily vocal production (Table 2.3). The degree to which this is true varies across age/sex classes (Fig. 2.3), with the proportion of specific calls contributing to the overall call production lowest in the male (13.5%), intermediate in females (26.8%) and highest in immatures (58.3%).

Discussion

Western Gorilla Vocal Repertoire

Western and mountain gorillas diverged recently (approximately 1.75 million years ago) with evidence of even more recent gene flow (Thalmann et al. 2007; Scally et al. 2012), which together might lead to an expectation of high similarity between the two species. Accordingly, we found that the vocal behavior of the two species was very similar. We distinguished 17 call types produced by wild western gorillas on the basis of acoustic characteristics and behavioral contexts in which they were used. In both species, the silverback male had the widest repertoire and vocalized more often than either females or immature individuals (mountain gorillas: Fossey 1972; Harcourt et al. 1993; western gorillas: this study). Each age/sex class used exclusively some calls: whinnies, hoot-chest beat, roar, and bark were given only by the male, screams only by females and whimper and cry only by infants. As in mountain gorillas (Schaller 1963; Fossey 1972), the repertoire is fairly graded and call types are not discrete units. However, our analysis showed that call types were misclassified most exclusively within calls sharing similar acoustic properties (i.e., broad acoustic categories: grunt-like sounds within themselves, horse-like sounds within themselves, grumbles with hums, etc.).

In some cases, call variation was consistent with a general tendency of having specific acoustic characteristics linked to the presumed emotional state/level of arousal experienced by the animal (Motivational Structural rules; Morton 1977). This has been documented to be the case in many mammalian and avian vocalizations (Morton 1977; Owren and Rendall 2001), although it remains controversial in primates (Hauser 1993). As the Motivational Structural rules predicts, low frequency, abrupt atonal western gorilla calls were produced when the caller was being aggressive both at close and long distance (i.e. cough grunts, barks), whereas moderate and high frequency tonal calls (i.e. singing, hoots, whimpers and screams) were produced in affiliative or fearful situation (i.e. maintenance activities and when distressed or receiving aggression). In contrast, the structure of some gorilla calls and the motivational state in which they were given did not support the Motivational Structural rules. Affiliative sounds not always displayed high frequency and pure tonal structure, as also found in other species (e.g., Peters 1984). For instance, western gorilla single and double grunts were produced during non-aggressive contexts (i.e., foraging, resting traveling) but were noisy calls of low frequencies. Furthermore, as suggested by Fichtel and colleagues, calls produced in more aggressive circumstances, although they exhibit more non-harmonic energy (more noise in the call), display higher frequencies and peak frequencies (i.e. whimpers vs. cries; cough grunts vs. screams and barks), in contrast to what suggested by the MS rules (Fichtel et al. 2001; Fichtel and Hammerschmidt 2002; Fichtel and Hammerschmidt 2003).

When compared to mountain gorillas, western gorillas exhibit several noteworthy differences in their repertoire and usage of calls. For instance, their vocal repertoire includes an additional call type, the sex-whinny, not described for mountain gorillas, and directed towards a specific receptive female, seemingly as an invitation to mate. Second, only females use screams, whereas, likely due to the presence of multiple males in their groups, both sexes in mountain gorillas give screams during within-group escalated aggression (Schaller 1963; Fossey 1972). Third, although both species produce the hoot series (long call), all western gorilla age/group classes use it during within-group communication, while just male mountain gorillas use it and only during intergroup encounters (Schaller 1963; Fossey 1972). Finally, western gorillas use a higher number of calls associated with specific contexts (i.e., humming, singing, and sex-whinny) than mountain gorillas (Schaller 1963; Fossey 1972; Harcourt et al. 1993). Therefore, our study adds and complements to the data previously collected on mountain gorillas, building a detailed understanding of gorilla vocal communication, and how it varies between the two gorilla species.

Behavioral Context of Western Gorilla Vocalizations

A strong association between a vocal signal and a specific context provides the opportunity for listening individuals to gather information about the activity or context of unseen calling individuals and their surroundings. The use of distinct call types during specific contexts is extremely valuable, particularly for social species living in forested habitats (Morton 1975), allowing the coordination of group movements and activity patterns between individuals that are not in visual contact (e.g., Boinski 1991; Boinski 1993). Accordingly, more than half of the call types used by western gorillas were context- and/or signal-specific, with seven of these being given in a single clearly defined context that was similar to those described in mountain gorillas (Tables 2.1 and 2.3).

In addition, we identified three specific call types: humming, singing, and the sex-whinny. Humming and singing were interpreted in mountain gorillas as signs of contentment during a range of activities (i.e. feeding, resting, and traveling; Schaller 1963; Fossey 1972; Harcourt et al. 1993), rather than in any particular context. In contrast, the same call types were much more context-specific in western gorillas, with individuals using them nearly exclusively during foraging. The third call, the sex-whinny, has not been documented for mountain gorillas, although a horse-like sound was anecdotally described to occur in some cases before copulation (Watts 1991a). In contrast, in western gorillas it was clearly identified as a separate call, based on its acoustic properties and the behavioral context in which it was primarily given (i.e., male courtship before copulation). Since our study was mostly based on one adult male, the result needs to be confirmed by future works in other wild western gorilla groups, to exclude the possibility of the call being idiosyncratic to that specific male. If we assume that it is part of the male western gorilla repertoire, the fact that it was not described in mountain gorillas raises interesting questions. Signaling an imminent copulation has different costs and benefits depending on the social organization of a species, as well as the age, sex, and rank of individuals under consideration (Pradhan et al. 2006). Although several hypotheses have been proposed to explain the function of pre, during and post copulation calls, especially in female primates, their specific adaptive function and how this varies across species remains obscure (reviewed in Pradhan et al. 2006). Due to the long shared evolutionary history and morphological constraints inherent in vocal production (Hammerschmidt and Fischer 2008), the sex-whinny might also be present in the mountain gorilla repertoire but the call might not have been described in their repertoire because it is rarely or never given, or because its production was influenced by the level of the habituation (i.e., Schaller 1963; Fossey 1972). Alternatively, mountain gorillas might not use the call to avoid increasing competition between reproductively active males in the group (Bradley et al. 2005), a situation that does not occur in western gorilla bisexual groups, which have only one adult male (Gatti et al. 2004).

In mountain gorillas only one call type was more context-specific than those of western gorillas, the hoot series (Fossey 1972), given during male extra-group displays. However, in western gorillas this call is produced during multiple non-aggressive contexts (e.g., travelling, foraging, and resting). The hoot series is exchanged within the group (R. Salmi unpublished data), and by all age/sex classes, suggesting that this call type might serve to maintain contact and regain proximity among dispersed group members. This condition is not experienced by mountain gorillas, in which group members are at all times in close proximity to each other (Watts 1991b). Further analysis of inter-individual distances, and its dynamics in relation to calls is needed to determine the role of the hoot series in maintaining western gorilla group cohesion.

Importance of Specific Signaling

Recent work on African ape vocal communication has focused on specific calls, providing deeper insights into their functions and potential referential meaning (e.g., Seyfarth et al. 1994; Stewart and Harcourt 1994; Crockford and Boesch 2003; Slocombe and Zuberbühler 2006; Slocombe et al. 2009; Clay and Zuberbühler 2011). Since the majority of call types produced by western gorillas were context and/or signal specific, which are both prerequisites for referential signaling, future studies on these call types might reveal that also gorillas use referential communication, as recently shown in other ape species (e.g., Slocombe et al. 2009; Clay and Zuberbühler 2011). Most of these calls were also age/sex specific, being used in typical age/sex specific activities. As in mountain gorillas, the male is the center of the group, protecting both females and offspring from conspecific and non-conspecific danger (R. Salmi pers. obs.; Watts 2000). Not surprisingly, calls uniquely used by one age/sex-class were those given by the male during group defense or mating, and by female and immature gorillas during alarm and distress situations.

Nevertheless, specific calls constituted less than 13-27% of total adult daily call production. Furthermore, while males used a larger number of specific call types, immature gorillas used them more frequently. Immature gorillas might benefit the most from the ability to precisely communicate distress to other group members, because they are the most vulnerable individuals in gorilla groups, with the highest mortality rate compared to all other age/sex classes (D. Doran-Sheehy pers. obs.). Alternatively, because non-specific signals are given during many contexts, with their meaning potentially varying in relation to other factors, immature gorillas might require longer time to socially learn how to use them correctly, as has been documented for other behaviors in apes (e.g., feeding behavior: Boesch and Boesch-Achermann 2000; Jaeggi et al. 2010; Byrne et al. 2011; cultural behavior: Matsuzawa et al. 2001; Lonsdorf et al. 2004). More information about the ontogeny of vocal production and its perception might help explain the observed differences in call usage across western gorilla age/sex classes.

General call types (i.e., grunts and grumbles), given during many contexts, were used most frequently, contributing more than 80% to the adult calling rate. They also presented more intermediate variants than other call types (R. Salmi, pers. obs.), raising the possibility that they convey different kinds of information (e.g., arousal and identity of the caller) and may include acoustically different subtypes, as described in other non-human primate species (e.g., Green 1975; Seyfarth and Cheney 1984; Owren et al. 1997). Furthermore, studies on these general calls might facilitate the study of behavioral flexibility in both production and perception, which are considered crucial in gestural studies, but have received limited study in primate vocal studies (Slocombe et al. 2011; Wheeler and Fischer 2012). The evolution of auditory genes has been linked to the evolution of language in humans (Clark et al. 2003), with the recent analysis of the gorilla genome indicating that several genes associated with hearing exhibit patterns of accelerated evolution similar to those in humans (Scally et al. 2012). Therefore, the study of gorilla vocal production and perception gains crucial importance in interdisciplinary efforts to ascertain the origin and evolution of human language.

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Tables and Figures

Table 2.1. Mountain gorilla vocal repertoire. Call types, proposed contexts, and age/sex differences [silverback/adult male (M), adult female (F), juvenile (J), infant (I)] in call usage. Context is distinguished between within- (WG) and extra-group (EG) and whether the call type is used in one or more (multiple) contexts.

Call type	Other names	Proposed contexts	M	F	J	I
Single grunt	Belch vocalization[2]	WG; multiple[1,2,3]	x	x	x	x
Double grunt	Belch vocalization[2]	WG; multiple [1,2,3]	x	x	x	x
Cough grunt	Staccato grunt[1];pig grunt[2]; pant series	WG; aggression[1,2,3]	x	x		
Copulation grunt	Copulatory grunt[1]	WG; copulation[1,2,3]	x	x*(c)		
Grumble	Belch vocalization[2]	WG; multiple [1,2,3]	x	x	x	x
Hum	Belch vocalization[2]	WG; multiple [1,2,3]	x	x	x	x
Sing	High hum [2]	WG; multiple [2,3]			x	x
Chuckle	Panting chuckle[1]	WG; play[1,2,3]				x
Whinny	Train grunt[3]; neighing horse sound[1,2]	WG; multiple [1,3,4,5]; idiosyncratic[2]	x			
Hoot series	Ho ho ho[1]	EG; interaction with extra-group male gorillas or humans[1,2,3]	x			
Hoot-chest-beat		EG; interaction with extra-group male gorillas or humans[1,2,3]	x	x*(1)		
Whimper	Whine[1]	WG; abandoned, injured, in danger [1]; distress[2]		x*	x*	x*
Cry	Infant scream: tantrum[2]	WG; left behind, in danger [1]; distress[2]				x*
Scream		WG/EG; aggression[1,2]; alarm[2]; human presence[1,2]	x*	x*	x*	x*
Bark	Hoot-, question-, hiccup-bark[2]	EG; aggression[1]; alarm[1,2]; human presence[1,2]	>x*	x*	x*	x*
Roar	Threat-, alarm-bark[2]	EG; attack[1,2]; human presence[1,2]	>x*	x*		

References: [1] Schaller 1963; [2]Fossey 1972; [3]Harcourt et al. 1993; [4]Watts 1991; [5]Sicotte 1994
***: Unhabituated animals; (c) only captive animals; (1) heard only once; > mostly this age-sex class.**

Table 2.2. Data set for western gorilla silverbacks/adult males (M), adult females (F), juvenile (J) and infants (I). These include number of focal follows (N_{FOLLOW}), total focal sampling time ($T_{SAMPLING\ (hrs)}$), total continuous sampling time ($T_{CONTINUOUS\ (hrs)}$), number of vocalizations heard during focal follows (N_{VOCS}), number of vocalization recordings selected for acoustic analysis (N_{CALLS}), and ratio of time spent in each time-period relative to the total follow time ($R_{TIME\text{-}PERIOD}$) [e.g., the juvenile (J1) was followed 12 times, 3 times in each of the four time-period 3/3:3/3:3/3:3/3 = 1:1:1:1].

Individual	N_{FOLLOW}	$T_{SAMPLING\ (hrs)}$	$T_{CONTINUOUS\ (hrs)}$	N_{VOCS}	N_{CALLS}	$R_{TIME\text{-}PERIOD}$
Habituated group						
M1	170	764	462	8,344	1,081	1.0:1.0:1.1:1.0
F1	84	176	87	1,149	401	0.9:1.0:1.1:1.0
F2	86	189	93	627	154	1.1:1.0:0.9:1.0
F3	75	154	72	228	75	1.0:0.9:1.2:0.9
F4	74	176	82	310	36	1.0:1.0:1.1:1.0
F5	-	-	-	-	17	1.0:1.0:1.0:1.0
F6	-	-	-	-	42	-
J1	12	54	53	296	45	1.0:1.0:1.0:1.0
I1	18	32	23	300	154	0.9:0.9:1.4:0.7
I2	14	28	19	106	50	0.8:0.8:1.2:1.2
Subtotal	**533**	**1,572**	**890**	**11,360**	**2,055**	
Semi-habituated group						
M2	17	54	54	378	68	0.9:1.1:1.1:0.9
F7	-	-	-	-	29	-
I3	-	-	-	--	11	-
Total	**550**	**1,625**	**944**	**11,738**	**2,163**	

Table 2.3. Summary of western gorilla vocal repertoire. For each call type the following are indicated: 1) call type assessed by distance category [close-range (C) or long-range (L)], 2) call specificity [signal and/or context-specific (S) or general (G)], 3) context, if specific, and whether is used in within- (WG) or extra-group communication, and 4) call rate for male (M), female (F), juvenile (J), and infant (I) gorillas.

Repertoire				***Call rates***			
Call	**Type**	**Specificity**	**Context**	**M**	**F**	**J**	**I**
Single grunt	C	G	WG; multiple	3.62 ±2.4	2.91±1.4	0.22±0.3	0.88±0.6
Double grunt	C	G	WG; multiple	10.42±1.1	0.71±0.7	0.01±0.0	0.08±0.1
Cough grunt	C	S	WG; aggression	0.55±0.2	0.29±0.2	0.04±0.1	0.14±0.1
Copulation grunt	C	S	WG; copulation	0.56±0.9	0.01±0.1		
Grumble	C	G	WG; multiple	1.68±1.0	1.01±0.8	1.60±1.5	2.41±0.8
Hum	C	S	WG; foraging	0.60±0.4	1.38±1.2	2.00±2.8	0.83±0.9
Sing	C	S	WG; foraging			0.89±0.8	
Chuckle	C	S	WG; playing	0 (o)	0.03±0.1	0.63±1.0	1.68±4.1
Whinny	C	G	WG; multiple	0.60±0.3			
Hoot series	L	G	WG; multiple	0.56±0.4	0.08±0.1	0.09±0.3	0.51±0.6I
Hoot-chest-beat	L	S	EG; interaction	0.05±0.1			
Whimper	C	S	WG; nursing attempt				1.75±0.1
Cry	L	S	WG; nursing denied				0.24±0.1
Scream	L	S	WG; aggression; alarm		0.03±0.1	0	
Bark	L	S	EG; alarm; human presence	0.16±0.03			
Roar	L	S	EG; attack; human presence	0*			
Sex whinny	C	S	WG: mate- courtship	0.16±0.3			

(o): Rare and only observed during non-focal sampling; *: only heard from non-habituated animals

Table 2.4. Percent of calls assigned to each of 14 call types by cross-validated DFA. Call type abbreviation include: single grunt (SG), double grunt (DG), cough grunt (CG), copulation grunt (COG), grumble (GR) hum (HM), sing (SI), whimper (WP), whinny (WH), sex-whinny (SWH), hoot-series + chest beats (HCB), hoot-series (HO), scream (SC), cry (CR). Bolded numbers indicate the percentage of calls assigned correctly to each call type. Call types are grouped in call categories (i.e., call types with similar broad acoustic structure), which are divided by solid lines.

Call type	***Cross-validated DFA: Predicted group membership***													
	SG	DG	CG	COG	GR	HM	SI	WP	WH	SWH	HCB	HO	SC	CR
SG	**62**	17	2	1	4	4	0	0	0	0	0	0	0	0
DG	24	**65**	3	5	9	1	2	0	0	0	1	0	0	0
CG	11	0	**66**	14	0	0	8	0	0	0	1	0	0	0
COG	18	18	12	**39**	0	0	8	0	0	0	5	1	0	0
GR	20	1	0	0	**40**	38	1	0	0	0	0	0	0	0
HM	9	3	1	1	39	**44**	2	0	0	0	0	0	0	0
SI	0	4	0	4	4	0	**89**	0	0	0	0	0	0	0
WP	0	0	0	0	0	0	5	**59**	0	2	0	32	0	2
WH	0	3	0	0	3	10	0	3	**70**	7	3	0	0	0
SWH	0	0	0	0	0	0	0	18	27	**55**	0	0	0	0
HCB	1	0	1	3	0	0	6	1	0	0	**79**	8	0	0
HO	0	1	0	3	0	0	3	0	0	0	34	**58**	0	0
SC	0	0	4	0	0	0	0	0	8	0	4	0	**60**	24
CR	0	0	0	0	0	0	0	9	0	0	2	0	8	**81**

Table 2.5. Mean (±SE) of the major acoustic parameters that distinguished among the 14 call types in adult male (M), adult female (F), as well as those of juvenile (J) and infant (I) western gorillas for the few calls uniquely given by immatures. The number of call segments used in the analysis is indicated by N_C.

Call	*C*	N_C	*duration*	*tonality*	*dfa2mean*	*df1mean*	*df2mean*	*fp1mean*	*fp1amean*	*pfmax*
Double grunt	M	171	838.3±25	1.8±0.3	227.7±5	109.9±1	165.7±2	151.3±3	759.7±19	244.5±8
	F	56	668.4±52	4.0±1	304.5±14	94.5±2	166.6±5	114.0±6	221.2±16	273.0±26
Single grunt	M	74	785.0±56	5.8±1	197.8±6	112.6±2	182.3±6	121.9±3	581.3±30	186.2±7
	F	76	495.4±35	4.1±1	316.5±13	91.0±1	174.1±7	102.8±5	240.3±15	225.7±26
Cough grunt	M	66	209.5±1.5	16.8±4	357.9±16	99.4±2	169.1±6	144.8±10	263.2±16	246.4±19
	F	156	206.5±0.9	11.4±2	407.6±16	98.7±2	174.0±4	188.1±10	240.4±10	300.4±19
Cop. grunt	M	73	416.1±28	5.4±2	236.5±5	113.8±3	170.3±4	173.0±6	615.9±33	218.6±10
	F	73	224.5±6	20.7±4	288.5±4	129.3±7	242.8±23	232.0±9	396.9±231	271.6±9
Grumble	M	45	1568.1±74	22.1±4	208.5±7	99.8±2	192.8±7.4	78.56±4	205.5±13	175.7±14
	F	34	2068.8±206	35.7±4	274.7±11	88.5±1	150.9±4.7	83.7±7	164.7±20	266.6±27
Hum	M	39	1817.2±88	8.9±2	243.8±7	96.9±2	158.5±3.8	93.1±4	239.0±27	249.1±16
	F	25	1971.2±170	42.3±5	292.2±16	87.1±3	144.0±7.1	83.3±9	209.7±16	224.7±29
Sing	J	26	373.9±52	70.0±4	327.5±25	120.6±6	249.7±11	129.9±11	139.0±14	213.0±30
Whimper	I	62	687.8±70	75.6±3	1357.3±106	460.7±13	1341.2±90	429.8±24	300.6±28	2748.9±35
Cry	I	62	609.5±39	57.1±4	2649.8±73	1235.7±35	2302.6±72	1477.9±50	422.58±28	3840.7±24
Scream	F	14	911.6±288	11.9±7	1613.6±124	616.6±61	1044.5±71	1048.1±10	724.2±111	1608.9±11
Whinny	M	31	1848.6±92	21.0±3	387.0±64	196.2±8	573.39±34	73.35±5	898.8±60	753.8±23
Sex-whinny	M	12	1680.3±208	7.4±3	1417.3±27	330.4±34	1010.8±97	111.4±24	342.6±77	2799.3±50
Hoot CB	M	316	158.6±3	64.2±2	308.4±11	208.3±1	601.5±31	154.2±4	659.0±21	244.4±9
Hoot series	M	321	171.1±3	63.7±2	282.9±5	214.1±2	529.0±26	170.6±4	734.8±19	247.2±4
	F	328	222.2±12	58.1±2	478.2±9	347.8±3	749.6±24	366.4±4	606.4±15	414.0±6

Table 2.6. Call context-specificity: the percent of calls given in each of context. Contexts include: aggression (AG), alarm (AL), display between-group (DPE) and within-group (DP-WG), forage (FO), courtship (CO), sex (SE), play (PL), rest (RE), travel-pose (TRP), travel (TR), seek nipple contact (NPA), and nipple contact rejected (NPR). Context-specific calls (i.e. for which ≥ 75%) are indicated in bold. Sample size (N_{VOC}) includes total number of each call type heard during continuous focal follows.

Calls/sounds		***Contexts***												
Calls	**N_{VOC}**	**AG**	**AL**	**DPE**	**DPW**	**FO**	**CO**	**SE**	**PL**	**RE**	**TRP**	**TR**	**NPR**	**NPC**
Single grunt	2776	0	0	0	0	48	0	0	0	29	11	12	0	0
Double grunt	4944	0	0	0	0	59	0	0	0	24	8	9	0	0
Cough grunt	361	**100**	0	0	0	0	0	0	0	0	0	0	0	0
Cop. grunt	29	0	0	0	0	0	0	**100**	0	0	0	0	0	0
Grumble	1192	0	0	0	0	26	0	0	0	22	23	28	0	1
Hum	836	0	0	0	0	**91**	0	0	0	3	1	5	0	0
Sing	26	0	0	0	0	**100**	0	0	0	0	0	0	0	0
Sex-whinny	64	0	0	0	0	0	**97**	0	0	0	3	0	0	0
Whinny	302	0	1	0	1	6	2	0	0	37	47	6	0	0
Hoot chest beats	14	0	0	64	36	0	0	0	0	0	0	0	0	0
Hoot series	256	0	3	0	3	23	0	0	0	49	18	4	0	0
Whimper	83	0	0	0	0	0	0	0	0	0	0	0	**100**	0
Cry	12	0	0	0	0	0	0	0	0	0	0	0	1	**99**
Scream	1[a]	**100**	0	0	0	0	0	0	0	0	0	0	0	0
Bark	10	0	**100**	0	0	0	0	0	0	0	0	0	0	0
Chuckle	35	0	0	0	0	0	0	0	**100**	0	0	0	0	0
Miscellaneous	112	0	0	0	0	38	1	0	0	38	12	11	0	0

Table 2.7. Call signal-specificity: the percent of 14 call types given in each context. Vocalizations include single grunt (SG), double grunt (DG), cough grunt (CG), copulation grunt (CPG), grumble (GR), hum (HM), sing (SNG), whinny (WH), sex-whinny (SWH), hoot series ± chest-beats (HC), hoot series (HS), whimper (WP), cry (CRY), scream (SC), bark (BK), chuckle (CK), and miscellaneous calls (MI). Signal specific calls (i.e. those for which ≥ 75% are given in a single context) are indicated in bold. Sample size is based on the number of calls given in each behavioral context (N_{CC}). The amount of time spent in each context (N_{HR}), and the total number of each call type (N_{VOC}) are also noted.

Context	N_{CC}	N_{HR}	*SG*	*DG*	*CG*	*CPG*	*GR*	*HM*	*SNG*	*SWH*	*WH*	*HC*	*HS*	*WP*	*CRY*	*SC*	*BK*	*CK*	*MI*
Aggression	362	5.9	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alarm	27	2	7	7	0	0	7	0	0	0	11	0	30	0	0	0	38	0	0
Display-extra-group	9	0.6	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0
Display-within-group	17	0.7	0	6	0	0	0	0	0	0	24	29	41	0	0	0	0	0	0
Forage	5441	435.4	24	54	0	0	6	14	0	0	0	0	1	0	0	0	0	0	1
Courtship	75	2	5	3	0	1	0	0	0	**83**	7	0	0	0	0	0	0	0	1
Sex	29	0.5	0	0	0	100	0	0	0	**0**	0	0	0	0	0	0	0	0	0
Play	41	1.7	7	0	0	0	7	0	0	0	0	0	0	0	0	0	0	**86**	0
Rest	2583	262.8	31	47	0	0	10	1	0	0	4	0	5	0	0	0	0	0	2
Travel-pose	1149	44.9	26	32	0	0	24	1	0	0	12	0	4	0	0	0	0	0	1
Travel	1214	75.3	28	37	0	0	28	4	0	0	1	0	1	0	0	0	0	0	1
Nipple-contact	93	2.3	3	0	0	0	8	1	0	0	0	0	0	**88**	0	0	0	0	0
Nipple-conflict	13	0.3	0	0	0	0	0	0	0	0	0	0	0	8	**92**	0	0	0	0
N_{VOC}	**11053**	**834.4**	**2776**	**4944**	**361**	**29**	**1192**	**836**	**26**	**64**	**302**	**14**	**256**	**83**	**12**	**1***	**10**	**35**	**112**

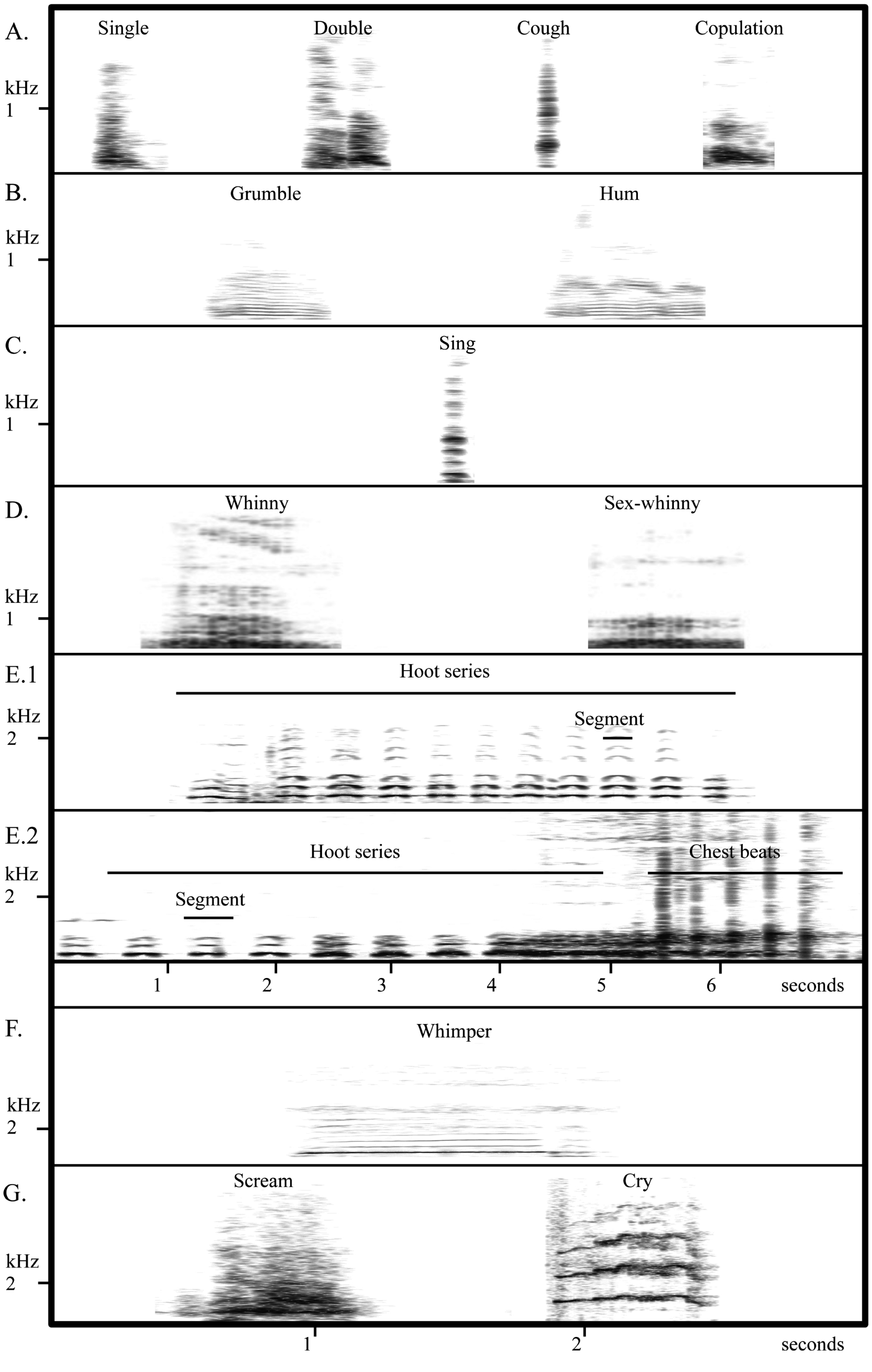

Fig. 2.1. Spectrograms of 14 western gorilla call types, grouped in 7 broad acoustic categories, including: grunts (A.), grumbles (B.), singing (C.), whinnies (D.), hoots (E.1 and 2), whimper (F.) and screams (G.).

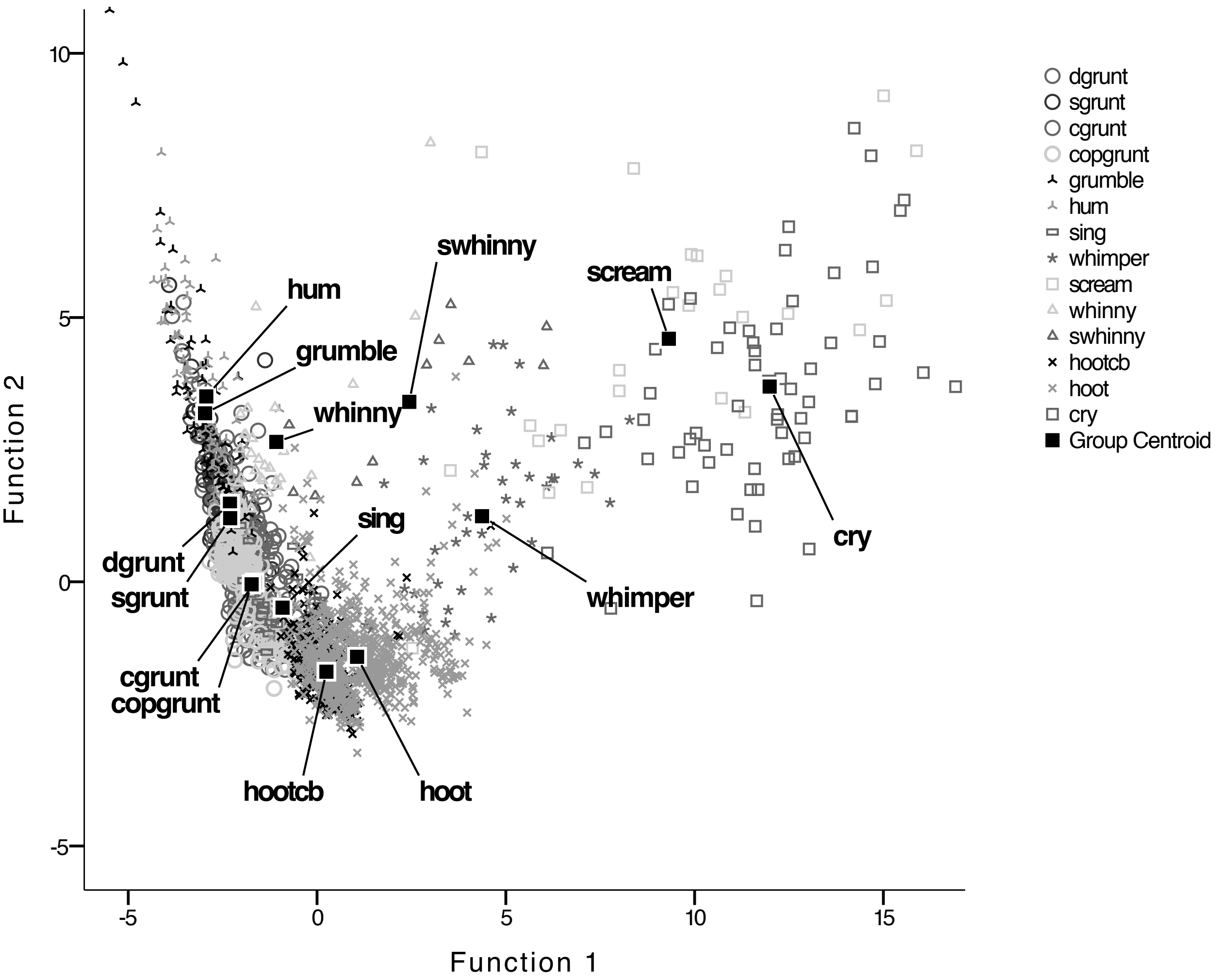

Fig. 2.2. Distribution of the discriminant scores for the 14 call types (abbreviated call types: sgrunt = single grunt; dgrunt = double grunt; cgrunt = cough grunt; copgrunt = copulation grunt; swhinny = sex whinny; hoot = hoot series; hootcb = hoot-chest beat).

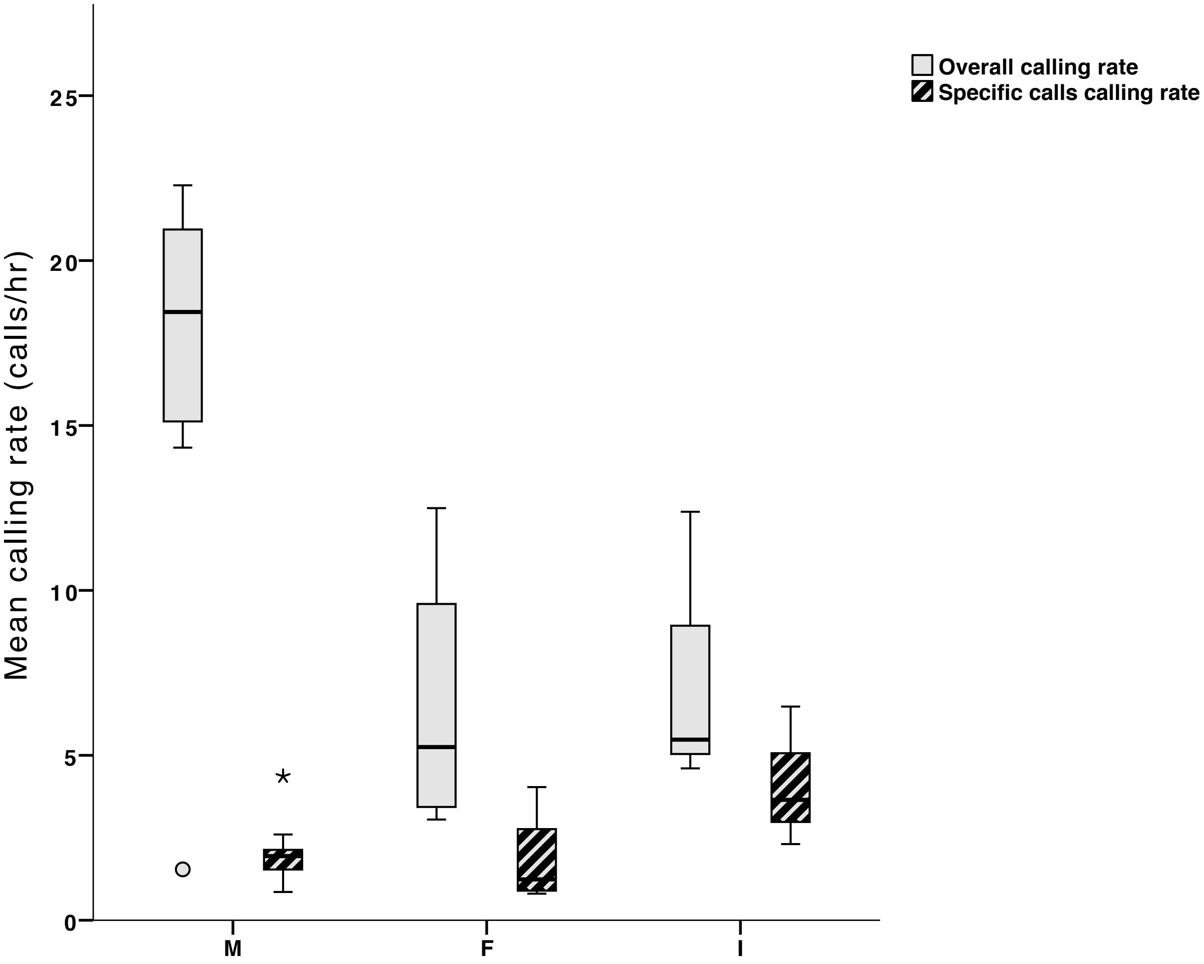

Fig. 2.3. Overall calling rate across age-sex classes and average rate for all specific call types combined. Male (M), female (F), immature [including both juvenile (J) and infant (I)] data were calculated from the mean monthly rates ($n_{M, F1-4} = 12$; $n_J = 2$, $n_{I1} = 10$, $n_{I2} = 7$) and monthly rates have been calculated by averaging across daily rates. Box plots show the median values (solid lines) and first and third quartiles (bottoms and tops of boxes); circle and star indicate outliers.

CHAPTER THREE

Wild Western Gorillas (*Gorilla gorilla*) Use "Hoot Series" to Regain Spatial Proximity[2]

Abstract

Although the use of long-range vocal signals to increase proximity with social partners (i.e., long contact, lost, or isolation calls) is well documented in many different species, the underlying mechanisms and how they differ across species remain unclear. The western gorilla's (*Gorilla gorilla*) vocal repertoire offers an opportunity to investigate these questions as it includes a long call (i.e., hoot series) used by all age-sex classes in non-aggressive contexts. We tested whether the hoot series functions as a contact call, and predicted that to do so it should be: 1) individually distinct, 2) given when individuals are separated, 3) replied to and by group members, and 4) result in decreased inter-individual distances. We also examine which party is responsible for decreasing distance between individuals to better understand its function and cognitive implications. Behavioural, spatial, and acoustic data were collected over 15 months at the Mondika Research Center, Republic of Congo and Central African Republic. During 659 focal follows (1,458 hrs) we collected behavioural data on 5 gorillas, while digitally recording their calls. Results indicate that hoot series were individually distinct in both acoustic and

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[2] This chapter will be submitted for publication to Animal Behaviour with D.M. Doran-Sheehy, Department of Anthropology, Stony Brook University, as co-author.

temporal characteristics. Hoot series were given by both male and female gorillas when at least one female (in case of a male caller) or a male (in case of a female caller) was separated from the caller's party at a distance that was significantly greater than maximum and mean daily distance between sexes. In almost all cases (21/22), inter-individual distance between the caller and at least one separated member of the group decreased significantly following hooting. We conclude that western gorillas use hoot series to regain (and negotiate) proximity among separated individuals. Since mountain gorillas use the call differently, i.e., as an agonistic signal during intergroup encounters, our results suggest that, although the acoustic features of vocal signals are highly constrained in closely related species, the function and usage of particular calls can be flexible.

Introduction

Long contact calls, also known as lost or isolation calls, are loud vocalizations used by individuals when separated from other group members. They are thought to function to reduce distances between individuals and coordinate group movements (Marler and Slabbekoorn 2004; Kondo and Watanabe 2009; Teixeira da Cunha and Byrne 2009). These calls are of particular importance for group-living species with members spread over great distances and especially for those living in environments where visibility is reduced, since they might represent the only means through which individuals can remain in contact with each other. Like other long distance calls, they may be acoustically adapted to travel long distances and have acoustic properties that allow them to overcome background noise and optimize sound propagation (e.g., birds: Sharp and Hatchwell 2005; elephants: Leighty et al. 2008b; primates: Palombit 1992a; Mitani and Stuht 1998; Sugiura et al. 2006; Schneider et al. 2008). In order to reunite group members, the call should be long enough (or contain a large number of call segments) to facilitate the localizability of the caller (reviewed in: Brumm and Slabbekoorn 2005). In addition, the call should be individually distinct (e.g., bats: Boughman 1997; birds: Berg et al. 2011; dolphins: Caldwell and Caldwell 1965; elephants: Soltis et al. 2005; manatees: Sousa-Lima et al. 2002; primates: Brown et al. 1978; Snowdon et al. 1983), allowing call receivers to recognize group members and respond differentially to specific individuals (e.g., Boinski 1991; Boinski 1993; Digweed et al. 2007; Leighty et al. 2008b). More importantly, calls that function as long contact calls, should elicit vocal responses from other individuals within the group to facilitate the reduction of the distance among separated group members (Waser 1977; Snowdon et al. 1983; Biben 1993; Digweed et al. 2007; Leighty et al. 2008a; but see Rendall et al. 2000).

In addition, long contact calls are of particular interest to biologists investigating animal cognitive abilities because they have been suggested to provide information about whether animals attribute mental states to others, that is, whether they exhibit a “theory of mind” (Cheney et al. 1996). If lost calls are replied to, it might indicate that the responder understood the “lost condition” of the caller, which might be considered a manifestation of the ability to attribute a mind state to others that differs from one’s own. The fact that baboons do not respond to the lost calls of other group members unless they themselves are also separated from the group (Cheney et al. 1996) has been considered as evidence that monkeys do not understand the state of mind of other individuals (Cheney et al. 1996; Rendall et al. 2000; Seyfarth and Cheney 2012). This interpretation, however, has been criticized since a simpler interpretation might explain the occurrence of vocal exchanges without alluding to a theory of mind (Byrne 2000). More precisely, if both the caller and receiver benefit from being reunited, a strong association would evolve between the signal and the outcome (reduced distance), which only implies that individuals can attribute a certain meaning to a signal, with no need of higher cognitive capacities (Byrne 2000; Teixeira da Cunha and Byrne 2009). Under this interpretation, answering is expected to be influenced by kin or rank, with replies more commonly given by close relatives and/or lower-ranking individuals (Teixeira da Cunha and Byrne 2009). This hypothesis might explain the presence of long contact calls that function to reunite group members (as well as mothers and infants) in many primates (e.g., Digweed et al. 2007), in line with the absence of evidence of a theory of mind in most of these species.

Among primates, however, chimpanzees (and bonobos) are thought to exhibit a theory of mind (Premack and Woodruff 1978), or some rudimental aspects of it, with supporting evidence coming from both captivity (Call and Tomasello 2008) and the wild (Crockford et al. 2012). Whether other apes also exhibit a theory of mind is less clear because data from wild populations are scarce and captive studies generally focus on chimpanzees (but see Poss et al. 2006; Okamoto-Barth et al. 2007; Zimmermann et al. 2009; Gretscher et al. 2012). Here we examine a long contact call used by wild western gorillas to gain a clearer idea of the mechanisms behind its use and to provide a better understanding of the function and evolution of these calls in gorillas.

Gorillas are large-bodied, sexually dimorphic, predominantly herbivorous primates that live in cohesive one- or multimale groups (Watts 1996; Harcourt and Stewart 2007). At present, two species are recognized, eastern (*Gorilla beringei*) and western gorillas (*G. gorilla*) (Groves 2001). Recent work has shown differences in some aspects of the ecology and ranging behaviour of the two species, including greater frugivory and longer daily distances travelled in the western species (e.g., Doran-Sheehy and Boesch 2004; Doran-Sheehy et al. 2004; Masi et al. 2009). Currently no systematic assessment of spatial proximity exists for western gorillas, although it has been suggested that they tend to be less cohesive than mountain gorillas (Watts 1991; Goldsmith 1999; Doran-Sheehy and Boesch 2004). In both species, the alpha or the only male is the center of social activity in the group (Watts 2000). As a result, the male has a higher rate of vocalization compared to other individuals (mountain gorillas: Harcourt et al. 1993; western gorillas: Salmi et al. in prep.), frequently initiating calls and responding to those of others (R. Salmi unpublished data).

Western gorillas use two variants of a loud call (i.e., the hoot series, Salmi et al. in prep.). Both variants are composed of monosyllabic harmonic call segments of medium-range frequencies (i.e., hoots), which are given repeatedly in rapid sequences at regular intervals (Fig. 2.1.). The first is a hoot series followed immediately by chest beats (i.e., the hoot series-chest beat), which is used by both mountain and western gorillas in the same context. It is given exclusively by silverback males during aggressive displays, and is most frequently directed towards extra-group males (mountain gorillas: Fossey 1972; Harcourt et al. 1993; western gorillas: Salmi et al. in prep). The second variant is a hoot series without subsequent chest beating, referred to hereafter simply as a hoot series. Mountain and western gorillas use the hoot series differently. In mountain gorillas, it is given exclusively by males and primarily in extra-group encounters, i.e., in the same way as the hoot series-chest beat (Fossey 1972; Harcourt et al. 1993). By contrast, in western gorillas, both females and males use the call but during non-aggressive contexts and never during intergroup encounters (Salmi et al. in prep). Here we test whether western gorillas use the hoot series as long contact call, examine the role it plays in coordinating group spatial patterns, and discuss the mechanisms behind its use and the process by which similar vocalizations can be adapted to function in novel ways.

First, we examine the general properties of hoot series and whether they are acoustically distinct among individuals in both temporal and frequency characteristics (e.g., Cheney and Seyfarth 1982; Mitani et al. 1996; Rendall et al. 1996; Dallmann and Geissmann 2001; Fischer et al. 2002; Wich et al. 2003).

Next, we consider the function of the hoot series. It has been suggested that most primate long calls are used to advertise group location (i.e., territorial calls) and facilitate spacing between groups, rather than functioning as a means of within-group communication (e.g., Marler 1972; Waser 1975; Waser 1977; Waser 1982; Mitani 1985a; Mitani 1985b; Raemaekers and Raemaekers 1985; Wich et al. 2002; da Cunha and Jalles 2007). Typically these calls are given on a daily basis and at specific times of day, usually at dawn and dusk. However, when long calls serve as contact calls to reunite group members, they should be less consistent in their timing, with individuals giving them when they are separated from other group members, regardless of the time of day. Thus we predict that hoot series will occur: 1) throughout the day rather than at dawn and dusk, 2) when individuals (or parties) are separated and 3) when the distance between the separated individuals/parties exceeds typical spatial patterning (i.e., mean and maximum daily distance) of individuals within the group. A long contact call used to increase group cohesion, must not only occur in the proper situation, but it should also reduce spatial distances between separated individuals (e.g., Palombit 1992b). Therefore we predict that distance between separated individuals will decrease between the onset and ending of hooting events.

Next we explore how hoot series contribute to regaining group cohesion. In mountain gorillas, males are thought to be the main decision makers and the ultimate arbiters of movement direction (Byrne 2000; Watts 2000). Males typically lead from behind (Kummer 1968; Byrne 2000). Although they may appear to follow females, if a dispute in travel arises, the male’s path is ultimately the chosen one (Byrne 2000). If the same pattern holds true in western gorillas we would predict that when individuals become separated, females would travel towards the male following hooting sequence. Finally we examine whether gorillas respond to the hoot series of other gorillas to facilitate reunion.

Methods

Study Site and Species

Behavioural data and vocal recordings were collected during 15 months (April 2009-June 2010) at the Mondika Research Centre, Central African Republic and Republic of Congo (Doran-Sheehy et al. 2004) from a single, well-habituated group of gorillas that has been studied since 2001 (Doran-Sheehy et al. 2007). During most of the study the group consisted of 6 adult individuals: one adult silverback male, five adult females, and two infants. Study subjects included the adult male and four females who were present throughout the entire study.

Behavioral and Acoustic Data Collection

Two teams of two researchers each (led by RS) collected simultaneous focal animal samples (2-3 hours) (Altmann 1974) of the silverback and one of the four adult females, rotating evenly among females. A total of 659 focal samples were collected during 1459 contact hours, including 340 male (764 hours) and 319 female (695 hours) samples, with an average of 80 follows (SD = 6, range = 74-84) and 173.8 hours (SD = 14.5, range = 154-189) of sampling per female (for summary of data collected see Appendix 4).

During focal follows (Altmann 1974) we conducted six 5-minute periods of continuous sampling alternated by six 5-minute periods of scan sampling (Martin and Bateson 1993). During continuous sampling periods we recorded all hoot series given by the focal subject and also recorded: a) the time at which it was given, b) whether it was apparently given spontaneously (i.e., no preceding hoot(s) within 5 min) or in response to another hoot series (i.e., < 1 min after a preceding hoot series, although in fact all responses were given within 30 s), c) whether it elicited a vocal response by a conspecifics (and the type of call), and d) the GPS location (Lat/Long) of the caller/focal animal at the onset of hooting (with accuracy < 15 m). We also continuously recorded aggression to construct ranking scores for the adult individuals using the David's score (Gammell et al. 2003), considering both all aggression and only those with decided outcome. We then used the David's scores to assign cardinal ranks for the focal females (for matrices, calculations and scores see Appendix 5).

During scan sampling both teams recorded the GPS location of the focal animal and proximity data, including the distance and the identity of all other adult group members within 50 meters of the focal animal. Recording the location of all individuals within 50 meters was possible because one of each pair of researchers per focal subject was dedicated to monitoring the arrivals, departures and locations of all individuals. On some occasions all females were within 50 meters of the silverback and the group was considered complete (i.e., comprising a single party). On other occasions, one (or more) female(s) were known to be more than 50 meters away from the male, and the group was classified as being in separate parties. When all other adult individuals were absent (>50 m) the focal individual was considered to be "alone". The two research teams communicated with each other using two-way radios, facilitating the complete description of the location of all group members relative to the focal subjects.

During focal animal sampling we acquired digital recordings of hoot series, recorded from ≤ 10 meters from the individual using a portable Marantz recorder (PMD671) and a Sennheiser MKH 416 short shotgun microphone [equivalent noise 13 dB, minimal impedance 25 Ω, sensitivity in free field, no load (1 kHz) 25 mV/Pa ± 1 dB] protected by a foam windshield. Recordings were taken at a sampling frequency of 48 kHz.

Individual Distinctiveness

We chose the entire hoot series for the analysis of temporal characteristics, and the single call segment, the hoot, as the unit of the analysis of frequency characteristics. Using the Avisoft SASLab Pro 5 software (R. Specht, Berlin, Germany), we generated spectrograms. On the basis of acoustic quality (i.e., background-noise ratio) we selected 52 complete hoot series, including 30 for the male (M) and 17 and 5 for the two females (Female 1 and 2 respectively), and 96 hoot segments from 20 hoot series (M = 8, F1 = 7, F2 = 5) for further acoustic analysis. We used a custom software program (LMA 2011, Schrader and Hammerschmidt 1997) to calculate 4 temporal parameters of the hoot series (i.e., number of segments, mean and max segment duration and location of the longest segment in the hoot series; see Table 3.1) and 5 acoustic parameters of the hoot segment (i.e., distribution of frequency energy, 1st dominant frequency band, amplitude ratio between 1st and 2nd dominant frequency bands, mean frequency first peak, mean frequency of the highest energy, Table 3.1). We excluded measurements of frequency modulation because it was not a noticeable property in hoot series and parameters (i.e., start and end call segment frequency measurements) shown to be more influenced by external factors (Maciej et al. 2011).

To determine if hoot series and hoot segments carried cues to individual identity, we performed a multilevel analysis of variance, following a two-step procedure: a) we first conducted Discriminant Function Analysis (DFA and cross-validated DFA; Klecka 1980) for the 52 complete hoot series as well as the 288 call segments of the 3 adult individuals; b) we then used linear mixed modelling (LMM; West et al. 2006) or multivariate analysis of variance (MANOVA, adjusting for unequal sample size as needed, Pillai's Trace; Miller 1997) to test whether call parameters differed significantly among adults. LMM results were adjusted using Hochberg's correction for multiple analyses when necessary (Hochberg 1988).

Spatial proximity and Communication Analysis

During simultaneous follows of the male and one female, we used GPS data collected during scan samples to determine the distance separating the male and female at 10-minute intervals, using the haversine formula in Microsoft Excel 2011, for data with decimal degree latitude and longitude values. We averaged these distances across the two-hour focal follow to produce for each female a daily distance to the male, which we then averaged for each female across all follows (mean samples per female = 67 ± 4; n = 268; Appendix 4). This yielded for each female a mean daily distance to the male. To better assess group spread, we also recorded the maximum distance separating a focal female from the male during scans of simultaneous focal follows, and then averaged these across all follows for a female to obtain her mean maximum distance to the male. We then tested for individual variation in mean and maximum distance to the male using Linear Mixed Models (West et al. 2006) and pairwise comparisons adjusted by Bonferroni correction (Miller 1981). Values were log-transformed to meet the assumption of normal distribution of the residuals.

When a gorilla hooted, it could give either a single hoot series or multiple hoot series separated by pauses. Call receivers could either hoot in response to some (or all) of the hoot series, or simply ignore the call. Therefore, when hooting occurred, it frequently happened in bursts of non-independent hoot series produced by one or more callers. To insure independence of data, we collapsed these hooting series into independent hooting events, which began when the first hoot series occurred, ended when the last hoot series was given, and included all hoot series by any group members during that time. Typically (98%), only a single hooting event occurred per day, although on occasion more than one could occur. In these cases, events were always separated by at least one hour. For each hooting event we determined the 1) time of onset and end, 2) identity of the first individual to hoot, and 3) number of individuals that hooted during the event (one, two or more). Using distance data from focal follows we also noted 4) whether the hooting event initiator was alone or with other group members at onset of hooting event, and 5) whether any individual that hooted in reply was alone or with other group members. From male distance data taken at the scan nearest to the onset (<5 min) of the hooting event, we noted whether any female was absent from the male party. From simultaneous focal follows, we measured the distance separating focal male and female at the scan samples closest to hooting onset and the first scan immediately following the end of the hooting event. We then tested whether distances at the onset of hooting were significantly greater than the mean and maximum daily distance of females to the male, using Linear Mixed Models (West et al. 2006) to control for pseudo-replication by including female identity as a random effect. We used Paired Samples T Test (Siegel and Castellan 1988) to determine whether the distance between the male and female had decreased overall (n = 21) at the end of hooting events, and we used Wilcoxon Signed Ranks Tests (Siegel and Castellan 1988; 1-tailed testing) to determine whether the distance between the male and female decreased for each individual female (n = 5-7) and for female mean values (n = 4).

To test whether hooting events occurred throughout the day, we first assigned the onset of a hooting event into one of five two-hour classes (between 0700 and 1700) and then tested, using the Chi-square goodness of fit test, whether the distribution of hooting events differed from what would be expected from the observation time spent in each 2-hour blocks.

To determine which individual, if any, was responsible for a decrease in distance during hooting events, we analysed the changes in distance and travelling directions of the focal individuals with respect to their initial positions. We considered an individual responsible when it either a) travelled towards the other focal individual (within 45 degrees from the line between the two initial focal positions) and moved more than 30m or b) travelled further (≥ 2/3 of the distance) when both individuals travelled toward each other. In contrast, when both individuals travelled towards each other but neither individual covered 2/3 or more of the initial distance, both individuals where considered responsible.

We measured hooting rates for each focal follow as the number of hoot series divided by sampling time. We then calculated the daily mean for each individual. We tested for individual variation in hooting rates using LMM and pairwise comparisons (Bonferroni correction) after log-transforming the data and adding a constant (0.2) to meet the assumption of normally distributed residuals. All means are reported as means ± SD. All statistical tests were conducted using SPSS 20.0, with *p-value* set at 0.05 if not otherwise specified.

Results

General Properties of Hoots and Hoot series

On average, a hoot series lasted 5.0 ± 1.5 seconds and was composed of 18.1 ± 5.0 hoots, each separated by 0.15 ± 0.3 seconds (average of 3 individuals based on 52 complete hoot series). The call has a low Fundamental frequency (ranging from 200 to 400 Hz) and presents a narrow spectrum and a low frequency modulation (Fig. 3.1).

Individuals exhibited significant variation in hooting rate (LMM: $F_{4, 42.14} = 16.22$, $p < 0.001$). The mean male hooting rate of 0.56 ± 0.4 hoot series per hour (n = 170 mean daily calling rates) was significantly greater than that for any female (Fig. 3.2). Females also differed in their hooting rates (although the difference didn't reach significance), with the highest ranking female hooting at roughly half the male's rate (female 1: 0.26 ± 0.5 hoot series per hour, n = 84 mean daily calling rates), the second ranking female calling at a quarter of the first female's rate (female 2: 0.06 ± 0.12 hoot series per hour, n = 86 daily hooting rates), and the remaining two females hooting very rarely (females 3 and 4: 0.0 hoot series per hour, n = 75 and 74 mean daily calling rates for female 3 and 4 respectively; both were observed hooting as non-focal subjects).

Acoustical Distinctiveness of Hoot and Hoot series

Four temporal parameters suggested that hoot series could potentially be used by listeners to distinguish among individuals (Table 3.1). The DFA assigned 90.4% (88.5% cross validated DFA) of 52 hoot series to the correct caller, significantly more than the 33.3% that would be expected on the basis of chance (*Wilks' λ* = 0.13; $\chi^2 = 97.92$, df = 8; $p < 0.001$; Fig. 3.3.A; Table 3.2). Most (79.3%) of the variance was explained by individual differences in a single parameter, the maximum duration of a hoot within the hoot series (Function 1 in Fig. 3.3.A), with the females exhibiting greater values than the male (Table 3.1). An additional 21.0% (Function 2 in Fig. 3.3.A) of the variance was explained by differences in the number of hoots given per series (with females giving more than the male) and the location within the hoot series where the longest hoot occurred (Table 3.1). All four temporal parameters used to generate the DFA were significant in distinguishing among individuals, with no need to adjust for multiple analysis (LMM results: number of hoots: $F_{2, 49} = 9.74$; $p < 0.001$; hoot mean duration: $F_{2,49} = 13.44$; $p <$

0.001; maximum hoot duration: $F_{2,49} = 30.14$; $p < 0.001$; location in the hoot series of the longest hoot: $F_{2,49} = 30.67$; $p < 0.001$). Post hoc tests (Hochberg's correction) revealed that all but one parameter (mean duration of hoot/segment) differed in at least two of the three pairs of individuals (Table 3.1). Call duration and duration of mean and maximum hoots within the hoot series were more similar within versus between sexes. Other characteristics, including the number of hoots within a series and the location of the longest segment in the series, varied as much within as between the sexes (Table 3.1).

Hoots, the single syllable components of hoot series, were also acoustically distinct among individuals, based on the frequency parameters analysed. The DFA assigned 84% (84% for cross-validated DFA) of 288 hoots (96 for each of 3 individuals) to the correct caller, significantly greater than the 33.3% that would be expected by chance (*Wilks'* $\lambda = 0.14$; $\chi^2 = 551.32$, df = 10; $p < 0.001$; Fig. 3.3.B). Function 1 accounted for 93% of the variance and was significantly associated with distribution of frequency energy ($r = 0.95$), mean frequency first peak ($r = 0.92$), mean frequency of the highest energy ($r = 0.83$), and 1st dominant frequency band ($r = 0.81$), all variables associated with pitch. Function 2 accounted for 7% of the variance and was associated with the amplitude ratio between 1st and 2nd dominant frequency bands (0.80). Therefore, pitch characteristics are useful in discriminating between the male and the two females (Function 1), whereas the amplitude ratio between 1st and 2nd dominant frequency bands is more useful in discriminating between the two females (Function 2). A one-way MANOVA revealed a significant multivariate main effect for caller identity (*Wilks'* $\lambda = 0.15$, $F_{10, 562} = 88.67$, $p < 0.001$, partial $\eta^2 = 0.61$; power to detect the effect was 1.00). Post hoc tests confirmed that three of the four parameters differed between each pair of subjects, whereas the mean value of the first dominant frequency band (df1mean) did not differ between the two females (Table 3.1).

Since the homogeneity of variance assumption was violated, we also ran MANOVA and post hoc tests assuming unequal variance, but the results remained unchanged and are not reported here. The majority of calls were well classified, and male calls in particular were rarely misclassified (97% correctly classified; Table 3.2). In the 19-26% of times when female hoots were misclassified, they were nearly always assigned to another female, which was not the case when hoot series were misclassified.

The Function of Hooting

Hooting events (n = 79) occurred approximately every third day (65 days with one or more hooting events during 199 days of sampling), although this should be considered a minimum estimate because gorillas are active approximately 12 hours a day and our average time spent with the group was less than half of that (mean = 5.5 ± 1.8 hours, range = 2-10 hours, n = 199 sampling days). Most hooting events (81.0%, n = 79) involved a single caller, with two (8.9%) or more (10.1%) callers recorded in the remaining cases. The male initiated the majority (84.8%) of hooting events (67 of 79 events), and hooted at some point in nearly all (75 of 79 events) events. Females hooted less frequently, initiating 15.2% of events, and were hooting at some point during 17.7 % of events (n = 79). The average duration of hooting events was 18.5 ± 27.8 minutes (range = 1-138 min, n = 79), although events lasted significantly longer (Mann Whitney U Test: $U = 242$; $p = 0.004$) when there were two or more (mean = 37 ± 33.6 min, n = 15 events) versus a single caller (mean = 14.4 ± 24.8 min, n = 64 events).

The distribution of the onset of hooting events across two-hours blocks from 0700 and 1700 differs from what would be expected if calling was randomly distributed (Fig. 3.4; $\chi^2 = 11.3$, df = 4, $p < 0.05$). Overall, fewer hooting events were initiated during the earliest and latest part of the day (Fig. 3.4). Although both sexes initiated hooting events when they were alone, most male and female calls were given when the individuals were in the company of other adult individuals [% of calls initiated when alone: male = 30%, female = 17%; % of calls when with others: male = 70%, female = 83%; sample sizes, n (# of call initiated): male = 67, female = 12]. Nonetheless, hooting events typically began when one (or more females) was in a party separate from the silverback male. Male proximity data taken at the onset of male initiated hooting events (n = 67) revealed the absence of one or more female in 65 events (97%). Female proximity data taken at the onset of female-initiated hooting events (n = 12) revealed the absence of the silverback from her own party in all cases.

In the majority (73%) of hooting events (n = 79), although at least one female was separated from the male, the focal female was in the same party as the male, and therefore no GPS data were available for the separated female. However, in the remaining 21 cases the focal male and female were in separate parties with simultaneous GPS monitoring, which allowed us to measure the distance separating individuals at the onset of hooting events (for a summary of sample sizes see Appendix 6). In these cases, the mean distance separating the male and female at the onset of hooting events (mean = 196 ± 130; n = 21 events) was significantly greater than either the mean daily female distance to male (mean = 51 ± 15 m, n = 290; LMM: $F_{1,287} = 82.04$; $p < 0.001$) or the mean daily maximum to male (mean = 127 ± 16 m, n = 290; LMM: $F_{1,288} = 8.50$; $p = 0.004$) (Fig. 3.5). There was individual variation in female mean and maximum distance to the male, with some females ranging on some occasions as far as 700 meters from the male and Female 1 being significantly further than other females (LMM: mean distance: $F_{3, 286} = 8.26$, $p < 0.001$; max distance: $F_{3, 286} = 2.78$, $p = 0.04$; Fig. 3.6A and B).

In 21 of 22 cases (with GPS monitoring of separated parties), the distance between a female and the male decreased between the beginning and ending of the hooting event (Fig. 3.7; Paired Samples T Test: $t_{21} = 7.41$, $p < 0.001$). On average, the distance between the male and the female decreased from 196 ± 130 meters at the onset of the hooting event to 72 ± 134 meters at the end. We also tested for significant decreases in male-female distance between the start and end of hooting events within each female and using the mean value for each female (Wilcoxon Signed Ranks Test per female: Female F1: $Z = -2.37$, $p = 0.009$; F2: $Z = -1.75$, $p = 0.04$; F3: $Z = -1.60$, $p = 0.054$; F4: $Z = -2.37$, $p = 0.009$; Wilcoxon Signed Ranks Test of female means: $Z = -1.83$, $p = 0.03$; all one-tailed p-values).

Responsibility of Reunion and Function of Replies

The male approached the female most often (74%, n = 14) although the value was only marginally significant (Binomial test: $p = 0.06$) (n = 19 hooting events with GPS data available and one sex responsible for decreasing distance; in one case distance was not reduced and in the remaining two cases both individuals were responsible; total events n = 22).

We found that neither the hooter nor the recipient approached the other more than would be expected by chance [Hoot initiator: approaches recipient 58% of events (n = 11), is approached 42% (n = 8); expected by chance = 50%; Binomial test: $p > 1.0$]. Thus responsibility for reducing distance does not rest exclusively with the hooting initiator.

In the 22 hooting events where GPS data were available on the separated parties, the call recipient replied in roughly half (55%) of the cases and remained silent during the other half (45%) (Binomial test: $p = 0.8$). When remaining silent, the call recipient approached the hoot initiator in 78% of cases (Binomial test: $p = 0.4$; n = 9 events in which one party was responsible for re-establishing contact and no reply was heard). However, when the call recipient replied to the hooter, it (the recipient) was less likely to approach the hoot initiator (only 40% of cases), whereas the initiator was more likely to approach the replier (60%; Binomial test: $p = 0.7$; n = 10 events with replies when one party was responsible for re-establishing contact).

Both sexes replied to hooting events initiated by separated adults of the opposite sex, but the male replied more frequently to the hoots of a separated female (75% of 12 female initiated hoots) than females did to the male (7.5% of 67 male initiated hoots). On no occasion did an adult female respond to the hoot series initiated by another female. Replies occurred both when the replier was separated from all other group members (alone) and when the replier was in a party with other adult individuals [% of calls given in reply when alone: male = 56%, female = 60%; % of calls when with others: male = 54%, female = 40%; sample sizes, n (# of call initiated): male = 9, female = 5].

Discussion

The results presented here show that hoot series meet all criteria for a long contact call functioning to reunite group members, including: individual call distinctiveness, the context of separation and the function of reducing distance between the caller and recipient/replier. In addition, the acoustic characteristics of the call are in accordance with the hypothesized function. For example, the long duration of hoot series (3-9 seconds) might usefully increase transmission over long distance by reducing attenuation (Waser and Waser 1977), although the call displays a low fundamental frequency (200-400Hz), which is not optimal to avoid background noise (Schneider et al. 2008). In addition, its long duration and the repetition of segments with low modulation and narrow spectrum (Palombit 1992b) might facilitate the localization of the caller when ambient noise is high (Waser and Brown 1986). Therefore, although the acoustic characteristics of the call do not show a strong adaptation for long distance transmission, such as that observed in gibbons' long calls (Schneider et al. 2008) or elephants' rumbles (Soltis 2010), they clearly facilitate the localizability of the caller in the tropical rainforest environment (Waser and Brown 1986), which is an important factor if the call is used to reunite separated group members.

The fundamental segment of the call (i.e., hoot) differs among callers in the acoustic frequency characteristics. Most parameters, however, distinguished between sexes rather than within sex (females), potentially due to the extreme sex dimorphism in gorillas (Smith and Jungers 1997) and the influence of body size on frequency characteristics (Janik and Slater 1997). The way in which the entire series was delivered (i.e., number of segments, mean and maximum segment duration and the location of the longest segment in the call), however, differed equally within and between sexes, which is not surprising as the temporal parameters are less constrained by body size (Janik and Slater 1997; Ey et al. 2007). Together, these results show that the western gorilla hoot series are individually distinct, potentially allowing the recognition of caller identity by listeners from its acoustic structure alone, as is true for many other primates and non-primate species long contact calls (e.g., bats: Boughman 1997; birds: Berg et al. 2011; dolphins: Caldwell and Caldwell 1965; elephants: Soltis et al. 2005; manatees: Sousa-Lima et al. 2002; primates: Brown et al. 1978; Snowdon et al. 1983; Mitani et al. 1996).

Western gorillas use this call when one or more females are separated from the male, usually at distances approximately four times the daily mean distance (197 vs. 51 meters) and twice the daily maximum distance (197 vs. 126). As predicted, after calling, the distance among dispersed group members was significantly smaller than at the onset of the call, confirming its function in decreasing distances between group members. Our study, therefore, differs from previous ones (e.g., Snowdon et al. 1983; Leighty et al. 2008b) because we could simultaneously investigate whether all of the conditions (i.e., call distinctiveness, context and function) were met for a true contact call (but see Cheney et al. 1996). In contrast to long calls of species living in fission-fusion societies (e.g., chimpanzees, spider monkeys, elephants), in which the outcome of a contact call may be complicated by other factors like the identity of the caller, the presence of oestrus females or fruit trees (e.g., Chapman and Lefebvre 1990; Clark and Wrangham 1994), western gorilla hoot series almost always resulted in reduced distance between callers and recipients.

Western Gorilla Contact Calls and Social Structure

Since females seemed to not react to each other calls, hoot series function more specifically to reduce male-female distance as opposed to general inter-individual distances among all individuals. This likely reflects the influence of the social organization on the dynamics of within-group vocal communication (Marler 1976). Dispersal patterns have often been used to explain sex differences in giving and exchanging long/lost calls. For instance, in baboons, a female philopatric species, lost calls are more commonly used by females (Cheney et al. 1996; Fischer et al. 2001), whereas in chimpanzees, a male philopatric species, long calls are given more commonly by males (Clark 1993; Notman and Rendall 2005). Gorillas live in polygynous groups in which both sexes disperse. Consequently, the most important social relationship for each female is the one with the male and not those with other females (Stokes 2004; Harcourt and Stewart 2007). That the male initiates the majority (85%) of hooting events may indicate that he is monitoring each female in the group. That male gorillas generally monitor females was previously suggested also in mountain gorillas (Watts 2000; Byrne 2000; Stokes 2004). In support of this hypothesis, over the last ten years we observed three females dispersing from the group and in each of these cases the male hooted for hours after the female left (D. Doran and R. Salmi, unpublished data). Adult females occasionally initiate calls (15%) when separated from the male. Nevertheless, in the majority of the cases, calls were initiated when other individuals were with the hooter. Therefore, western gorilla hoot series cannot be described as lost or isolation calls of single individuals as in other species (e.g., Cheney et al. 1996; Digweed et al. 2007; Carter et al. 2012). The call is more commonly given by individuals when the group splits into subgroups or parties that have become separated from each other, similar to rumbles in elephants (Leighty et al. 2008b).

Although hooting did not occur randomly throughout the day, it was not concentrated at dawn and/or dusk like other long calls which have been suggested to indicate locations of groups to neighbouring groups (e.g., Waser 1975; Waser 1982). Instead, the call was given less frequently in early hours of morning, which is not surprising since western gorilla group members nest all together at night (Tutin et al. 1995; Mehlman and Doran 2002; Kalan et al. 2010), and thus group members would be least likely to be separated just after nesting.

To facilitate reunion, western gorillas not only give but also reply to calls from other group members. Female gorillas reply only to the male and never to other females. However, most hoot series are met with silence: when this occurs the separated party is most likely to approach the hooter, suggesting that the call meaning might be “come to me” and silence may indicate agreement (the following approach confirms it), in which case no response is necessary. In contrast, when the call recipient hoots in reply, he/she is less likely to approach the original caller, in which case the meaning of a reply might suggest, “no, you come to me.” In this case, the hooting event lasts longer and might represent disagreement between callers. Although our sample size is small, results suggest that individual travel direction can be influenced by whether hoot series are replied to or not, in which case, calling might represent an attempt to establish a consensus in traveling decision (Conradt and Roper 2005; Conradt and Roper 2007). Females might use hoot series not only to maintain and decrease distance to the male (and therefore secure protection for her and her offspring) but also to influence group travel direction and indicate specific foraging patches, which would otherwise be ignored by the male. If this is true, leadership in western gorillas might be at least partially shared, in contrast to the pattern described for mountain gorillas (Watts 2000).

Hooting rates vary across individuals and females differ in their average distance to the male. Since being farther apart should lead to higher hooting rates, one could predict that reduced average proximity to the male is associated with higher female hooting rate. However, this seems unlikely for two reasons. First, the two females with the highest calling rate are also the farthest and the closest to the male (female 1 and 2). Second, although females are most commonly with another female during hooting events, some females consistently hoot more than others. Hooting rate is directly linked to rank (as close call rates in mountain gorillas: Harcourt and Stewart 1996), with high-ranking females hooting more frequently than low ranking ones (F1-2 vs. F3-4). If so, high-ranking individuals (i.e., male and the highest ranking females) are also more likely to influence group travel than other individuals.

Variable Function of Hoot Series

The results of this study support the hypothesis that spatial cohesion is reduced in western gorillas relative to mountain gorillas (Goldsmith 1999; Doran-Sheehy and Boesch 2004). In western gorillas, although females nest with the silverback nightly, their distance to the male throughout the day fluctuates considerably, and females can range as far as 700 meters from the male. In addition, the average distance between each female and the male was equal to 50 meters although the average daily maximum was over 100 meters. This contrasts sharply with measures of group cohesion that have been reported in mountain gorillas (with comparable group size), in which group members are rarely separated from each other by 50 meters and never farther than that (Watts 1991). Previously, Doran-Sheehy and colleagues showed that western gorillas feed frequently on fruit trees (Doran and McNeilage 2001; Doran et al. 2002; Doran-Sheehy and Boesch 2004), which are extremely rare in habitats where mountain gorillas live. Typically, trees used by western gorillas are not large enough for all group members to feed together, so individuals separate to forage. The distance separating individuals at these times exceed the typical distance over which close vocalizations are used by mountain gorillas (Harcourt et al. 1993). These changes in diet and spatial cohesion produce different communication challenges, potentially explaining the different use of long calls in the two species. While mountain gorillas (and only males) give hoot series during intergroup encounters, western gorillas use them to communicate with dispersed group members. Our results support, therefore, previous findings showing that differing ecological and social constraints can strongly affect a species' vocal communication. For instance, the frequency and acoustic structure of calls have been found to differ in species inhabiting different environment and under differing social circumstances (proximity to other individuals), potentially enhancing the ability to locate the caller (Snowdon and Hodun 1981; Waser and Brown 1986; Oda 1996; Sugiura 2007; Ey et al. 2009).

Vocal production, however, is highly constrained by anatomy and phylogeny (Hauser 1993; Fitch and Hauser 1995; Fletcher 2004; Ey et al. 2007). Although western and mountain gorillas diverged 1.75 million year ago (Scally et al. 2012), there is clear evidence of more recent gene flow between the two subspecies (Thalmann et al. 2007; Scally et al. 2012), which might have impeded the evolution of new calls and favored instead the use of a call already in their repertoire in novel circumstances (as also observed in Guinea and chacma baboons: K. Hammerschmidt pers. obs., and in rhesus and Japanese macaques: Owren et al. 1993).

This suggestion can explain the use of hoot series in within-group communication for western gorilla males, but not for western gorilla females, raising the question of why western gorilla females started producing a call that was typically a male call. Yet this scenario assumes that the vocal behavior of the most recent common ancestor of western and mountain gorillas most closely resembled that of the extant mountain gorillas. If, instead, the vocal behavior before the split was more similar to the western species, the loss of hoot series to maintain cohesion in mountain gorillas might reflect the lowered group dispersion within this species. This view represents a more conservative explanation of the production of a new call by western gorilla females. Whichever scenario best reflects the evolutionary history of the hoot series, its different use in the two gorilla species illustrates a greater flexibility in both production and usage of ape acoustic signals than previously thought (see also Hopkins et al. 2007).

The Mechanisms Behind the Use of Hoot Series

Western gorillas give hoot series when separated from at least one group member of the other sex and not only when alone. In addition, both the male and females reply to the hoot series of other group members regardless of their own location (i.e., alone or in proximity to others). In contrast, baboons, who give lost calls when they are separated from other group members, do not respond to the lost calls of other group members unless they themselves are also separated from the group (Cheney et al. 1996), suggesting that they do not understand the state of mind of other individuals and that calling/replying is mostly a manifestation of the caller's emotional state (Cheney et al. 1996; Rendall et al. 2000; Seyfarth and Cheney 2012). Since previous research conducted in captive settings has demonstrated that chimpanzees and to some extent also other great apes, possess some rudimental aspects of theory of mind (Call and Tomasello 2008; Zimmermann et al. 2009; Herrmann et al. 2010; but see Gretscher et al. 2012) and might communicate intentionally (Poss et al. 2006; Crockford et al. 2012), it is not unlikely that wild western gorillas might understand the state of separation and/or the intention of other group members to re-establish proximity and call to facilitate reunion (Dennett 1988). This interpretation is further suggested by those cases in which responses were not given and the silent listening individual travelled towards the calling individual whether or not s/he was alone or with the rest of the group. However, since regaining proximity might be beneficial for both male and females, the association between the call and the subsequent outcome might represent a simpler and more parsimonious explanation of the mechanisms involved in the use of long contact calls in western gorillas, as well as in other primate species (Byrne 2000).

Although responses to separated individuals have been observed in other primate species, the probability of a response is generally dependent on the relative rank of the caller (i.e., individuals are more likely to answer to high ranking individuals; Digweed et al. 2007), which Teixeira da Cunha & Byrne (2009) have argued does not demonstrate evidence of understanding of others' statuses but rather reflects the general trend of increased attention to the behaviour of dominant individuals. In western gorillas, however, this explanation does not apply since high-ranking individuals were calling and responding much more than others (i.e., male vs. females; female 1 and 2 vs. female 3 and 4). Teixeira da Cunha & Byrne (2009) have labelled two hypotheses and formulated respective predictions to test the mechanisms behind the use of long contact calls: the personal-status hypothesis (from the baboon study; Cheney et al 1996) states that the calls are not given to inform others, and includes the prediction that calls are replied to only by isolated individuals, and the reunite hypothesis (Byrne 2000), which predicts that calling does not depend on the state of separation and replies will be more commonly given by low-ranking individuals. None of these hypotheses explain the use of long contact calls in western gorillas, because calls were given only when individuals were separated from specific individuals and not only when alone, and they were not replied to more often by low ranking individuals. This study, therefore, might represent the first evidence of perspective taking (i.e., understanding of others' state of mind) in wild western gorillas although future research implementing playback experiments is needed to assess the perception of these calls and to better explain the cognitive abilities behind their use.

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Tables and Figures

Table 3.1. Hoot series and hoot segment acoustic characteristics. Description and individual mean ± SD of temporal parameters of hoot series (n = 52; n_M = 30; n_{F1} = 17; n_{F2} = 5) and frequency parameters of hoot segments (n = 288; 96 segments for each caller). Parameters that differed between callers (Hochberg's correction) are indicated under posthoc by 1 if M ≠ F1, by 2 if M≠F2, and by 3 if F1≠F2.

1. Hoot series

Parameters	**M**	**F1**	**F2**	**posthoc**
Call duration [s]	4.1±0.9	6.4±3.0	6.5±3.2	n/a*
Number of segments in the series [n]	12.3±3.9	14.0±9.0	28.0±15.1	1, 2
Mean segment duration [s]	0.1±0.0	0.2±0.1	0.2±0.1	1
Maximum segment duration [s]	0.2±0.2	0.9±0.4	0.8±0.5	1, 2, 3
Location maximum segment duration within the call (as ratio = sequential number of the unit / number of units)	0.5±0.3	0.3±0.7	0.7±0.4	1, 3

2. Hoot segment

Parameters	**M**	**F1**	**F2**	**posthoc**
Mean frequency at which the first quartile of global energy is reached across all time segments [Hz]	216.6±23.4	351.9±39.8	380.1±43.6	1, 2, 3
1st dominant frequency band [Hz]	211.9±18.3	347.0±45.1	355.4±47.8	1, 2
Amplitude ratio between first and second dominant frequency bands	6.3±3.9	10.2±7.8	4.4±2.4	1, 2, 3
Mean frequency first peak [Hz]	165.5±54.9	348.2±48.0	376.5±44.9	1, 2, 3
Mean frequency of the highest energy [Hz]	218.7±27.0	352.8±46.8	378.0±45.8	1, 2, 3

Table 3.2. DFA cross-validated classifications. For each individual the percentage of hoot series (1) and hoots (2) correctly assigned (in bold) and those misclassified (not in bold) are indicated.

1. Hoot series temporal characteristics

Individual	n calls	M	F1	F2
M	30	**90**	7	3
F1	17	12	**88**	0
F2	5	0	20	**80**

2. Hoot segment frequency characteristics

Individual	n segments	M	F1	F2
M	96	**97**	3	0
F1	96	4	**74**	22
F2	96	3	16	**81**

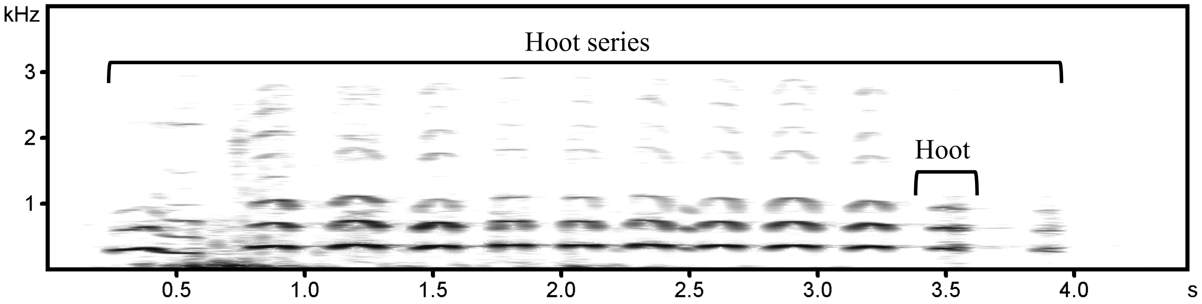

Fig. 3.1. Spectrograms of hoot series. The entire call (Hoot series) and the call segment (Hoot) are indicated.

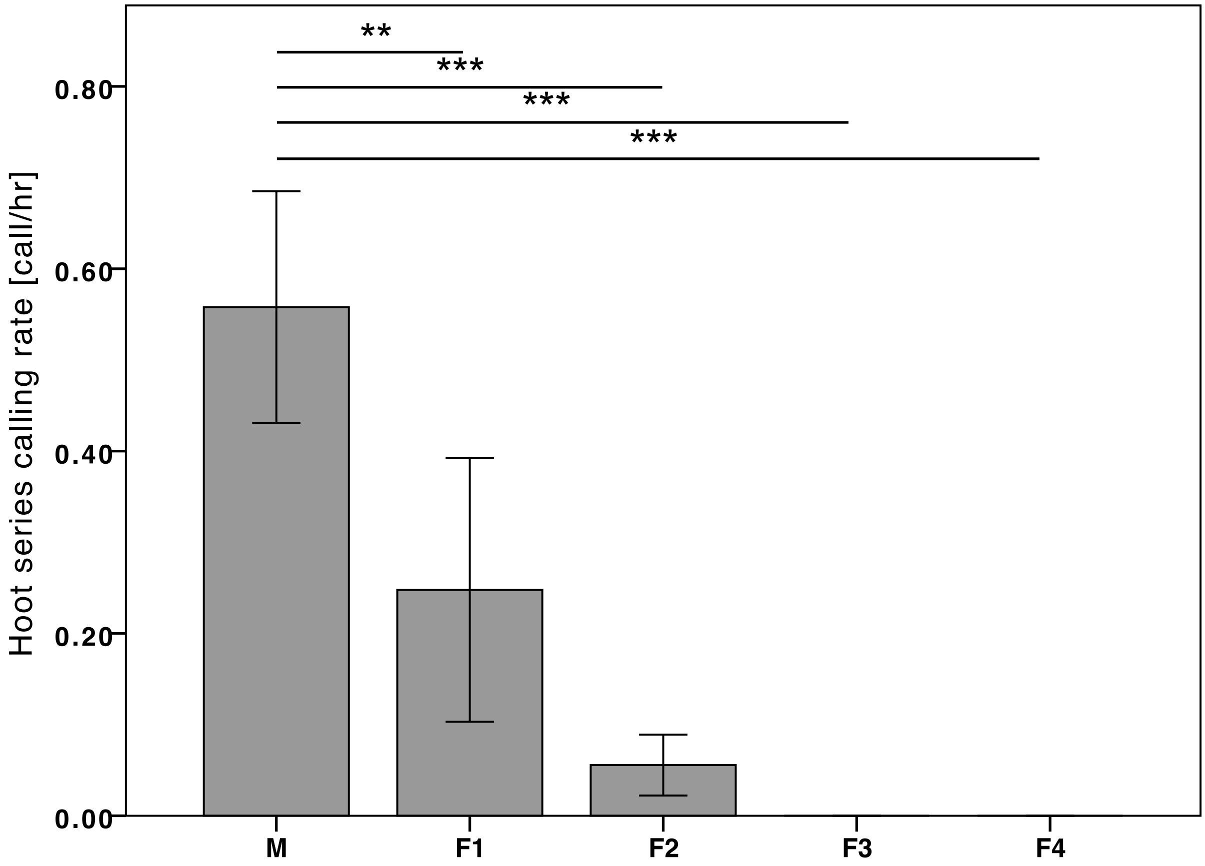

Fig. 3.2. Individual variation in male (M) and females (F) gorilla hoot series mean calling rates (Error bars: ± SE/; n = 12 monthly means of daily hoot series calling rates per individual). Significant differences (see text) are indicated with ** = $p < 0.01$ and *** = $p < 0.001$.

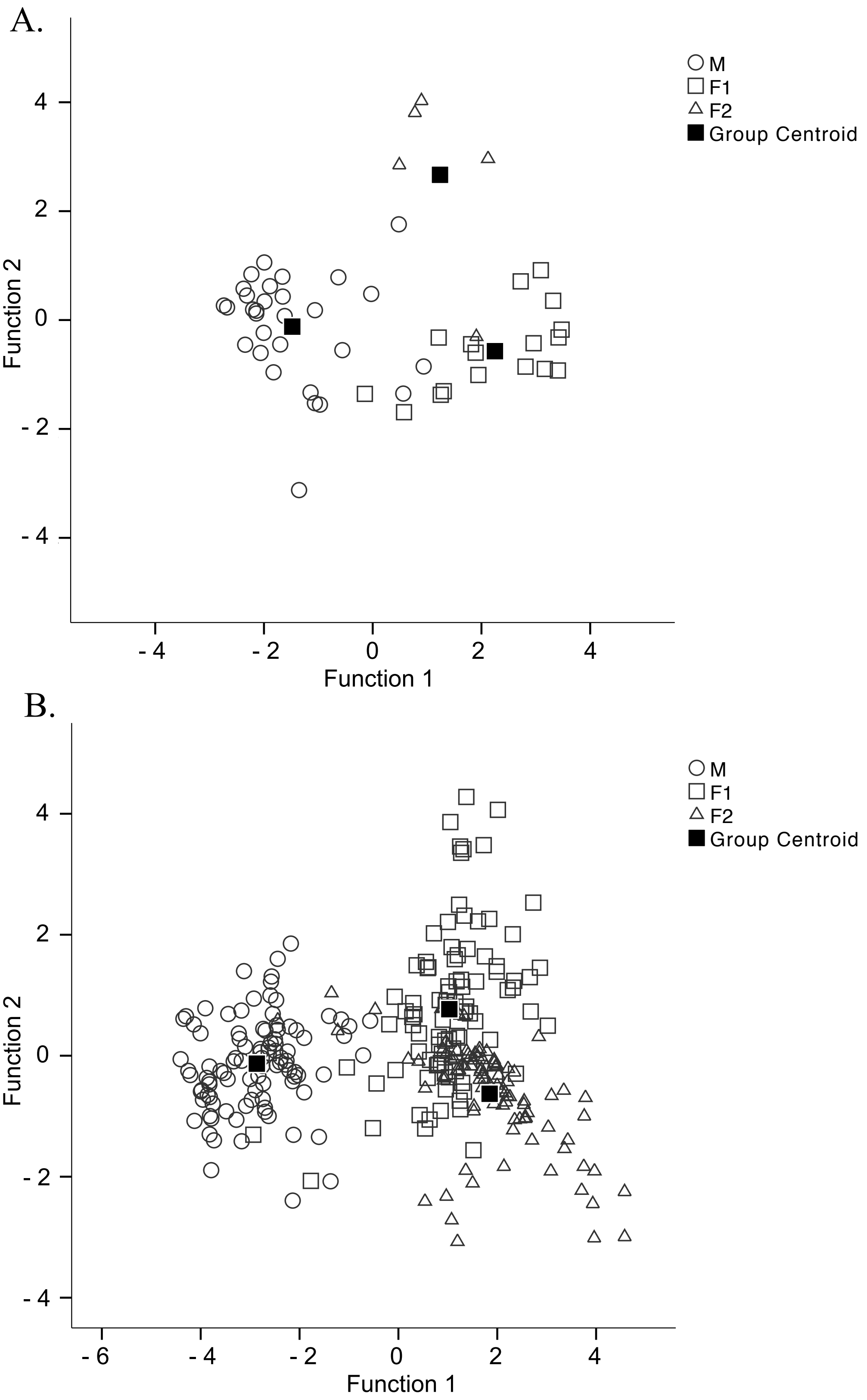

Fig. 3.3. Discriminant function analysis of individual distinctiveness of a) hoot series and b) hoot segments (A; $n_M = 30$; $n_{F1} = 17$; $n_{F2} = 5$; B; $n_{M,\, F1,\, F2} = 96$).

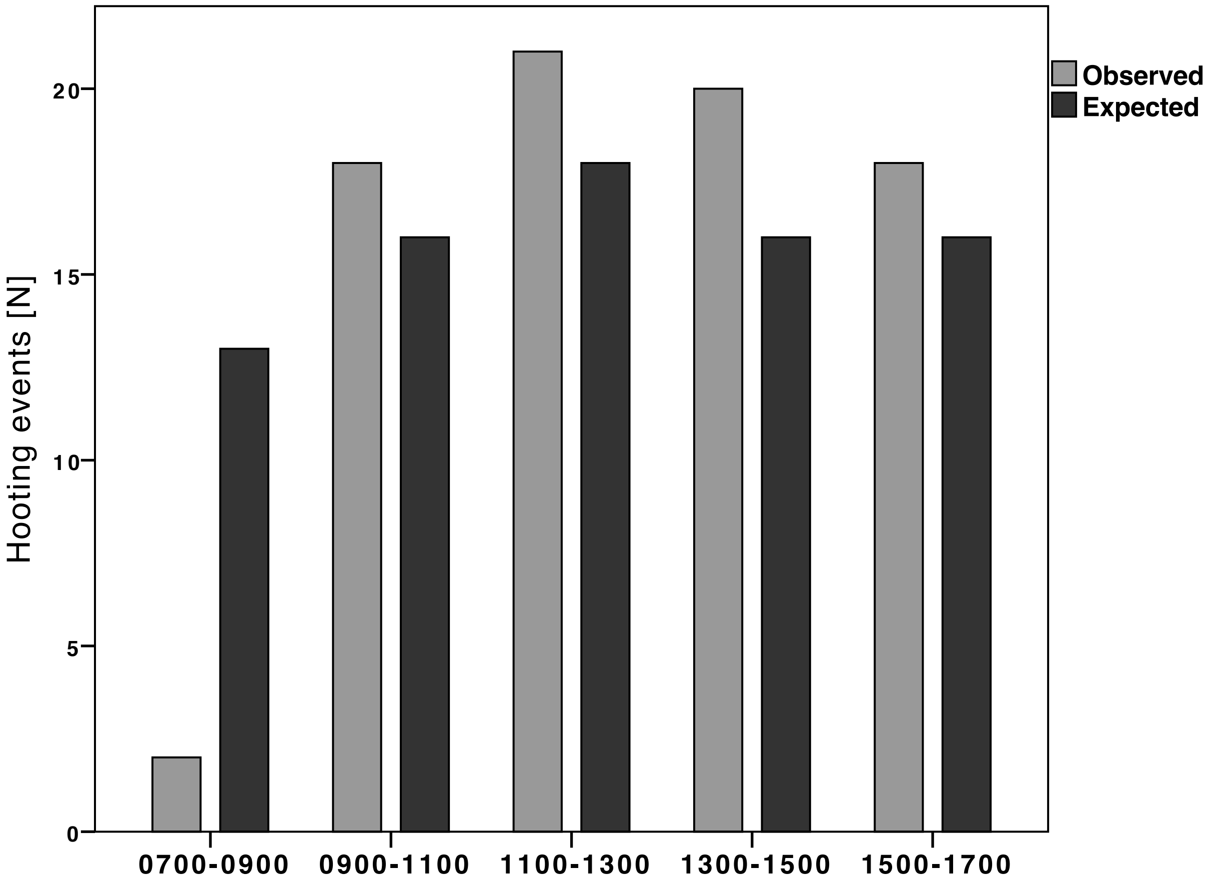

Fig. 3.4. Observed and expected distribution (calculated from the observation time spent in each time block) of hooting events (n = 79) during five 2-hour blocks.

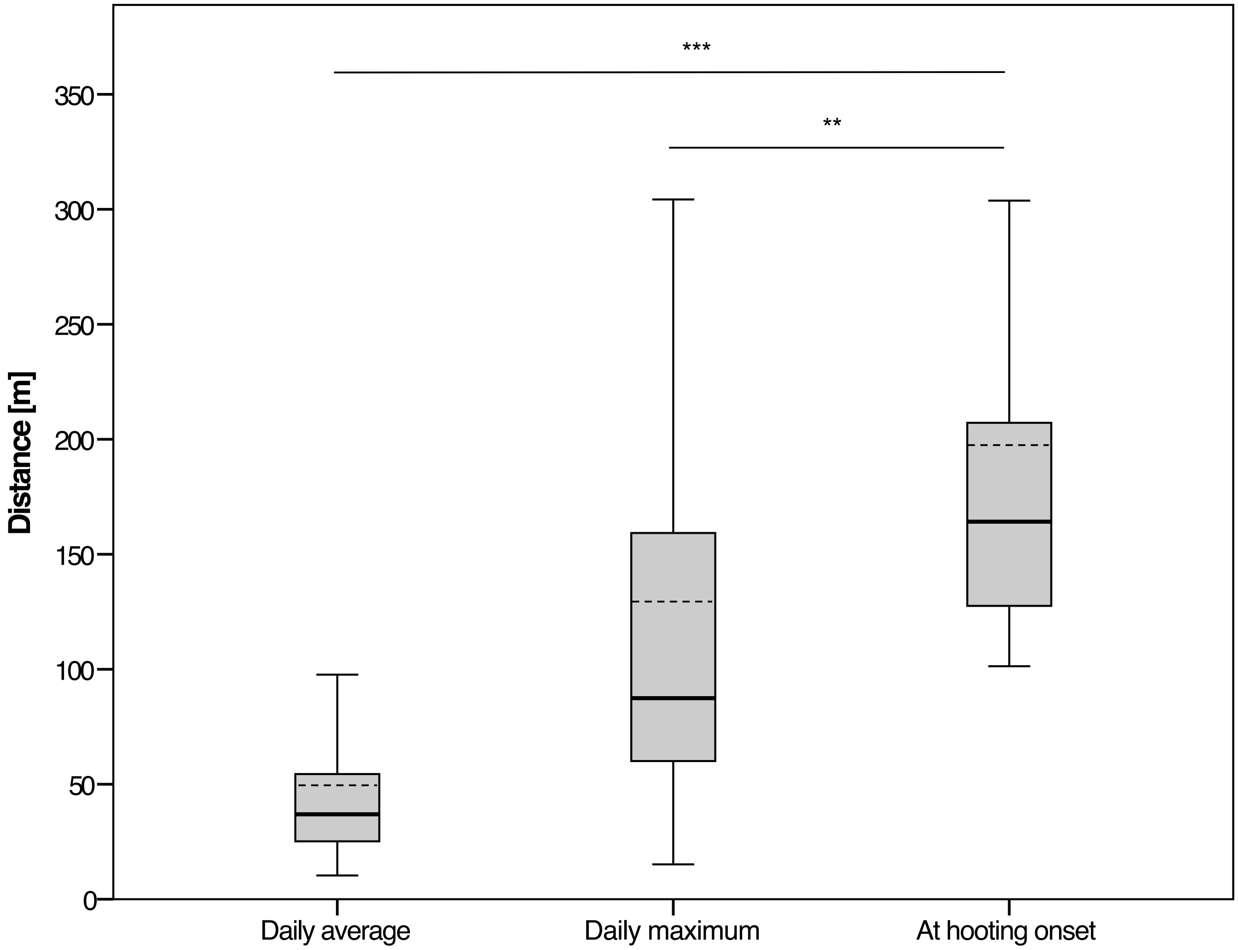

Fig. 3.5. Distance of females to the male at hooting onset compared to daily average and maximum distance. Box plots include median (solid lines), mean (dashed lines), first and third quartiles (bottoms and tops of boxes), and interquartile range (whiskers). Significant differences (see text) are indicated with ** = $p < 0.01$ and *** = $p < 0.001$.

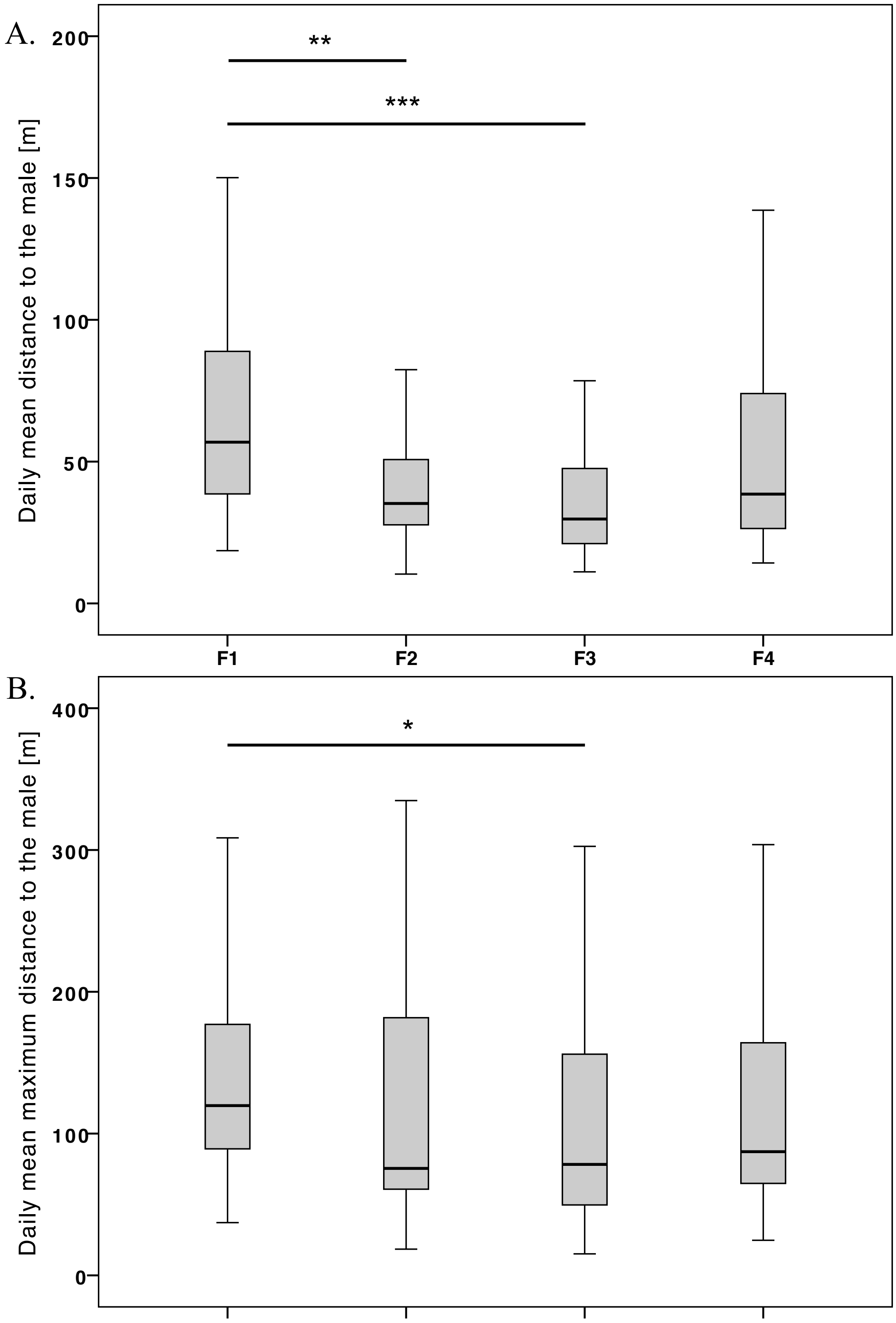

Fig. 3.6. Individual variation in female distance to the male. Box plots show median (solid lines) and first and third quartiles (bottoms and tops of the boxes) of daily mean (A) and maximum distance (B) of each female (F1-4) to the male. Whiskers show minimum and maximum values. Significant differences (see text) are indicated with * = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$.

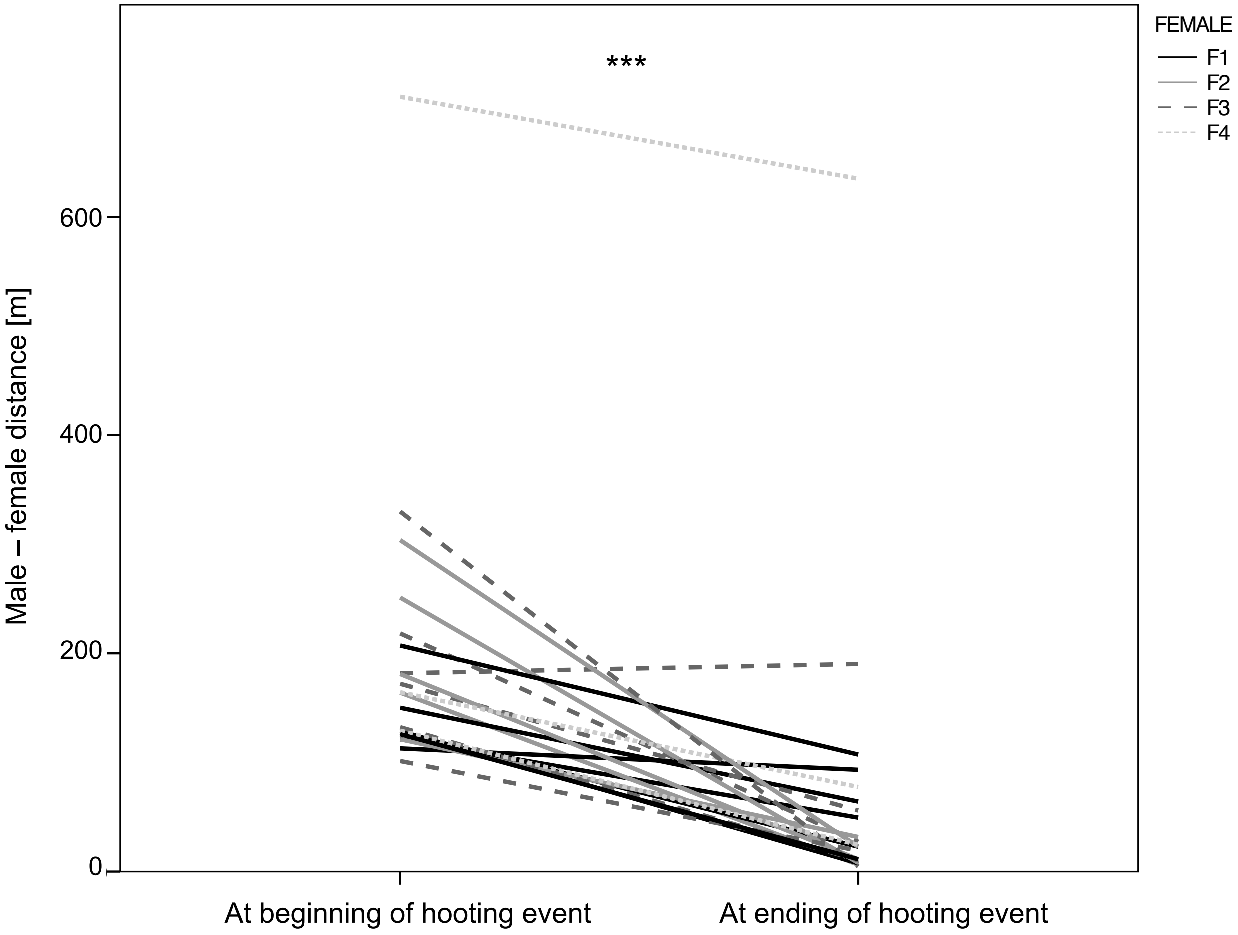

Fig. 3.7. Male-female proximity at onset and end of hooting events (n = 21). Significant difference (Paired t-test) is indicated with *** = $p < 0.001$.

CHAPTER FOUR

Acoustic Variation and Individual Distinctiveness throughout the Vocal Repertoire of the Wild Western Gorilla (*Gorilla gorilla*)[3]

Abstract

Individually distinct vocalizations play an important role in animal communication, allowing call recipients to respond differentially based on caller identity. However, which of the many calls in a species' repertoire should have more acoustic variability and be more recognizable is less apparent. One proposed hypothesis is that calls used over long distances (long calls) should be more distinct because visual cues are not available to identify the caller. An alternative hypothesis proposes that close calls should be more recognizable because of their importance in social interactions. To examine which hypothesis garners more support, we selected 1,594 calls from 1 male and 6 adult female gorillas (*Gorilla gorilla*) during focal follows conducted over 16 months at the Mondika Research Center (Republic of Congo). We measured call coefficients of inter- and intra-individual variation, and the potential for individual coding for each acoustic parameter (n = 20) for each call type (n = 6). Using discriminant function analysis, we measured the proportion of calls that could be correctly assigned to their caller. Acoustic variability, and especially intra-individual variation was high in all gorilla calls. Results indicated that all calls were individually distinct: loud calls (i.e., hoots), social (i.e.,

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[3] This chapter will be submitted for publication to Journal of the Acoustical Society of America with D.M. Doran-Sheehy, Department of Anthropology, Stony Brook University and K. Hammerschmidt, Cognitive Ethology, German Primate Center as co-authors.

screams, threat and copulation calls) and contact calls (i.e. grumble, single, double and copulation grunts) were equally individually distinct, suggesting that both the distance at which communication occurs and the call social function have played an important role in the evolution of identity signaling in western gorilla vocal communication.

Introduction

Advances in the study of animal vocal communication have shown that many species display higher inter- and intra-individual acoustic variability in their vocal signals than previously thought (e.g., birds: Robisson et al. 1993; Evans and Evans 2007; Berg et al. 2011; bats: Boughman 1997; Arnold and Wilkinson 2011; Carter et al. 2012; ungulates: (Reby et al. 2005; Vannoni and McElligott 2007; carnivores: Theis et al. 2007; Schehka and Zimmermann 2009; primates: Hauser 1991; Fischer et al. 2001; Fischer et al. 2002; Clay and Zuberbühler 2011b; Leliveld et al. 2011). Although it is less clear if these subtle acoustic differences are always meaningful for the animals, it is now recognized that vocal signals have the potential to carry different kinds of information, which include: (a) diverse external events (i.e. predators, food) and behavioral contexts experienced by the callers (birds: Evans and Evans 2007; mammals: Macedonia and Evans 1993; primates: Seyfarth and Cheney 2003b); (b) caller internal state (birds: Leavesley and Magrath 2005; elephants: Soltis et al. 2005; tree shrew: Schehka and Zimmermann 2009; hyenas: Theis et al. 2007; marmots: Blumstein and Armitage 1997; primates: Seyfarth and Cheney 2003a; Lemasson et al. 2012); and (c) caller identity (birds: Jouventin and Aubin 2002; koalas: Charlton et al. 2011; pandas: Charlton et al. 2009; deer: Vannoni and McElligott 2007; hyraxes: Koren and Geffen 2011; hyenas: Theis et al. 2007; primates: Cheney and Seyfarth 1980; Snowdon and Cleveland 1980; Miller and Thomas 2012).

Individual differences in vocal signals could reflect both physical and social characteristics. Physical characteristics are those related to morphological differences including age, sex, and body size (goats: Briefer and McElligott 2011; hyenas: Theis et al. 2007; deer: Reby et al. 2005; primates: Rendall et al. 2004; Pfefferle and Fischer 2006; Ey et al. 2007; Bouchet et al. 2010), whereas social characteristics are those reflecting specific social categories including rank, kinship, and even group membership (bats: Boughman 1997; birds: Price 1999; Sharp et al. 2005; dolphins: Hawkins 2010; Hoffmann et al. 2012; Boughman and Wilkinson 1998; seals: Charrier et al. 2003; primates: capuchin monkeys: Rendall et al. 1996; Weiss et al. 2001; Crockford et al. 2004; Digweed et al. 2007).

Individually distinct vocalizations play an important role in animal communication, since they may reduce the uncertainty of the external world experienced by listeners, allowing them to respond differentially based on caller identity, age, sex, social rank, and group membership. However, there are many questions not yet fully answered regarding animal identity signaling (Ghazanfar and Santos 2004; Ghazanfar 2007; Rendall et al. 2009). First, is inter- and intra-acoustic variability similar across all calls? Second, are all calls in a species' vocal repertoire individually distinct or has natural selection for individual uniqueness been stronger on some calls and less on others? In the latter case, which of the many calls in a species' repertoire should be more individually recognizable? Third, what acoustic characteristics are responsible for generating distinctive voice cues, and are those the same across call types? Although systematic study of individual distinctiveness and acoustic variability across an entire species' vocal repertoire is needed to understand the adaptive functions they play in the animal's communication systems, few attempts have been made so far (skuas: Charrier et al. 2001; primates: Leliveld et al. 2011; Lemasson and Hausberger 2011; Bouchet et al. 2012), while the majority of studies has focused on the analysis of only one vocalization at a time (e.g., Fischer et al. 2001; Fischer et al. 2002; Spillmann et al. 2010) or at maximum two (e.g., chimpanzees: Mitani et al. 1996; baboons: Owren and Rendall 2003; Rendall et al. 2009; putty-nosed monkeys: Price et al. 2009).

Four non-mutually exclusive hypotheses, based on the distance at which calls are given (Marler 1967), the social (Snowdon and Elowson 1997) or spatial context (Janik and Slater 1998) in which they are produced, and the direct effects to the nervous system they can elicit in receivers (Owren et al. 1997; Owren and Rendall 2001), have been proposed to explain the evolution of individually distinct vocal signals and their variation across a species' vocal repertoire. So far, among nonhuman primates studies have yielded differing results, supporting two of the hypotheses proposed: the distance communication hypothesis and the social context hypothesis. Under the distance communication hypothesis, calls given or exchanged over long distance are expected to be more distinct among individuals than those given at close distance, since no other cues could be simultaneously used to enable listeners to recognize the identity of the caller (Marler 1967). Support for this hypothesis comes from studies conducted in chimpanzees and mouse lemurs, two primate species in which individuals forage commonly alone or in fission-fusion system. In both species long-distance calls, used when individuals are not in visual contact, were more individually distinct than calls exchanged over close distance (Mitani et al. 1996; Leliveld et al. 2011). In contrast, under the social context hypothesis, calls used in intragroup social interactions at close distance, such as affiliative or threats calls (those calls given toward a specific target and generally when individuals are relatively close to each other) are expected to be more distinct than long-distance calls directed to a more generalized audience (e.g. the entire group) (Snowdon and Elowson 1997). Support for this hypothesis has been found in primate species that are more spatially cohesive. For instance, among red-capped mangabey and female Campbell's monkey vocalizations, although all calls are individually distinct, those emitted during social/affiliative interactions showed higher acoustic variation and were more individually distinct than either long or alarm calls (Lemasson and Hausberger 2011; Bouchet et al. 2012).

Here we test which of these two hypotheses better explains the pattern occurring in the wild western gorilla's (*Gorilla gorilla*) vocal repertoire. We explore whether the acoustic variability differs across gorilla call types, and since they are highly social animals, we expect higher acoustic variability in calls used during social interactions than those directed to a more generalized audience and/or exchanged over long distance. If gorilla calls are acoustically distinct among individuals, we also determine whether some call types are more than others. We then explore which vocal characteristics are responsible for generating distinctive voice cues, and if they are the same across call types. We finally explore whether the acoustic characteristics that distinguish among individuals (only females) and those that distinguish between sexes are the same.

Western gorillas are the appropriate species for this study since: (a) they inhabit the dense tropical rainforest and vocal signals represent an important communicative channel; (b) they live in cohesive polygynous groups and, in contrast with chimpanzees, individuals often interact with each other (R. Salmi pers. obs.), and many of their calls are used for regulating these important social interactions (Harcourt et al. 1993; Harcourt and Stewart 1996); and finally (c) since group members are, in some cases, separated by over 700m all age classes need to communicate with dispersed group members using loud broadcast calls (Salmi & Doran-Sheehy in prep.).

The species' vocal repertoire has been described recently and includes 17 call types (Salmi et al. in prep.). Since the male body size is more than double than that of the female (170 vs. 71 kg; Smith and Jungers 1997) and we have data only from one male, to investigate both acoustic variability and individual distinctiveness we examined only calls among adult females. We considered eight call types grouped into four major categories (Salmi et al. in prep.; Salmi and Doran-Sheehy in prep.): long-distance calls (one type), soft food calls (one type), contact calls (three types) and social calls exchanged during close interactions between individuals (three types). We measured the same acoustic parameters in all calls and determined both acoustic variability and individual distinctiveness. If the distance at which communication occurs has shaped the acoustic properties of western gorilla vocalizations, we would expect loud calls, such as long contact calls, to have both higher acoustic variability and individual distinctiveness, and calls exchanged at close distance such as contact, food, copulation, and aggressive calls to show lower values. However, if the social context better explains the variation across call types, we would expect to find contact and social calls to display higher levels of acoustic variability and individual distinctiveness; food calls (for their indiscriminate target and quiet nature) to exhibit intermediate values; and long-distance calls to display lower ones (see Table 4.1 for a schematic explanation of our predictions).

Methods

Subjects and Study Area

Seven adult wild western gorillas (1 silverback, 6 females) from one habituated group were observed for 16 months (May-June 2007, April 2009-May 2010) at the Mondika Research Center (02° 21′ 859″N; 016° 16′ 465″E), Republic of Congo (for study site description, see

(Doran-Sheehy et al. 2004). Three of the group's females were not present for the entire study, as a result of death, emigration and immigration. All individuals (with the exception of one newly immigrated female) were fully habituated, permitting digital recordings of calls at very close range (<10 meters). Precautionary measures, following the guidelines of the Wildlife Conservation Society (WCS), were adopted to prevent any disease transmission between human observers and animals.

Data Collection

We conducted 489 focal follows of 2-4 hours for a total of 1,572 focal hours. They include 170 male follows (764 hours) and 319 female follows (695 hours, including an average of 80 ± 6 follows and 173.8 ± 14.5 hours for each of four females and 54 hours, from 12 follows, for a fifth female). Additionally, we also used ad lib sampling of rare vocalizations (n = 71) for a sixth unhabituated female. During focal follows, we continuously collected digital recordings of all focal vocalizations, using a portable Marantz recorder (PMD671) and a Sennheiser MKH 416 short shotgun microphone (equivalent noise 13dB, minimal impedance 25Ω, sensitivity in free field, no load (1kHz) 25mV/Pa ± 1dB), handled with a shock mount and protected by a foam windshield (MZW415ANT). Recordings were taken at a sampling frequency of 48kHz.

Description of Call Types and Call Categories

We examine eight call types: the scream (SC), a very loud call with high and sparse harmonics with varying degree of noise, given as a sequence of screams of different length; the threat grunt (TG), an abrupt, close call of short duration, given in irregular bouts of 1- 30 calls; the copulation grunt (CG), soft, close call emitted in long sequences (>80 calls) with some frequency modulation; the single grunt (SG), a soft, guttural, single -syllable call of low frequency; the double grunt (DG), a soft guttural call composed by two syllables of varying length, normally the second longer than the first; the grumble (GR), a soft close call of irregular length defined by dense harmonics with some degree of noise, displaying higher percentage of tonal segments than grunts; the hum (HM), a soft call with dense harmonics and varying degree of noise; and the hoot series (HT), a vocalization composed by a sequence of calls/segments with 2-3 sparse harmonics given at regular intervals, with the highest percentage of tonality among all call types (Fig. 4.1). They are all used in within-group communication but they vary in several of their characteristics. For example, they differ in their directionality (i.e., whether they are directed to a specific individual or to a generalized audience), in the distance they travel and the context in which they are given. We grouped the eight calls in four major categories: social calls, contact calls, food calls, and long-distance calls (Table 4.2). Social calls include three call types directed to a specific individual and used during close social interactions: the threat grunt (TG) given during within-group aggression, the scream (SC) emitted during escalated within-group aggression (SC), and the copulation grunt (CG) used during sexual behavior. Contact calls include the three most frequent call types given in many different contexts and exchanged at close distance but generally not directed to a specific individual: the single grunt (SG), double grunt (DG) and grumble (GR). Food calls include only one call type, given exclusively during foraging at intermediate distance but not directed to a specific individual: the hum (HM). Long-distance calls include also one call type, which is given when individuals are separated and directed to a broad audience: the hoot series (HT) (Table 4.2).

Data Analysis

Using the Avisoft SASLab Pro 5 software (R. Specht, Berlin, Germany), we generated spectrograms after converting the sampling frequency of the calls depending upon call frequency range (22,050 Hz, 11,025 Hz, or 4,000 Hz). Gorilla vocalizations are typically composed of one or more call segments, each of which may be given once or more than once (Fig. 4.1). We use the call segment (call), rather than the entire vocalization, as the unit for acoustic analysis, regardless of how often they are repeated (following Bezerra et al. 2010). Based on the acoustic quality (i.e. background-noise ratio), we selected 1,594 calls for the acoustic analysis from a total of 11,360 recorded. We used the custom software program LMA 2011 (Fischer et al. in press) to calculate twenty acoustic parameters related to time, frequency, energy, relative amplitude characteristics, and tonality (Table 4.3), for each call segment. In contrast to previous studies (e.g., Lemasson and Hausberger 2011) we did not consider the total call duration, the number of call segments in the call and the silent intervals between them, since our analysis was based on call segments. We excluded measurements of frequency modulation because it was not a noticeable property in gorilla calls and also those parameters (i.e. start and end call segment frequency measurements) shown to be influenced by external factors (Maciej et al. 2011).

Since individuals vary in calling rates and call rates vary considerably across call types, the sample sizes of calls vary among individuals (Salmi et al. in prep.). For each call type, only individuals with ≥ 4 calls were included in the analysis. In order to maintain the same number of subjects for the analysis of most adult call types, we used the same number of females as often as possible, varying their identity as needed.

Statistical Analysis

Acoustic Variability

We used the twenty call parameters as single acoustic characteristics. For each of them, across all call types, we calculated the inter-individual variation means ($\mathrm{MEAN}_{\mathrm{inter}}$ calculated over the whole set of calls of a given type) and standard deviation ($\mathrm{SD}_{\mathrm{inter}}$ calculated over the whole set of calls of a given type), and the intra-individual means ($\mathrm{MEAN}_{\mathrm{intra}}$ calculated by averaging individual means) and standard deviations ($\mathrm{SD}_{\mathrm{intra}}$ calculated by averaging the SD of every individual's set of calls and totaling it with the SD calculated over the individual means values). We then computed the coefficients of variation, both inter-individually ($\mathrm{CV}_{\mathrm{inter}}$ = 100x $\mathrm{SD}_{\mathrm{inter}}$ / $\mathrm{MEAN}_{\mathrm{inter}}$) and intra-individually ($\mathrm{CV}_{\mathrm{intra}}$ = mean of individual CV values; with for each individual, CV = 100x SD / MEAN) for each parameter. We test whether the inter- and intra-individual coefficients of variation differed among call types using the Friedman test. Separately, we computed for each call type inter- and intra-individually mean coefficients of variation ($\mathrm{CV}_{\mathrm{mean}}$) averaged over all parameters studied ($\mathrm{CV}_{\mathrm{inter\text{-}mean}}$ and $\mathrm{CV}_{\mathrm{intra\text{-}mean}}$).

Individual Distinctiveness

We calculated individual distinctiveness of call types by determining the potential of identity coding (PIC) following Robisson et al. (1993) to be able to compare our results with those of previous studies in social monkey species (Lemasson and Hausberger 2011; Bouchet et al. 2012). The potential for individual identity coding (PIC) is the ratio between the two sets of coefficients of variation ($\mathrm{CV}_{\mathrm{inter}}$ / $\mathrm{CV}_{\mathrm{intra}}$), a PIC value > 1 indicates that the parameter can be used for individual recognition. We tested whether calls differed in their PIC values using the Friedman test. For each call we also calculated the overall potential for individual identity coding (overall PIC = $CV_{inter\text{-}mean} / CV_{intra\text{-}mean}$) to assess whether some calls display higher values than others.

We also examined individual distinctiveness using a multilevel analysis of variance, following a two-step procedure (Fischer et al. in press). We performed discriminant function analysis (DFA; Klecka 1980) of the acoustic parameters using the stepwise method and then testing for internal validation of the classification with a cross-validation procedure using the leave-one-out method (U-method) (Hair et al. 1995). The comparison of DFA and cross-validated DFA allows determining whether the profiles are stable (Barros et al. 2011), especially in those cases in which individual call samples are small (<10 calls). We then used linear mixed modeling (LMM; West et al. 2006) to test whether distinctiveness of call parameters (those which correlated > 0.45 with the functions generated by DFA) was significant after controlling for unequal samples and after adjusting for multiple analyses using Hochberg's correction (Hochberg 1988). To determine whether some calls were more individually distinct than others, we compared the cross-validated correct assignments of each female caller for the eight calls and ran a LMM, considering as fixed factor all call types or call categories (i.e., contact, social, food and long-distance calls) and as random factors caller identity and number of call used. Finally, to explore sex differences, and in particular which acoustic parameters were influenced by sex, we ran the same analysis (DFAs, LMMs and Hochberg corrections) for seven of the eight calls used by both females and the male. All statistical tests have been executed using SPSS 20.0.

Results

Acoustic Variability across Female Calls

Overall mean coefficients of inter- and intra-individual variation were above 40% for most call types (Fig. 4.2 and Table 4.4). Intra-individual variation differed significantly across call types (Friedman test on CV_{intra}: $\chi^2 = 16.33$, df = 7, n = 20, $p = 0.02$; Table 4.4). Coefficients of intra-individual variation ranged from 38% in food calls (HM) to 63% in one social call (Fig. 4.2). Inter-individual acoustic variation also differs among calls (Friedman test on CV_{inter} values: $\chi^2 = 15.10$; df = 7, n = 20, $p = 0.035$; Table 4.4), ranging from 47% in food calls to 67-75% in social calls given during aggression (TG and SC) (Fig. 4.2).

Individual Distinctiveness across Female Calls

All call types had overall PIC values > 1, ranging from 1.06 in one social call (TG) to 1.36 in screams, indicating they all display individual vocal cues (Fig. 4.3). However, PIC values did not vary significantly among call types (Friedman test: $\chi^2 = 3.95$, df = 7, n = 20, $p = 0.79$; Table 4.5).

The discriminant function analyses significantly distinguished among female callers for all eight calls, with classification accuracy ranged from 75% in single grunts to 100% in screams (cross-validated DFA = 75 to 100%; Table 4.6). The percentage of calls assigned correctly to each subject ranged from 50 to 100% (cross-validated DFA 50 to 100%). In each case, the correct classification was significantly greater than that predicted by chance (ranging from 33 to 50%, depending on the number of subjects included). The plots of the two discriminant functions for different call types based on the DFA of female calls show clear separation of individuals' calls (Fig. 4.4). In all cases DFA and cross-validated DFA produced similar results, indicating that the derived profiles were stable (Table 4.6). All parameters used by each DFA and correlated to one of the canonical factors for a value equal or greater than 0.45, maintained significance in the LMM after Hochberg correction for multiple analyses (Table 4.6; for calls' characteristics see Appendix 7).

No calls were more individually distinct than others, i.e., cross-validated classification assignments did not differ significantly among the eight call types (LMM: $F_{7, 14} = 1.51$; $p = 0.24$), or among the four behavioral call categories (i.e., social, contact, food and long-distance calls; LMM: $F_{3, 16.3} = 0.2$; $p = 0.89$).

Individual Distinctiveness when the Male is Included

When the male was added to the analysis, the DFA discriminated among callers in each call, with classification accuracy ranging from 62% in cough grunts to 89% in hoot series (cross-validated DFA = 58 to 88%; Table 4.7). The percentage of correct assignment for the male in each call type ranged from 49 to 100% (cross-validated DFA 47 to 100%), and in each case, the classification was significantly greater than that predicted by chance (25-33%). The call types in which the male was assigned the lowest accuracy were the threat grunt (corrected classification 49%, cross-validated classification 47%) and the food call (corrected classification 69%, cross-validated classification 67%). For all the other calls, correct call assignment was greater than 75% (cross-validated classification 72%). The plots of the two discriminant functions for different call types based on the DFA of female and male calls are shown in Fig. 4.5. DFA and cross-validated DFA produced similar results, indicating that the derived profiles were stable (Table 4.7). All parameters used by each DFA and correlated to one of the canonical factors for a value equal or greater than 0.45, remained significant in the LMM after Hochberg correction

(Table 4.7), with the exception of noise and the mean frequency of the first peak (fp1mean) for threat grunts (social call), and the minimum value of the frequency with highest energy (pfmin) for food calls (Table 4.8; for calls' characteristics see Appendix 1).

Important Acoustic Parameters

From PIC Analysis

Most of the 20 acoustic parameters had a PIC value > 1, and thus most parameters might be used to identify the caller (Table 4.5). Four of the 20 acoustic parameters displayed values above 1 in all call types (Table 4.5); these include the mean frequency range (ranmean), the minimum frequency of the first dominant band (df1min), the first peak mean frequency (fp1mean) and the percentage of noisy time segments (noise). However, the parameters with highest PIC values (> 2.0) were not consistent across call types. For instance, the minimum difference between first and second dominant frequency bands (diffmean) was important in long distance and copulation calls, but not in food calls or double grunts (Table 4.5).

From DFA of Females

In contrast, the DFA found that fewer acoustic parameters, on average two (range 1-4), were used to distinguish calls of females (Table 4.6). The set of acoustic parameters that significantly distinguished among callers was different for each call type and no single parameter was significant in all call types (Table 4.6). However, one parameter, the mean number of dominant frequency bands (diffreq), contributed to distinguish among female calls more often than any other, being significant in four call types, including the long call (hoot series), and three social calls (screams, threat and copulation calls). Two other parameters distinguished between callers in two calls: the location of the global energy in the first quartile of the call (dfa1maloc), differing in contact and long-distance calls (double grunt and hoot series); and the frequency of the global energy in the second quartile of the call (dfa2mean), differing in two social calls (screams and threat calls) (Table 4.6).

From DFA of Females and Male

When the male was added to the analysis, twice as many parameters were significant in distinguishing among individuals (Table 4.7 and 4.8). A common parameter across call types was the first peak mean amplitude (fp1amean). Nine of the fifteen parameters that were significant in distinguishing among female calls were also significant when the male was included. Twenty-two new parameters became important when the male was included (Table 4.7 and 4.8). These parameters may therefore be more related to body size and/or sex differences than individual differences, although larger sample size will be required to confirm this. For example, the mean amplitude of the first peak (df1amean) was commonly correlated to Function 1, which strongly discriminated between the calls of the male and females (Fig. 4.5; Table 4.8), especially in single grunts (contact call), double grunts (contact call), and hoot series (long-distance call).

Discussion

Acoustic variability was displayed by all eight western gorilla calls studied. Our results showed that intra-individual variation was generally higher than that of monkey species [red-capped monkeys (*Cercocebus torquatus*): 11-31%, Bouchet et al. 2012; Campbell monkeys (*Cercopithecus campbelli*): 20-50%, Lemasson and Hausberger 2011), ranging from 38 to 67%.

Inter-individual variation was instead intermediate between those of the other two species for which a similar analysis has been conducted (red-capped monkeys: 20-50%, Bouchet et al. 2012; western gorillas: 45-75%, this study; Campbell monkeys: 45-227%, Lemasson and Hausberger 2011). In western gorillas both intra- and inter-individual acoustic variations were highest in social calls (screams and threat grunts) and lowest in food calls (hums).

Individuals living in social groups are often monitoring the behavior of other group members (e.g., Cheney and Sayfarth 2007; Slocombe and Zuberbühler 2007; Wittig et al. 2007; Maciej et al. 2013). Since gorilla males protect the members of their groups from predation, harassment, and infanticide (Watts 1989; Harcourt and Stewart 2007) and serve as peacekeeper in female conflicts (Watts 1997; Harcourt and Stewart 2007), the higher acoustic inter-individual variation of calls given during conflicts among females (i.e., screams, threat grunts) might allow the male to identify who is participating in a skirmish when occurring out of sight, and to intervene when needed. The male intervention in ending the skirmish would therefore benefit the female who was receiving the aggression (and screaming). Although screams and cough grunts are used during close aggressive interactions between individuals, they might also function to recruit help form distant individuals (Gouzoules et al. 1984; Slocombe and Zuberbühler 2007; Eberle and Kappeler 2008). The higher intra-individual variation of these calls suggests instead that they might carry additional information, for example, the individual's emotional state and the urgency of the situation (Fichtel et al. 2001; Fichtel and Hammerschmidt 2002; Fichtel and Hammerschmidt 2003), the participants' rank (Bergman et al. 2003; Cheney and Seyfarth 2004; Kitchen et al. 2005), and the relative role each individual has in the conflict (Slocombe and Zuberbühler 2005).

The lower intra-individual variation of food calls might also be explained by the general function they serve. These calls are given during a specific context (i.e., during foraging) to potentially affect the spatial proximity among group members during feeding when individuals are generally not in visual contact. Intra-individual variation of gorilla food calls, however, is relatively low compared to other gorilla calls, but still high when compared to other monkey species (i.e., red-capped monkeys (Bouchet et al. 2012). This suggests that the acoustic structure of western gorilla food calls might also carry, as shown in other primate species, other types of information such as food distribution and abundance (e.g., Dittus 1984; Hauser et al. 1993), food type (Clay and Zuberbühler 2011a), and individual food preference (e.g., Elowson et al. 1991; Slocombe and Zuberbühler 2006).

For all calls, inter-individual variation was higher than intra-individual variation, and consequently, identity coding was above 1 in each of the calls tested. Our results are similar to those of other studies in finding that all calls possess substantial potential for identity coding and that parameters with high identity coding vary across call types (Lemasson and Hausberger 2011; Bouchet et al. 2012). The multivariate analysis, which provides information on how different calls relate to each other, allowing the comparison of a large number of samples and variables at the same time (Hammerschmidt and Todt 1995; Schrader and Hammerschmidt 1997; Fischer et al. in press), yielded similar results. The discriminant function analyses (DFA) confirmed that western gorillas calls were all individually distinct, suggesting that they all carry important individual cues that listeners might use to distinguish different callers. Another result shown by the multivariate analysis concerned the parameters used to distinguish among callers. Previous studies found that noisy calls were less distinct than harmonic ones (Leliveld et al. 2011), although this might be a consequence of the greater difficulties in estimating subtle differences in noisy sounds. In contrast, individual distinctiveness of gorilla calls was independent from the noise of the call and the grunts were as distinct as the harmonic hoot series (or even more). In each call type a differing set of acoustic parameters was useful to differentiate among callers, indicating that individual vocal cues do not depend on few acoustic parameters.

Our results suggest also that there are some differences in the parameters used to discriminate within and between sexes: the mean number of dominant bands was commonly used to distinguish among females, whereas the mean amplitude at first peak and the parameters describing the energy in the call were more important in distinguishing between male and females calls. These results however have to be taken with caution since we had calls from only one male and an equal sample size between sexes is crucial to assess sex differences in vocal signals. Nevertheless, since our unit of analysis was the call segment and not the entire call we might have underestimated both the variability and the individual distinctiveness of gorilla call types. For instance, temporal parameters of primate vocalizations, such as the entire length, the number of repetition of the call segment in the call and the silent space between them can increase the individual difference of vocal signals and have been found to differ significantly among individuals in other species (e.g., Lemasson and Hausberger 2011).

We tested between two of the hypotheses proposed to explain the adaptive function of individual distinctiveness across a species vocal repertoire. According to the social hypothesis (Snowdon and Elowson 1997), vocal signals used at close distance during social contexts should be more individually distinct than long-distance calls. In contrast, we found that not only contact calls (i.e., single grunt, double grunt, and grumbles) and those calls given during close social interaction between individuals (i.e., screams, threat calls and copulation calls) were highly individual distinct, but this feature was also present in long-distance calls (hoot series) used when individuals are not in visual contact (Salmi & Doran-Sheehy in prep.). Under the distance hypothesis (Marler 1967), calls exchanged over long distances were expected to be more distinct than those exchanged at close distance. However, among western gorillas not only long-distance calls, but also close-distance calls, and especially those emitted during social interactions (copulation grunts, cough grunts, screams), were acoustically different among callers. Thus, our results show that neither the distance communication hypothesis nor the social context hypothesis alone explains the adaptive function of individual distinctiveness in the vocal repertoire of western gorillas, in contrast to what has been shown by previous studies in strepsirrhines (Leliveld et al. 2011) or monkey species (Lemasson and Hausberger 2011; Bouchet et al. 2012). This lack of fit might be explained by the graded nature of apes' vocal systems (Marler 1976) and therefore the higher variability in the acoustic structures of their vocalizations compared to the more discrete or stereotyped calls of monkey species. In addition, in the case of female gorillas the lack of calls directed to a very broad audience such as those used by many primates to deter or announce the presence of predators and those territorial calls functioning in inter-group spacing, might explain the need of individual distinctiveness in all calls used in within-group communication.

Although different calls might serve different functions, individual distinctiveness might facilitate communication in different circumstances. For instance, when interacting at very close range during aggressive or affiliative situations (threat, screams and copulation calls), individually distinct calls might facilitate the monitoring of others' behaviors; at intermediate distances (contact and food calls), they might allow the coordination of group activity and spatial proximity; and when group members are spatially separated (long-distance calls), individually distinct calls might contribute to maintain vocal contact and allow regaining of inter-individual proximity. In short, individual distinctiveness and the potential ability to recognize the caller in western gorillas might have evolved to facilitate different functions. Alternatively, individual distinctiveness might be the result of chance, emerging from idiosyncrasies and differences in the development of the vocal tract of each individual (Rendall et al. 1998; Rendall et al. 2009). This explanation, however, has been considered too simplistic and potentially not able to account for the level of individual differences found in vocal signals of primates, who have been shown to be capable of vocal tract modulation (Hauser 1992; Riede and Zuberbühler 2003).

Regardless of the proximate causes of individual distinctiveness in primate calls, a more important step to understand the evolution and the adaptive function of individual vocal cues in our close relatives is testing whether these differences are meaningful and used by listeners to distinguish callers. That calls are individually distinct, in fact, does not mean that individuals can recognize the calls of different individuals, and playback studies are needed to this end (e.g., (Rendall et al. 1996; Hammerschmidt and Fischer 1998; Cheney and Seyfarth 2000; Fischer 2004; Rendall et al. 2009). In addition, evidence in primate literature suggests that acoustic recognition might not follow the same pattern of call distinctiveness. For example, Kojima et al. (2003) showed that although chimpanzee long-distance calls (pant hoots) were shown to be more individually distinct than close calls (pant grunts), a captive female chimpanzee easily recognized the different callers of not only pant hoots but also pant grunts and screams, and she could recognize the identity of more than one caller when calls of different callers were played simultaneously.

In conclusion, our study showed high levels of acoustic variation (especially intra-individual variation) across the entire vocal repertoire of western gorillas, with all calls being equally individually distinct. Our results did not support any of the hypotheses tested, since individual distinctiveness did not vary across calls. We suggest that the study of caller recognition is critical to elucidate the adaptive function of individual vocal cues, and playback experiments can contribute to this goal by revealing whether listeners use these acoustic differences to recognize caller identity and to better investigate what parameters are important for this end.

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Tables and Figures

Table 4.1. Hypotheses and predictions for acoustic variability and individual distinctiveness across western gorilla calls. The last column summarizes the results.

Call categories	***Calls***	**Distance Hypothesis**	**Social Hypothesis**	
		Predictions		***Result***
Long-distance calls	Hoot series	High	Low	High
Food calls	Hums	Low	Intermediate	High
Contact calls	Single grunt, double grunts, grumbles	Low	High	High
Social calls	Screams, copulation grunts, threat grunts	Low	High	High

Table 4.2. Description of western gorilla call types, including names, categories, distances at which they are exchanged, directionality (broad or specific audience) and contexts in which they are given.

Call type	**Category**	**Distance**	**Directionality**	**Context**
Single grunt [1]	contact call	close	broad	maintenance activities (forage, rest, travel)
Double grunt[1]	contact call	close	broad	maintenance activities (forage, rest, travel)
Grumble[1]	contact call	close	broad	maintenance activities (forage, rest, travel)
Copulation grunt[1]	social call	close	specific	sexual behavior
Threat grunt[1]	social call	close	specific	within-group aggression
Scream[1]	social call	close	specific	within-group escalated aggression
Hum[1]	food call	intermediate	broad	forage
Hoot series[1, 2]	long-distance call	large	broad	when individuals are separated

[1]: Salmi et al. in prep; [2]: Salmi and Doran-Sheehy in prep

Table 4.3. Acoustic parameters list. Name and description of parameters used.

Parameters	Description
duration	Duration from beginning to the end of the call [ms]
dfa1mean	Mean value of the frequency at which the first quartile of global energy is reached across all time segments [Hz]
dfa1maloc	Location of the maximum frequency at which the first quartile of global energy is reached across all time segments
dfa2mean	Mean value of the frequency at which the second quartile of global energy is reached across all time segments [Hz]
dfa2maloc	Location of the maximum frequency at which the second quartile of global energy is reached across all time segments
df1max	Maximum value of the first frequency in the call which contains more energy than a particular thresholds in all time segments (DF) [Hz]
df1min	Minimum value of the first frequency in the call which contains more energy than a particular thresholds in all time segments (DF) [Hz]
df1mean	Mean value of the first frequency in the call which contains more energy than a particular thresholds in all time segments (DF) [Hz]
diffmean	Minimum difference between first and second dominant frequency bands (DF) [Hz]
diffreq	Mean number of dominant frequency bands (DF)
ampratio1	Amplitude ratio between first and second dominant frequency bands
fp1max	Max frequency first peak (global frequency peak) [Hz]
fp1mean	Mean frequency first peak [Hz]
fp1amean	Mean amplitude first peak [rel. amplitude]
ranmean	Mean frequency range [Hz]
pfmax	Maximum value in all time segments of the frequency with the highest energy [Hz]
pfmin	Minimum value in all time segments of the frequency with the highest energy [Hz]
pfmean	Mean value across all time segments of the frequency with the highest energy [Hz]
noise	Percentage of noisy time segments [%]
tonality	Percentage of tonal time segments [%]

Table 4.4. Coefficient of intra- (a) and inter-individual variation (b) of each acoustic parameter and overall values for each call type.

	Long call (HT)		*Food call (HM)*		*Contact call (GR)*		*Contact call (DG)*		*Contact call (SG)*		*Social call (CG)*		*Social call (TG)*		*Social call (SC)*	
	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b
duration	122	94	38	45	55	59	35	40	36	50	14	19	5	6	50	48
dfa1mean	70	14	16	26	16	16	18	27	22	24	15	19	41	50	29	30
dfa1maloc	32	64	59	72	99	97	93	101	85	83	105	99	92	91	71	153
dfa2mean	67	33	25	25	25	23	24	35	32	31	13	12	37	49	25	30
dfa2maloc	41	66	43	66	51	54	115	84	69	70	103	94	47	49	64	129
df1max	23	56	46	48	44	47	42	66	42	44	25	41	46	46	31	29
df1min	16	22	4	4	5	7	4	6	7	7	26	39	20	21	33	35
df1mean	81	16	16	16	7	10	15	14	10	10	24	43	23	25	36	36
diffmean	35	105	44	42	33	42	52	49	55	60	60	137	56	55	26	25
dffreq	20	21	66	77	74	103	41	47	42	50	24	22	74	73	22	27
ampratio1	47	21	34	53	35	48	35	39	22	39	27	28	71	68	38	39
fp1max	49	45	43	40	45	73	43	35	34	40	34	49	49	50	53	58
fp1mean	25	55	27	28	23	32	31	48	38	38	28	41	36	43	63	70
fp1amean	22	25	52	67	48	64	65	75	70	76	26	25	61	80	21	25
ranmean	19	23	10	14	15	16	12	21	29	32	35	37	76	97	82	83
pfmax	79	20	27	39	27	30	30	31	26	37	23	26	60	77	35	36
pfmin	73	71	59	62	88	90	59	64	72	68	94	95	118	116	94	159
pfmean	26	76	66	70	112	106	65	68	65	60	98	100	87	90	122	206
noise	52	124	27	47	28	42	8	9	13	16	65	85	50	52	24	31
tonality	14	54	54	54	58	67	127	248	311	319	170	143	207	190	189	258
Overall CV	**46**	**50**	**38**	**45**	**44**	**51**	**46**	**55**	**54**	**58**	**51**	**58**	**63**	**66**	**56**	**75**

Table 4.5. PIC values of 20 acoustic parameters [CV_{inter}/CV_{intra}] and overall values [$CV_{mean-inter}/CV_{mean-intra}$] for each call type (HT = hoot series; HM = hum; GR = grumble; DG = double grunt; SG = single grunt; CG = copulation grunt; TG = threat grunt; SC = scream).

Parameters	*Long call (HT)*	*Food call (HM)*	*Contact call (GR)*	*Contact call (DG)*	*Contact call (SG)*	*Social call (CG)*	*Social call (TG)*	*Social call (SC)*
duration	0.77	1.19	1.06	1.16	1.39	1.37	1.20	0.95
dfa1mean	0.21	1.62	0.98	1.47	1.10	1.30	1.24	1.04
dfa1maloc	2.03	1.22	0.98	1.09	0.97	0.94	0.99	2.14
dfa2mean	0.50	1.01	0.92	1.44	0.97	0.91	1.31	1.22
dfa2maloc	1.59	1.53	1.05	0.73	1.02	0.91	1.04	2.01
df1max	2.43	1.04	1.07	1.58	1.05	1.60	1.01	0.94
df1min	1.42	1.02	1.29	1.54	1.01	1.49	1.03	1.04
df1mean	0.19	1.01	1.31	0.91	0.97	1.74	1.06	1.00
diffmean	3.00	0.96	1.26	0.94	1.09	2.27	0.97	0.95
dffreq	1.10	1.16	1.40	1.15	1.20	0.92	0.99	1.22
ampratio1	0.45	1.56	1.37	1.14	1.74	1.01	0.97	1.02
fp1max	0.92	0.93	1.63	0.81	1.17	1.45	1.02	1.10
fp1mean	2.17	1.07	1.40	1.55	1.01	1.46	1.17	1.11
fp1amean	1.16	1.30	1.33	1.15	1.08	0.96	1.32	1.20
ranmean	1.23	1.31	1.05	1.67	1.10	1.06	1.29	1.01
pfmax	0.26	1.44	1.11	1.04	1.43	1.13	1.29	1.03
pfmin	0.96	1.04	1.03	1.08	0.96	1.01	0.98	1.69
pfmean	2.88	1.05	0.95	1.04	0.93	1.02	1.03	1.68
noise	2.38	1.70	1.53	1.17	1.28	1.30	1.04	1.26
tonality	3.82	1.01	1.15	1.95	1.03	0.84	0.92	1.37
Overall PIC	**1.10**	**1.18**	**1.15**	**1.21**	**1.07**	**1.14**	**1.06**	**1.36**

Table 4.6. Call individual distinctiveness. Summary of eight discriminant function analyses, number of Functions (F #), Wilk's λ, Chi square (χ^2) and p-values, number of linear mixed models per call (# LMMs) and significant parameters after LMM and Hochberg's correction.

Call type	*Sex*	*n*	*DFA*	*Cross-DFA*	*Chance*	*F #*	*Wilk's λ*	*df*	χ^2	*p-value*	*# LMMs*	*Significant parameters*
Single grunt		***47***	***75.0***	***75.0***		***1***	***0.36***	***2***	***49.57***	***< 0.001***	***1***	***fp1mean***
	Female 1	16	62.5	62.5	*30.0*							
	Female 2	25	84.0	84.0	*30.0*							
	Female 4	11	72.7	72.7	*30.0*							
Double grunt		***38***	***86.8***	***84.2***		***2***	***0.33***	***4***	***38.69***	***< 0.001***	***2***	***pfmean, dfa1maloc***
	Female 1	26	84.6	84.6	*30.0*							
	Female 4	8	87.5	87.5	*30.0*							
	Female 6	4	100	75.0	*30.0*							
Threat grunt		***149***	***79.2***	***74.5***		***2***	***0.26***	***18***	***189.59***	***< 0.001***	***4***	***dfa2mean, diffreq, ampratio, duration***
	Female 1	62	82.3	80.6	*30.0*							
	Female 3	58	79.3	70.7	*30.0*							
	Female 4	29	72.4	69.0	*30.0*							
Cop. grunt		***59***	***86.4***	***83.1***		***2***	***0.21***	***4***	***88.04***	***< 0.001***	***2***	***diffreq, pfmean***
	Female 1	18	77.8	77.8	*30.0*							
	Female 4	8	87.5	75.0	*30.0*							
	Female 5	33	90.9	87.9	*30.0*							
Grumble		***24***	***87.5***	***79.2***		***2***	***0.13***	***6***	***40.28***	***< 0.001***	***2***	***tonality, fp1amean***
	Female 1	6	66.7	66.7	*30.0*							
	Female 2	12	91.7	75.0	*30.0*							
	Female 3	6	100	100	*30.0*							
Hum		***23***	***78.3***	***78.3***		***2***	***0.23***	***4***	***28.30***	***< 0.001***	***2***	***noise, pfmax***
	Female 1	14	78.6	78.6	*30.0*							
	Female 4	4	50	50.0	*30.0*							
	Female 6	5	100	100	*30.0*							
Hoot series		***319***	***78.1***	***77.2***		***1***	***0.67***	***7***	***126.95***	***<0.001***	***2***	***dfa1maloc, diffreq***
	Female 1	204	77.0	76.1	50.0							
	Female 2	115	79.1	79.1	50.0							
Scream		***12***	***100***	***100***		***1***	***0.00***	***5***	***81.80***	***< 0.001***	***1***	***diffreq***
	Female 1	7	100	100	50.0							
	Female 3	5	100	100	50.0							

Table 4.7. Call individual distinctiveness (+ male). Summary of seven discriminant function analyses, number of Functions (F#), *Wilk's λ*, *Chi square* (χ^2), *p-values*, number of linear mixed models per call (# LMMs) and significant parameters after LMM and Hochberg correction.

Call type	*Sex*	*n*	*DFA*	*Cross-DFA*	*Chance*	*F #*	*Wilk's λ*	*df*	χ^2	*p-value*	*# LMMs*	*Significant parameters*
Single grunt		*77*	***84.4***	***79.2***		***3***	***0.10***	***12***	***166.07***	***< 0.001***	***4***	***fp1amean, df1mean, dfa1maloc, df1max***
	Male	25	92.0	84.0	*25.0*							
	Female 1	16	68.8	62.5	*25.0*							
	Female 2	25	92.0	88.0	*25.0*							
	Female 4	11	72.7	72.7	*25.0*							
Double grunt		***186***	***88.7***	***86.6***		***2***	***0.25***	***18***	***251.68***	***< 0.001***	***4***	***fp1amean, df1mean, fp1mean, duration***
	Male	148	94.6	93.9	*25.0*							
	Female 1	26	64.4	61.5	*25.0*							
	Female 4	8	75.0	50.0	*25.0*							
	Female 6	4	50.0	50.0	*25.0*							
Threat grunt		***198***	***62.1***	***57.6***		***3***	***0.32***	***24***	***215.42***	***< 0.001***	***8***	***dfa2mean, ampratio, dfa1maloc, duration, pfmin, pfmean***
	Male	49	49.0	46.9	*25.0*							
	Female 1	62	66.1	59.7	*25.0*							
	Female 3	58	67.2	62.1	*25.0*							
	Female 4	29	65.5	62.1	*25.0*							
Cop. grunt		***132***	***80.3***	***73.5***		***3***	***0.11***	***18***	***277.48***	***< 0.001***	***5***	***dfa1mean, fp1amean, diffreq, df1max, pfmean***
	Male	73	75.3	72.6	*25.0*							
	Female 1	18	72.2	61.1	*25.0*							
	Female 4	8	87.5	50.0	*25.0*							
	Female 5	33	93.9	87.9	*25.0*							
Grumble		***68***	***82.4***	***75.0***		***3***	***0.18***	***15***	***105.80***	***< 0.001***	***3***	***fp1amean, tonality, diffreq***
	Male	44	79.5	77.3	*25.0*							
	Female 1	6	66.7	50.0	*25.0*							
	Female 2	12	91.7	83.3	*25.0*							
	Female 3	6	100	66.7	*25.0*							
Hum		***39***	***79.5***	***71.8***		***3***	***0.18***	***9***	***78.57***	***< 0.001***	***3***	***tonality, ranmean***
	Male	16	68.8	68.8	*25.0*							
	Female 1	14	92.9	78.6	*25.0*							
	Female 4	4	50.0	50.0	*25.0*							
	Female 6	5	100	80	*25.0*							
Hoot series		***638***	***88.6***	***88.0***		***2***	***0.10***	***24***	***1458.11***	***<0.001***	***5***	***dfa1mean, fp1mean, pfmean, df1min, dfa1maloc***
	Male	319	100	100	33.0							
	Female 1	204	79.4	78.5	33.0							
	Female 2	115	73.9	72.2	33.0							

Table 4.8. Parameters associated to (Parameters) and variance explained by (V%) the canonical functions generated by the discriminant function analyses (F) of eight western gorilla calls. Analyses of adult individuals are divided in those performed within females (DFA-females) and those including also the male (DFA-females-male).

Call	**F**	***DFA-females***		***DFA-females-male***	
		V%	**Parameters**	**V%**	**Parameters**
Single grunt	**1**	100	fp1mean*	72.8	fp1amean*
	2	-		27.1	fp1mean*
	3	-		0.1	df1mean*, duration*
Double grunt	**1**	98.1	parameters not used in the analysis[1]	87.9	fp1amean*, df1mean*
	2	1.9	dfa1maloc*, pfmin*	8.1	dfa1maloc*, dfa1max*
Threat grunt	**1**	64.8	dfa2mean*, diffreq*	66.1	dfa2mean*
	2	35.2	ampratio*, duration*	28.5	ampratio*, dfa1maloc*, duration*
	3	-		5.4	pfmin*, noise, pfmean*, fp1mean
Copulation grunt	**1**	90.1	diffreq*	87.8	dfa1mean*
	2	9.9	pfmean*	90	fp1amean*, diffreq*, df1max*
	3	-		3.2	pfmean*
Grumble	**1**	77.9	tonality*	78.9	parameters not used in the analysis[1]
	2	22.1	fp1amean*	18.3	fp1amean*
	3	-		2.8	tonality*, diffreq*
Hum	**1**	84.3	noise*	94.1	tonality*
	2	15.7	pfmax*	5.7	pfmin*
	3	-		0.2	ranmean
Hoot	**1**	100	dfa1maloc*, diffreq*	95.1	dfa1mean*, fp1mean*, pfmean*, df1min*
	2	-		4.9	dfa1mean*
Scream	**1**	100	tonality*, dfa2mean*, diffreq*		

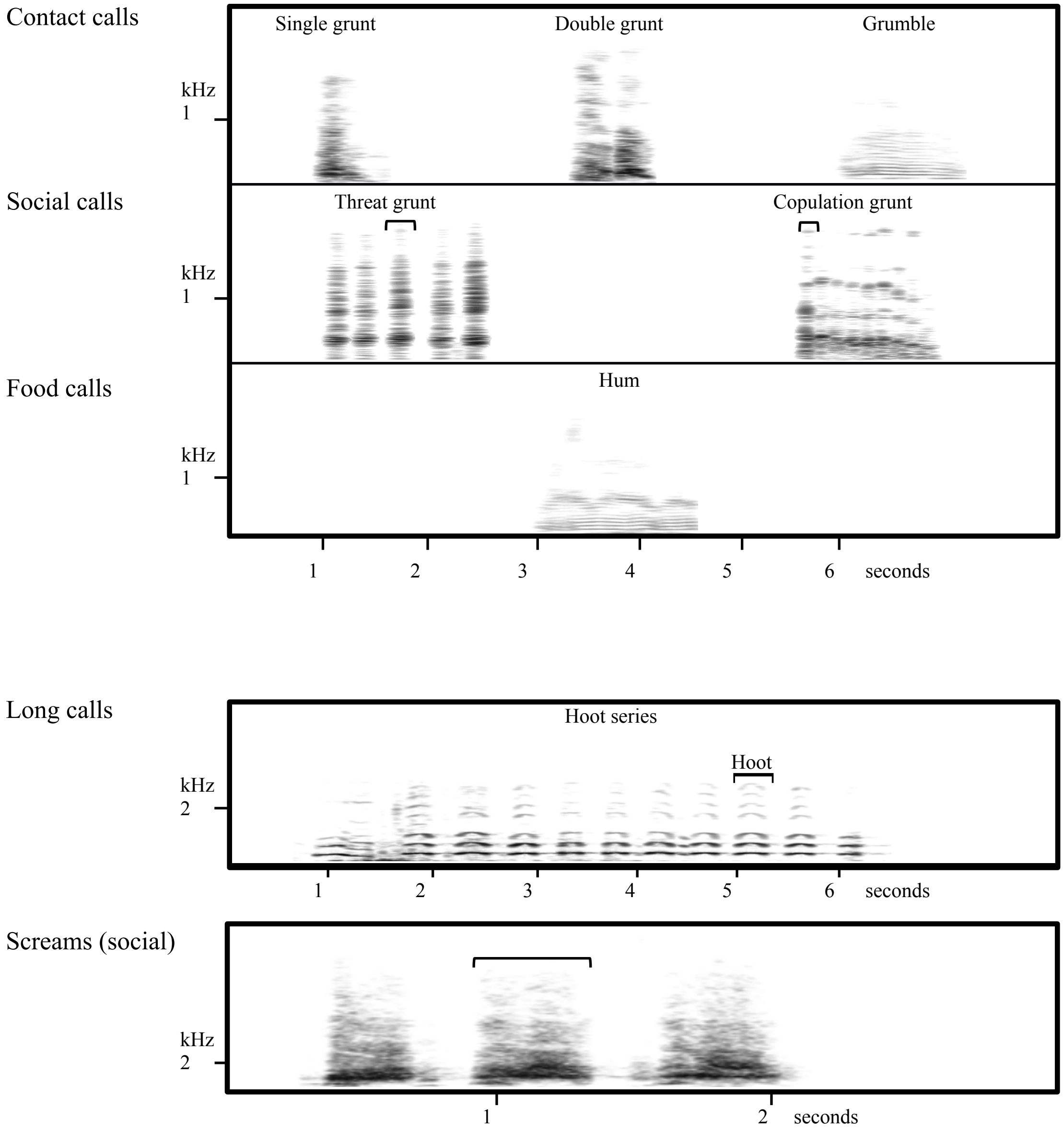


Fig. 4.1. Spectrograms of gorilla call types include hoot series (HT), hum (HM), grumble (GR), double grunt (DG), single grunt (SG), copulation grunt (COG), threat grunt (TG), scream (SC), with unit of analysis (call segment) indicated in brackets.

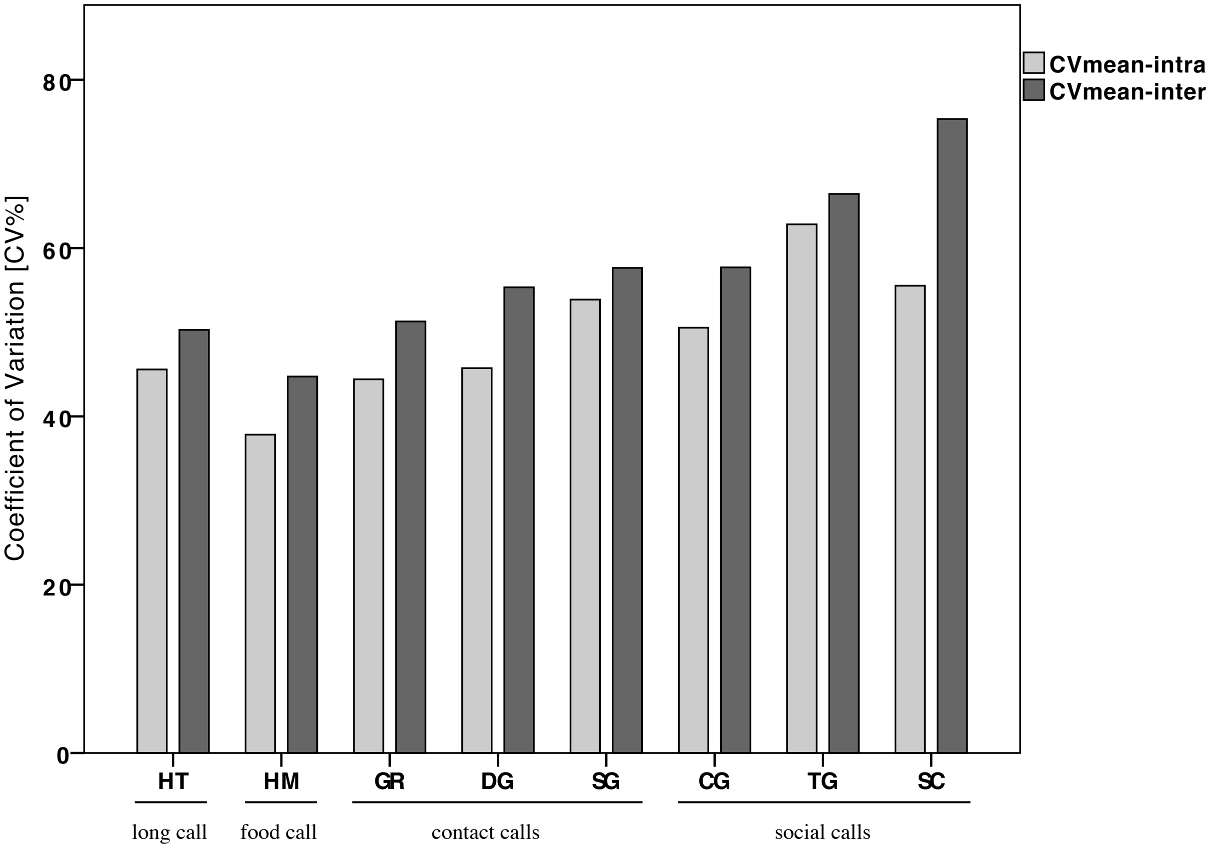


Fig. 4.2. Inter- and intra-individual mean coefficient of variation for eight female gorilla call types.

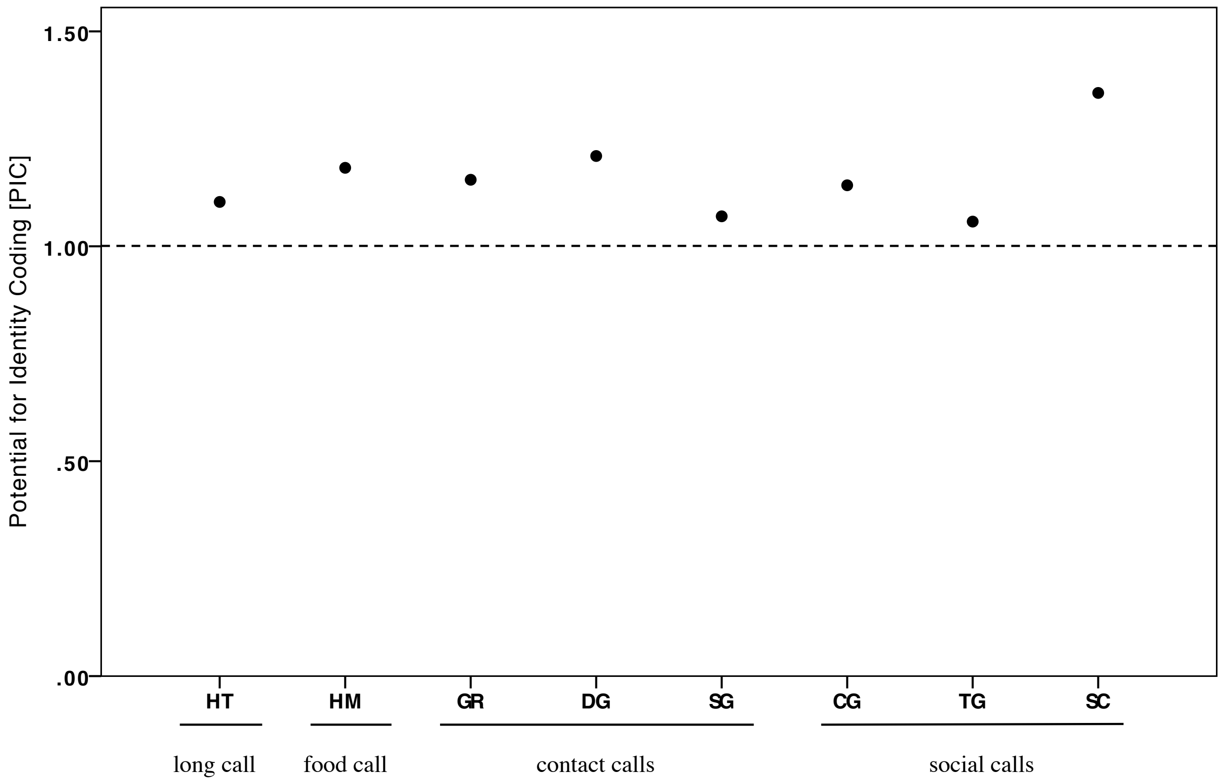
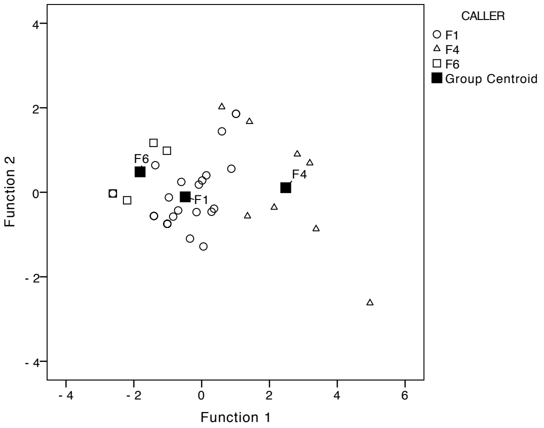


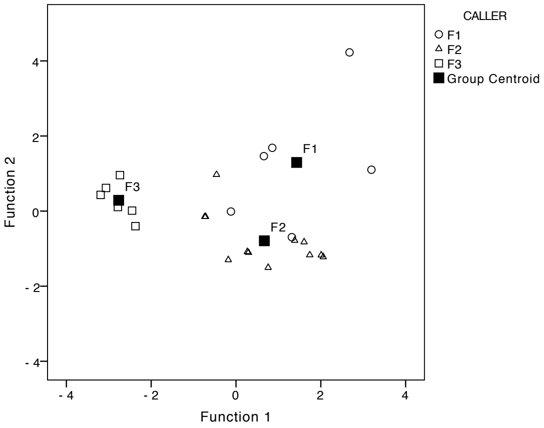
Fig. 4.3. Potential for Identity Coding [PIC = $CV_{mean\text{- }inter}/CV_{mean\text{-}intra}$] for each call type (HT = hoot series; HM = hum; GR = grumble; DG = double grunt; SG = single grunt; CG = copulation grunt; TG = threat grunt; SC = scream).

Contact calls:

Double grunt

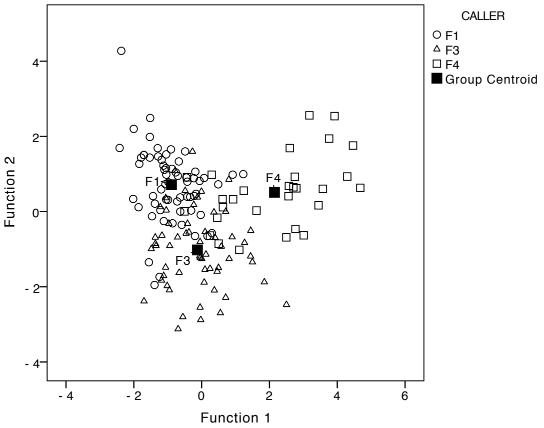


Grumble

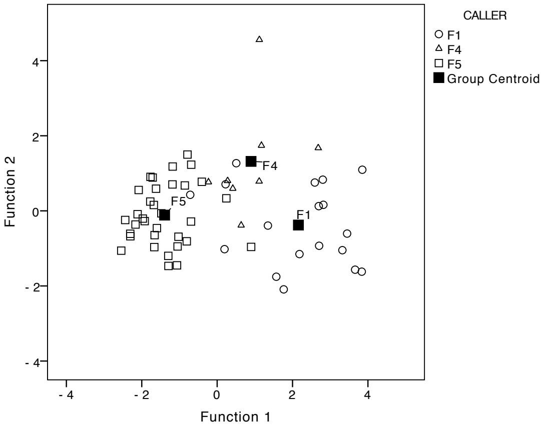


Social calls:

Threat grunt



Copulation call



Food calls:

Hum

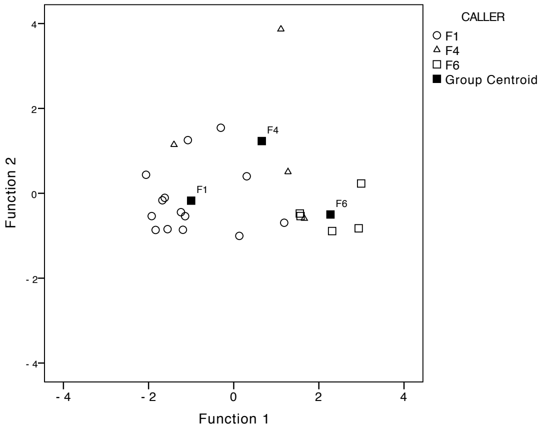
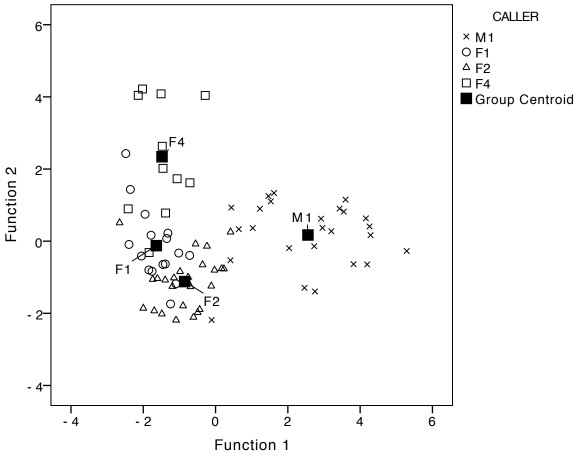


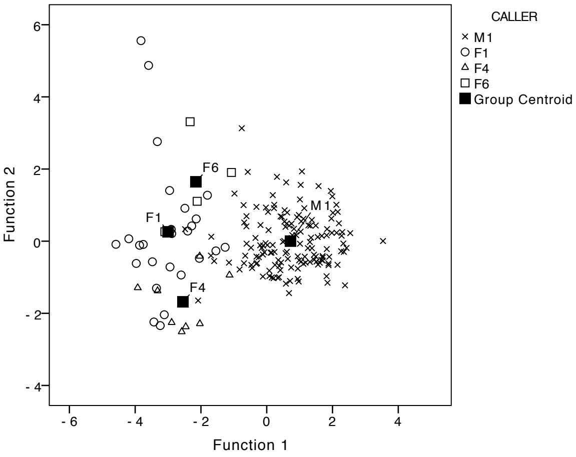
Fig. 4.4. Distribution of the discriminant scores for five gorilla calls among females (NOTE: no plot is generated when testing between two callers or when only one Function distinguishes among callers).

Contact calls:

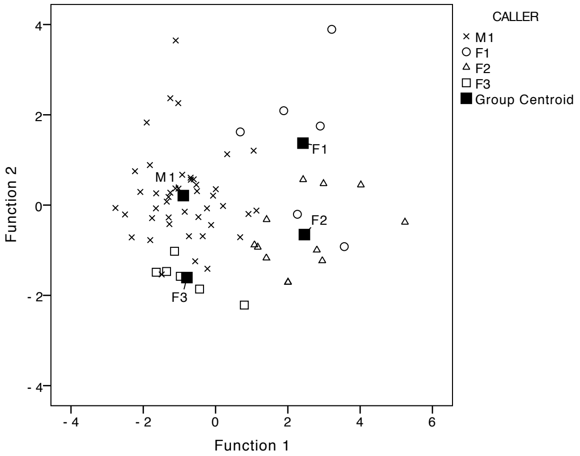
Single grunt

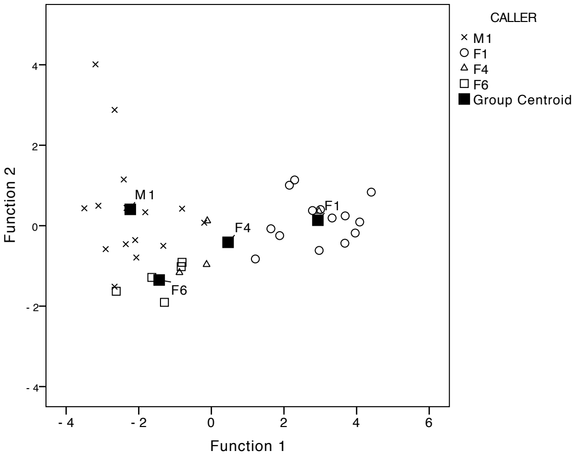


Double grunts



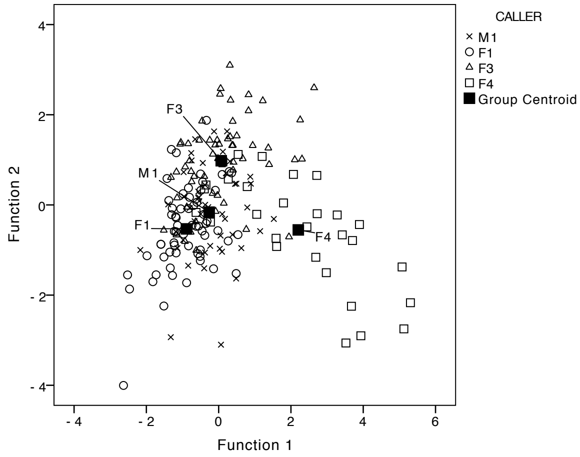
Food calls:



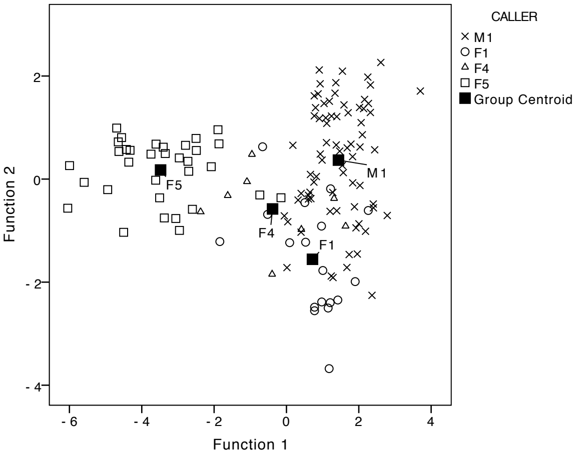


Social calls:

Threat grunt



Copulation grunt



Long-distance calls

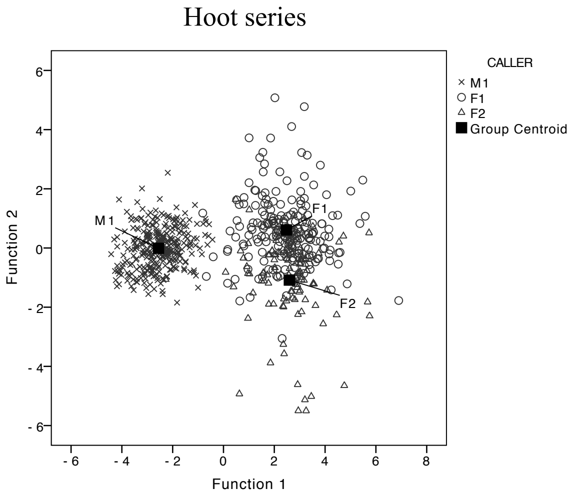

Hoot series

Fig. 4.5. Distribution of the discriminant scores for seven gorilla calls among females and the male.

CHAPTER FIVE

The Vocal Behavior of Western Gorillas: Summary, Synthesis, and Future Directions

In this dissertation, I investigated the vocal behavior of the least known ape species, the western gorilla (*G. gorilla*). More specifically, the goals of this study were to: 1) identify how social and ecological variation affect gorillas' vocal repertoire and call usage, 2) assess the function and mechanisms of long calls in within-group communication, and 3) examine the adaptive function of individual vocal cues across the entire species' vocal repertoire. Despite considerable interest in the vocal communication of non-human primates and its possible relevance to theories of language evolution (Pinker and Bloom 1990; Seyfarth 2005; Zuberbühler 2006), work has primarily focused on monkeys; thus, we know surprisingly little about vocal communication in our closest living relatives, the great apes (Slocombe et al. 2011). Furthermore, most of the studies on great apes have focused on the contexts and functions of chimpanzee vocalizations (e.g., Crockford and Boesch 2003; Laporte and Zuberbühler 2010; Slocombe et al. 2010b), and to a lesser extent on those of bonobos (e.g., Clay and Zuberbühler 2011; Clay and Zuberbühler 2012) and specific vocalizations of orangutans (Delgado 2003; Delgado 2007; Spillmann et al. 2010). The vocal behavior of gorillas has been studied in only one subspecies of one of the two gorilla species, the mountain gorilla (*G. beringei beringei*) (e.g., Schaller 1963; Fossey 1972; Harcourt et al. 1993). Since western and eastern gorillas are now known to differ in some aspects of their ecology and sociality (Doran and McNeilage 1998), this study was aiming to expand our understanding of how socio-ecological factors have shaped their vocal communication systems.

Summary of the Dissertation

In Chapter Two, I provided the first data on the vocal repertoire of western gorillas, with a focus on the context of emission and calling rates. The results are compared with studies on mountain gorilla vocalizations and used to determine whether differences in call usage between the two species can be explained by their socio-ecological differences. I described one call type not found in the mountain gorilla repertoire, the sex whinny, as well as several differences in the usage of some call types. Most importantly, it emerged that western gorillas produce more context-specific calls than mountain gorillas (Fossey 1972; Harcourt et al. 1993), which may be related to the differences in habitat structure and group cohesion of these two species. Furthermore, western and mountain gorillas differ in the usage of one particular long-distance call, the hoot series.

In Chapter Three, I investigated the function of the hoot series in greater detail in order to gauge whether western gorillas use this call in within-group communication, particularly as a mechanism to regain proximity among dispersed individuals. My results confirmed previous suggestions that group spread is greater in western versus mountain gorillas (male-female maximum distance: mountain gorillas = 50 m, western gorillas > 100 m), with individuals separated at times by over 600 meters. Under these circumstances, it is not surprising that western gorillas use vocal signals that travel long distances not only when communicating with other groups but also when communicating among group members. This study showed that hoot series were individually distinct, potentially allowing call recipients to distinguish among the calls of different group members. As predicted, they were given when individuals were alone or separated from other group members. More specifically, I showed how both males and females call when separated from each other, reply to the calls of others, and how calling is followed by reunion. Individuals appear to respond to others' hoot series conditionally; they vocally respond (hoot series in reply) when not actually moving towards the caller and they do not call back when they instead moved toward the caller. This hints at the possibility that western gorillas use vocal signals (i.e., hoot series) to negotiate who approaches whom, and the final direction of travel.

In Chapter Four, I examined the adaptive functions of vocal cues across the vocal repertoire of western gorillas. Individually distinct vocalizations play an important role in animal communication, allowing call recipients to respond differentially based on caller identity. However has been a subject of controversy whether natural selection should act more on some calls than others, resulting in some call types being more individually acoustically distinct than others. This study showed that call types were equally individually distinct suggesting that neither the distance at which communication occurs nor the social context in which individuals call played alone an important role in the evolution of identity signaling in western gorilla vocal communication. Instead, it appears there may be some benefit to western gorillas being able to distinguish individuals in within-group communication regardless of the call type.

The Vocal Repertoire of Western Gorillas: A Synthesis

This study provided the first quantitative description of western gorillas' vocal repertoire and their vocal behavior. They produce at least seventeen call types, most of which are used during specific contexts. As expected, given that gene flow between western and mountain gorillas was interrupted only recently (Thalmann et al. 2007; Scally et al. 2012), the vocal behavior of the two species is very similar (Chapter 2). However, although primate vocal production is highly constrained by body size, vocal tract morphology, and phylogeny (Hauser 1993; Fitch and Hauser 1995; Fletcher 2004), differing ecological and social constraints, such as changes in habitat, diet, group composition and cohesion, and daily travel distances may also affect vocal communication (Snowdon and Hodun 1981; Waser and Brown 1986; Oda 1996; Sugiura 2007; Ey et al. 2009). Accordingly, the results of this dissertation have shown several noteworthy differences between the vocal behavior of western and mountain gorillas including: 1) the production, context, and function of one long-distance call, the hoot series, and 2) the presence of more calls associated with specific behavioral contexts in western gorillas.

Group cohesion in western gorillas is reduced compared to that of mountain gorillas. This is probably due to more widely spaced resources, resulting from a more frugivorous diet. This in turn has triggered the use of a long call for within-group communication (Chapter 2 and 3). Thus, a call type similar to that of mountain gorillas is used by a broader array of individuals in a different context (Chapter 3). Individuals call when separated from specific group members, the male from females and females from the male, and although call receivers reply half of the time, calling alone lead to reduction in distances (Chapter 3). In mountain gorillas, the equivalent call is used instead exclusively by males and during inter-group encounters (Schaller 1963; Fossey 1972). Mountain gorillas might in fact not need long calls when communicating among group members, since group spread is reduced and very rarely are individuals found more distant than fifty meters (Vedder 1984; Watts 1991). This alternate use of the long call illustrates unexpected plasticity in the production and usage of gorilla acoustic signals.

A large proportion of western gorilla calls were context- and/or signal-specific. Compared to mountain gorillas, they use three additional specific call types: the sex whinny, humming, and singing (Chapter 2). The sex whinny, given by the male before copulation, has not been described in mountain gorillas. In contrast, humming and singing have been previously observed in mountain gorillas, although they occurred in many different contexts compared to the single context seen in western gorillas (i.e., foraging). Again, this might be a consequence of their more frugivorous diet, with these calls serving to decrease feeding competition if group members use them to avoid overlapping foraging areas (Robinson 1982; Palombit 1992).

Having distinct call types and using them during specific contexts might be very valuable, particularly for species living in forested habitats (Morton 1975; Boinski and Campbell 1996; Brown and Handford 2000; Uster and Zuberbühler 2001). The strong association between vocal signals and contexts might allow receivers to gather information about their surrounding and specifically the activity or context of the caller, allowing the coordination of group movements and activity patterns between individuals out of visual contact (e.g. Boinski 1991; Boinski 1993). Specific calls although numerous were used much less often than more general calls and therefore their limited use raises compelling new questions. For example, are context-specific calls also produced infrequently in other primate species, or do the ecological and social characteristics of the species influence the proportion of specific calls across the species repertoire? Second, how does their importance to each age-sex class vary across species?

Calls used more commonly, such as grunts and grumble, contributed more than 80% to the adult calling rate. These calls were given during many different contexts and presented more intermediate variants than other call types (R. Salmi, pers. obs.). Closer examination, therefore, is needed to determine whether call subtypes exist, with different variants consistently given during different contexts, as described in other non-human primate species (e.g., Struhsaker 1967; Green 1975; Snowdon et al. 1983; Seyfarth and Cheney 1984; Seyfarth et al. 1994; Owren et al. 1997). This is suggested by the high intra-individual acoustic variation observed within the entire western gorilla vocal repertoire. Further studies should therefore explore whether there are context-specific acoustic subtypes of common calls such as grunts and grumbles. Additionally, it would be interesting to see if more context-specific calls such as screams, threat grunts, copulation grunts, and food calls have acoustic subtypes. Further studies that focus on the functions of these calls and call subtypes might reveal referential communication in gorillas, as well as a better understanding of their social knowledge, a topic that remains surprisingly understudied.

The analysis of individual distinctiveness across the entire western gorilla repertoire allowed for exploration into the adaptive function of individual vocal cues. The results did not support any of the hypotheses tested. Rather all call types were equally individually distinct (Chapter 4), suggesting that individually distinct calls are advantageous in many different circumstances. Therefore, selection is likely acting on distinctiveness in gorilla vocalizations not only in terms of the distance at which communication occurs but also in terms of the many functions these calls serve during within-group communication. It remains unclear, however, whether this is a major difference between monkeys and apes or a specific characteristic of western gorilla vocal signals. Furthermore, to determine whether some calls are more recognizable than others and what factors might affect the ability of listeners to distinguish among calls of different callers, future studies will need to include playback experiments.

Suggestions for Future Research

While this study provides an interesting addition to our understanding of a topic that remains poorly studied (gorilla vocal communication), further analyses are needed to determine the function additional calls play in the organization of group life and whether acoustic variants of the same call type exist and carry additional information. Furthermore, the use of playback experiments will be necessary to determine the function of specific calls or acoustic variants of calls and test whether western gorillas are able to recognize caller identity based on acoustic structure of calls. These experiments also would help test whether recognition and individual distinctiveness is asymmetrical, as found in other primate species (Kojima et al. 2003; Rendall et al. 2009). Finally, since this study is based mostly on one group of wild western gorillas, further research should be conducted on additional groups, potentially living in different areas, both to corroborate these results, as well as assess whether geographical or cultural differences exist in western gorilla vocal behavior, as shown in other ape species (e.g., Mitani et al. 1999; Wich et al. 2012).

The Functions of Other Call Types

Contact Calls

Western gorillas produce different types of close calls that are given during an extensive range of circumstances and may encode numerous kinds of information (e.g., identity, location, activity, rank, and familiarity), suggesting that they may serve several ecological and social functions (see Boinski and Campbell 1996). In contrast to other call types given in very specific contexts, single grunts, double grunts, and grumbles were given at a high rate during different behavioral contexts and elicit vocal responses by conspecifics (R. Salmi unpublished data) while the caller exhibits a relaxed behavior. These are all characteristics used to define primate "contact calls" (Pola and Snowdon 1975; Snowdon and Cleveland 1984).

One proposed function of contact calls is to reduce the likelihood of an individual becoming separated from a group (Caine and Stevens 1990; Boinski 1991; Uster and Zuberbühler 2001), with alteration in the rate serving to maintain cohesion. For example, contact call rates were observed to increase in response to increased distance to the closest neighbor and/or group spread (Palombit 1992; Oda 1996; Uster and Zuberbühler 2001), when environmental visibility decreases (Byrne 1981; Koda et al. 2008), and during potentially separating activities (i.e. traveling) (Boinski and Mitchell 1992; Koda et al. 2008). In gorillas close/contact calls may contribute to synchronization of time and type of activities among group members, and especially to coordinate group movement, conveying information about the identity and location of the caller plus the direction and intention of traveling (Byrne 1981; Robinson 1982; Boinski 1991; Boinski 1993; Stewart and Harcourt 1994).

Finally, more research is needed to determine whether contact calls in gorillas facilitate interaction between the caller and the recipient and promote reconciliation after aggression as shown in other species (*Macaca spp*: Bauers and de Waal 1991; Bauers 1993; Silk et al. 2000; *Papio spp*: Cheney et al. 1995; Silk et al. 1996; Cheney and Seyfarth 1997; Palombit et al. 1999; Wittig et al. 2007).

Food Associated Calls

Although this study showed that western gorillas use a specific call (the hum) exclusively during feeding, its specific function remains unclear. Food calls may be used to notify other group members of food to be shared, conveying information about the location, quality of foraging patches, and individual preference (e.g., Dittus 1984; Di Bitetti 2003; Slocombe and Zuberbühler 2006; Clay and Zuberbühler 2009). In these cases, food calls would function to reduce inter-individual distances attracting individuals to a specific location (Dittus 1984). Recently, food calls have been found to be referential (i.e., supplying information regarding an external event or object) in chimpanzees and bonobos, a possibility that still needs to be tested in western gorillas.

Alternatively, food-associated calls may maintain spacing between potential foraging competitors, reducing overlap of individual foraging areas (Robinson 1981; Janson 1990). In this context, calls may be used either *aggressively* to deter competitors from approaching and attempting to share an individual's foraging patch (Marzluff and Heinrich 1991; Boinski and Campbell 1996; Gros-Louis 2004) or non-*aggressively* to announce a forager's current position, thus reducing the chance of another individual approaching (Robinson 1982; Palombit 1992). If food associated calls in western gorillas are not referential and do not attract others to a specific location they might function in spacing individuals during foraging to reduce feeding competition, an hypothesis worth to be tested.

Acoustic Subtypes of Calls

Further investigation is needed to determine whether western gorillas produce acoustic variants that are salient to listeners. In fact, although primates have limited repertoires, many species produce variants of the same call type in a broad range of contexts, and acoustic features have been shown to vary according to the context, suggesting that they can differentiate a large number of vocal signals (e.g., Snowdon and Pola 1978; Cheney and Seyfarth 1982; Fischer 1998).

Context-specific variants are abundant in alarm and food calls, in which they encode for specific predators (reviewed in: Zuberbühler 2007) or for specific characteristics of food resources (reviewed in: Clay et al. 2012), but they are not limited to these two contexts. For example, the coo calls of Japanese macaques include nine acoustic subtypes, each of which is emitted during a particular context (Green 1975). In cotton-top tamarins and squirrel monkeys, some variants of a call type are used only during feeding while other variants are used during other activities (Elowson et al. 1991; Boinski and Mitchell 1997), allowing activity coordination among individuals. In mountain gorillas, the acoustic structures of spontaneous and replying double grunts were found to differ significantly (similar to western gorillas, R. Salmi unpublished data), although no playbacks were conducted to determine whether listeners were able to perceive the differences (Seyfarth et al. 1994). Furthermore, gorillas exchange different types of calls (R. Salmi unpublished data) and it would be worthwhile to investigate whether other calls, such as long-distance calls (Chapter 3) or even screams and threat grunts differ in structure when given or when replied. In other primates, the acoustic features of agonistic screams vary depending on the social role the individual plays during the conflict (Slocombe and Zuberbühler 2005a) or the severity of the conflict (Gouzoules et al. 1995); characteristics that still need to be tested for in western gorillas. Recently, Crockford & Boesch (2003) reported that chimpanzees use context-specific signals, combining barks and drums. These signal combinations increased specificity levels up to 90% in three of the six contexts analyzed (a value similar to those of alarm calls in vervet monkeys). The presence and functions of combinations of calls in gorillas were not addressed in this study and need further investigation.

The Implementation of Playback Experiments

To determine the functions of different calls, several studies have used playback experiments to record the behavioral or vocal responses to a specific stimulus, controlling for other variables impossible to rule out during behavioral observations. For example, to determine whether food calls attract others or maintain separation among individuals would require the use of playback experiments, in which calls are played to specific individuals and during differing circumstances, allowing better understanding of their specific functions. Furthermore, if acoustic variants of the same calls exist in the vocal repertoire of western gorillas, playback experiments would help to determine whether those subtle differences are salient to listeners. Since referential communication has been recently recognized in apes (e.g., Slocombe and Zuberbühler 2005b; Clay and Zuberbühler 2011), playbacks are indispensable in determining whether gorillas have the ability to extract specific information about external events from acoustic variants of their calls.

Since my results showed that individual differences in calls' structure was present in all call types (Chapter 4), the next step in assessing the adaptive function of vocal cues is to determine whether individuals are able to distinguish caller identity and if recognition differs across call types. This is particularly important because asymmetries between individual differences in call acoustic structures and the ability to recognize caller identity have already been recognized in some primate species (Kojima et al. 2003; Rendall et al. 2009).

Employing experimental design has been very valuable not only in determining context- or caller-related acoustic differences, but also in answering more complex questions regarding the importance of social relationships (Palombit et al. 1997; Fischer 2004; Wittig et al. 2007; Lemasson et al. 2008; Slocombe et al. 2010a) and social knowledge in primate species (Cheney et al. 1995; Bergman et al. 2003; Crockford et al. 2007). Recent field experiments demonstrate that baboon social knowledge shares some properties with human language (Seyfarth et al. 2005), supporting the hypothesis of the social origin of language, which argues that internal representations of language meaning evolved partly from our ancestors' knowledge of social relationships (Worden 1998; Cheney and Seyfarth 2007). Future studies on gorilla communication should address similar questions to better comprehend their cognitive abilities and social knowledge, both understudied topics despite being critical in our understanding of the evolution of human language and intelligence.

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Appendix 1. Definition, code and description of behavioral contexts of wild western gorillas.

Context	*Code*	*Description*
Within-group aggression	AG	Aggressive behavior toward a specific individual, escalating from staring/vocal aggression to physical charge with open mouth, intent of grabbing/stopping/biting the opponent
Alarm/alertness	AL	Attentive looking/sensing/listening behavior accompanied by a stiff body position, pilo-erection, and rapid changes of the direction of gaze or face
Within-group display	DPW	Not directed toward a single individual, includes charges, tree kicking, destruction of trees or tree branches, etc.
Extra-group display	DPE	In response to the presence or vocalizations of other males, accompanied by stiff body position, pilo-erection, vocalizations (hoot series followed by chest-beats), occasionally by charges
Nipple contact	NPA	Infant approaches the mother to nurse
Nipple conflict	NPR	When nursing was denied: the mother actively prevented the infant to access the nipples, by covering her body, or leaving/biting the infant
Foraging	FO	Feeding and movements of < 5 meters during feeding
Play	PL	Playful chasing and wrestling
Resting	RE	Sitting and laying down (includes sleeping)
Pre-mating courtship	CO	Quadrupedal standing, looking and approaching a specific female, preceded copulation
Copulation	SE	Sexual intercourse: post-ventral or ventral-ventral sex
Travel-pause	TRP	Quadrupedal standing prior to or during travel, resting, and climbing
Traveling	TR	Movements greater than 5 m; includes climbing up and down trees
Other	OT	When the focal animal is out of sight as well as grooming or self-grooming (<0.1% of budget activity)

Appendix 2. Acoustic parameters of western gorillas included in the analysis.

#	*Parameters*	*Description*
1	duration	Duration from beginning to the end of the call [ms]
2	dfa1mean	Mean value of the frequency at which the first quartile of global energy is reached across all time segments [Hz]
3	dfa1maloc	Location of the maximum frequency at which the first quartile of global energy is reached across all time segments
4	dfa2mean	Mean value of the frequency at which the second quartile of global energy is reached across all time segments [Hz]
5	dfa2maloc	Location of the maximum frequency at which the second quartile of global energy is reached across all time segments
6	df1max	Maximum value of the first frequency in the call which contains more energy than a particular thresholds in all time segments (DF) [Hz]
7	df1min	Minimum value of the first frequency in the call which contains more energy than a particular thresholds in all time segments (DF) [Hz]
8	df1mean	Mean value of the first frequency in the call which contains more energy than a particular thresholds in all time segments (DF) [Hz]
9	df1maloc	Location of the maximum value of the first frequency in the call which contains more energy than a particular thresholds in all time segments
10	df1miloc	Location of the minimum value of the first frequency in the call which contains more energy than a particular thresholds in all time segments (DF)
11	df1trfak	Factor of linear trend of 1st dominant frequency band (DF)
12	df2max	Maximum value of the second frequency in the call which contains more energy than a particular thresholds in all time segments (DF) [Hz]
13	df2mean	Mean value of the second frequency in the call which contains more energy than a particular thresholds in all time segments (DF) [Hz]
14	df3mean	Mean value of the third frequency in the call which contains more energy than a particular thresholds in all time segments (DF) [Hz]
15	diffmean	Minimum difference between first and second dominant frequency bands (DF) [Hz]
16	diffreq	Mean number of dominant frequency bands (DF)
17	ampratio1	Amplitude ratio between first and second dominant frequency bands
18	fp1max	Max frequency first peak (global frequency peak) [Hz]
19	fp1mean	Mean frequency first peak [Hz]
20	fp1amean	Mean amplitude first peak [rel. amplitude]
21	ranmean	Mean frequency range [Hz]
22	pfmax	Maximum value in all time segments of the frequency with the highest energy [Hz]
23	pfmin	Minimum value in all time segments of the frequency with the highest energy [Hz]
24	pfmean	Mean value across all time segments of the frequency with the highest energy [Hz]
25	pfmaloc	Location of the maximum value in all time segments of the frequency with the highest energy
26	pftrfak	Factor of linear trend of pick frequency
27	noise	Percentage of noisy time segments [%]
28	tonality	Percentage of tonal time segments [%]

Appendix 3. Description of western gorilla broad acoustic categories and call types.

1. The acoustic category “Grunts” consisted of calls with noisy harmonics/spectral-structured noise (Beeman 1998; brief, atonal, staccato sounds defined as “syllabled calls” by Harcourt et al. 1993) and included four call types: single grunts, double grunts, cough grunts, and copulation grunts (Fig. 2.1.A).

a. Single grunt: soft, guttural, single -syllable call, uttered with open or closed mouth at low frequency (Table 2.7). *Single grunt, belch vocalization* in Mountain gorillas (MG; Fossey 1972; Harcourt et al. 1993)

b. Double grunt: soft guttural call composed by two syllables of varying length, normally the second longer than the first. Triple and inverted grunts, as in Mountain gorillas, were also recorded, but they were extremely rare, thus are here not included. *Double grunt, belch vocalization* in MG (Fossey 1972; Harcourt et al. 1993).

c. Cough grunt: loud, close call emitted with open mouth by all age sex classes of short duration (Table 2.7). Generally it was given in irregular bouts of 1- 30 calls or even more. *Cough or pig grunt* in MG (Fossey 1972; Harcourt et al. 1993).

d. Copulation grunt: soft, close call emitted with open or closed mouth by all adult individuals in long sequences (>80 calls) with some frequency modulation (Fig. 2.1). Males give long grunts at the end of each call bouts (3-20ca.). *Copulatory grunt* in MG (Fossey 1972; Harcourt et al. 1993).

2. “Grumbles” were characterized by a mixture of low dense harmonics and spectral-structures noise” (long, tonal, non-staccato sounds defined as “non-syllabled calls” by Harcourt et al. 1993) and included two call types: grumbles and hums (Fig. 2.1.B).

a. Grumble: a soft close call of irregular length defined by dense harmonics with some degree of noise, displaying higher percentage of tonal segments than grunts (Table 2.7). Mostly given with closed mouth as single call, but it could solicit choruses in which many individuals grumble at the same time. *Rumbles, grumbles* in MG (Fossey 1972; Harcourt et al. 1993).

b. Hum: a call with dense harmonics and varying degree of noise. *Hums* in MG (Fossey 1972; Harcourt et al. 1993).

3. “Singing” presented a clear tonal structure and was considered a distinct acoustic group from “grumbles” (Fig. 2.1.B), although described as a variation of grumble in mountain gorillas (Fossey 1972; Fig. 2.1.B).

a. Sing: was heard only by a juvenile female and given alternating to hums. Over 70% of segments were tonal (Table 2.7), and sounded similar to the “he, he he” of humans. *High hum or singing* in MG (Fossey 1972; Harcourt et al. 1993).

4. “Whinnies” were characterized by long, noisy, pulse repetition sounds with clear frequency dominant bands (Fig. 2.1.C). We distinguished two whinnies in the field based on the context in which they were given (sex versus other activities).

a. Whinny: pulse repetition, low sound with several dominant frequency bands (Fig. 2.3). Normally given as single call, rarely as a sequence of two calls and rarely combined with grunts. *Whinny or train grunt* in MG, poorly described (Fossey 1972; Harcourt et al. 1993; Sicotte 1994).

b. Sex-whinny: a pulse repetition sound with few dominant frequency bands (Fig. 2.1. C). Normally given as a sequence of bouts of two to four calls. *Train grunts (whimpers?)* in MG, not differentiated from the other whinny (Fossey 1972; but see Watts 1994).

5. “Hoots” were sparse harmonics, given as sequences of 15 ± 7 ($n = 89$) of tonal segments at regular intervals. We distinguished two hoots based on whether they were given alone or were immediately followed by chest beats (Fig. 2.1.D.1 and 2).

a. Hoot series: vocalization composed by a sequence of calls/segments with 2-3 sparse harmonics given at regular intervals, with the highest percentage of tonality among all calls. In contrast to MG, all individuals emitted this call. *Hoot series* in MG were described only for males during intergroup encounters (Fossey 1972; Harcourt et al. 1993).

b. Hoot series ± chest beats: a rare vocalization uttered only by adult males combining the hoot and a sequence of 10-16 chest beats. *Hoot chest beat* in MG (Fossey 1972; Harcourt et al. 1993).

6. "Whimpers" were call presenting soft, sparse, irregular harmonics (Fig. 2.1.E).

a. Whimper: very harmonic call, characterized by sparse, long, irregular harmonics, with lower frequencies than screams and given only by infants. Calling rates were between 2.2 and 1.4 calls/hr. *Whimpers* in MG (Fossey 1972; Harcourt et al. 1993).

7. "Screams" were sparse harmonic sounds with variable noise; we distinguished adult screams and infant cries (Fig. 2.1.G).

a. Scream: call with high and sparse harmonics with varying degree of noise, given as a sequence of screams of different length, potentially depending on the gravity of the conflict/danger. *Screams* in MG (Fossey 1972; Harcourt et al. 1993).

b. Cry: very sparse harmonic call, with noisy elements, given only by infants. *Cries or tantrums* in MG (Fossey 1972; Harcourt et al. 1993).

8. "Barks" were loud and harsh spectral-structured noise and included two call types: bark and roar (spectrograms not available).

a. Bark: loud, harsh and abrupt sound, given as single call but also in repetition only by adult males. Barks were common for the non-habituated male (2.2 calls/hr) and rare for the habituated male (0.02 calls/hr), indicating a clear evidence of the influence of the habituation process in the vocal behavior of gorillas (see also Fossey 1972; Harcourt et al. 1993). *Barks* in MG (Fossey 1972; Harcourt et al. 1993).

b. Roar: an extremely loud bark-like sound, only heard from unhabituated gorillas, elicited always by human presence (never heard by focal animals).

9. "Laughs" were irregular noisy chuckle sounds (spectrogram not available).

a. Chuckle: irregular chuckle/grunt-like sound given in sequence and simultaneously to other players. *Play chuckle and/or laughs* in MG (Fossey 1972; Harcourt et al. 1993).

Appendix 4. Summary of data collected. Data are shown for adult male (M), and each adult female (F1-4) western gorilla. Data include the number of focal follows (N_F), the number of simultaneous focal follows of male and female with GPS locations (N_{GPS}), total focal sampling time ($T_{S\ (hrs)}$), total continuous sampling time ($T_{C\ (hrs)}$), number of digitally recorded hoots or segments (N_{HOOT}) and hoot series (N_{HS}) used in acoustic analysis, and number of independent hooting events with simultaneous GPS points ($N_{E\text{-}H}$) used in the behavioural analysis.

Subject	N_F	N_{GPS}	$T_{S\ (hrs)}$	$T_{C\ (hrs)}$	N_H	N_{HS}	$N_{E\text{-}H}$
M1	340	-	764	462	96	30	
F1	84	65	176	87	96	17	5
F2	86	69	189	93	96	5	6
F3	75	72	154	72			3
F4	74	62	176	82			5
Total	**659**	**268**	**1 459**	**795**	**288**	**52**	**21**

Appendix 5. Interaction matrices for all aggression (A. n = 217) and for aggression with decided outcome (B. n = 116) with dominance proportion (in parenthesis), dominance ranks (RANKS) calculated using David's Score (DS) and values for their calculations (w1, w2, l1, l2).

A.

	M	*F1*	*F2*	*FN**	*F3*	*F4*	*W1*	*W2*	*DS*	*RANK*
M		28(0.88)	25(1.0)	7(1.0)	38(0.79)	13(1.0)	4.67	8.59	***12.01***	***1***
F1	4(0.13)		17(0.89)	5(1.0)	9(0.9)	25(0.93)	3.85	5.60	***7.15***	***2***
F2		2(0.11)		3(1.0)	3(1.0)	6(0.86)	2.96	2.86	***1.92***	***3***
FN					3(0.75)		0.75	0.95	***-6.00***	***4***
F3	10(0.21)	1(0.1)		1(0.25)		10(0.71)	1.27	1.90	***-7.33***	***5***
F4		2(0.07)	1(0.143)		4(0.29)		0.50	1.07	***-7.73***	***6***
l1	0.33	1.15	2.04	3.25	3.73	3.50				
l2	0.92	1.14	1.86	4.45	6.78	5.81				

B.

	M	*F1*	*F2*	*FN**	*F3*	*F4*	*W1*	*W2*	*DS*	*RANK*
M		19(1.0)	15(1.0)	7(1.0)	16(1.0)	9(1.0)	5.00	9.00	***14.00***	***1***
F1			5(0.84)	3(1.0)	4(1.0)	19(1.0)	3.84	4.65	***7.04***	***2***
F2		1(0.16)		2(1.0)	1(1.0)	5(1.0)	3.16	2.61	***2.96***	***3***
FN					2(0.67)		0.67	0.69	***-6.28***	***4***
F3				1(0.33)		5(0.7)	1.03	0.43	***-8.85***	***5***
F4					2(0.3)		0.30	0.31	***-8.87***	***6***
l1	0.00	1.16	1.84	3.33	3.97	3.70				
l2	0.00	0.29	0.97	4.31	6.34	5.78				

***FN was not included in the focal individuals since she was not fully habituated during the data collection of this study.**

Appendix 6. Hooting events sample sizes.

Hooting events	***M***	***F***	***Total***
Total – initiated by	67	12	79
With simultaneous GPS location of separated parties (GPS-SP) – initiated by	14	8	22
GPS-SP ended in reunion – initiated by	13	8	21
GPS-SP ended in reunion both individuals responsible– initiated by	2		2
GPS-SP ended in reunion one individual responsible– initiated by	11	8	19
GPS-SP ended in reunion one individual responsible – initiated by - no reply	6	3	9
GPS-SP ended in reunion one individual responsible – initiated by - reply	5	5	10
GPS-SP ended in reunion one individual responsible – replied by	4	6	10

Appendix 7. Acoustic characteristics (mean ± SD) of call types (SG = single grunt; DG = double grunt; TG = threat grunt; CG = copulation grunt; GR = grumble; HM = hum; HT = hoot series; SC = scream).

CALL	*ID*	*duration*	*dfa1mean*	*dfa1maloc*	*dfa2mean*	*dfa2maloc*	*df1mean*	*df1max*	*df1min*	*diffmean*	*dffreq*	*ampratio*
SC	F1	211.7±100	1038.6±318	0.5±0.4	1807.4±563	0.5±0.5	541.4±227	906.1±264	246.6±94	435.6±100	6.8±2.1	1.8±1.2
	F3	233.2±124	869.8±230	46.2±30.6	1380.4±258	56.4±17	631.2±188	888.8±294	319.4±91	389.6±117	462.8±94	88.0±27.1
TG	M	205.9±10	177.5±48	0.3±0.4	365.2±138	0.7±0.4	100.2±18	122.7±39	84.3±18	71.5±41	9.5±3.5	1.2±0.5
	F1	199.7±11	179.6±66	0.2±0.4	324.9±101	0.7±0.4	97.3±20	118.5±33	79.7±16	76.2±40	8.5±3.1	1.2±0.5
	F3	210.6±11	208.9±80	0.6±0.4	382.8±187	0.8±0.3	97.8±30	136.8±63	76.9±17	74.3±38	9.5±4.7	0.9±0.3
	F4	211.0±7	337.5±158	0.6±0.4	645.9±207	0.8±0.3	104.9±20	140.5±91	86.2±16	79.3±52	14.3±3.8	1.3±0.3
CG	M	416.1±241	156.6±20	0.3±0.3	236.5±42	0.3±0.3	113.8±22	140.0±34	88.8±16	56.3±22	6.1±2	1.1±0.3
	F1	241.3±74	175.7±25	0.3±0.3	290.8±33	0.4±0.4	92.4±19	111.2±30	79.2±15	59.3±21	7.8±1.8	0.9±0.2
	F4	220.5±14	204.8±34	0.4±0.4	303.6±52	0.4±0.5	106.0±16	139.4±34	80.6±12	60.9±12	7.3±1.7	0.8±0.3
	F5	213.1±43	238.8±32	0.3±0.3	285.3±30	0.4±0.4	160.6±60	230.2±59	97.6±44	163.6±205	3.5±1.2	1.3±1.5
SG	M	850.2±489	125.5±17	0.2±0.3	205.7±56	0.4±0.4	114.2±12	193.2±104	75.8±9	81.6±43	4.1±1.1.	1.5±0.5
	F1	391.3±126	141.6±	0.4±0.4	304.4±87	0.7±0.4	86.5±7	136.0±35	67.3±2	64.1±19	7.0±2	1.2±0.2
	F2	540.8±296	132.7±	0.4±0.4	311.6±97	0.5±0.5	88.0±6	151.4±74	69.0±4	102.1±52	5.8±1	1.5±0.3
	F4	377.1±80	169.6±	0.5±0.5	318.6±117	0.7±0.4	92.6±13	135.3±69	68.3±7	84.6±72	7.4±2	1.0±0.2
DG	M	780.3±228	146.8±25	0.4±0.2	224.7±54	0.3±0.3	109.9±9	169.0±35	70.2±6	57.3±19	5.4±1.7	1.1±0.3
	F1	599.2±241	149.4±48	0.3±0.3	296.1±117	0.5±0.5	90.7±11	174.3±123	67.8±4	63.7±23	7.1±2	1.2±0.3
	F4	472.140	157.3±19	0.7±0.3	269.8±64	0.7±0.4	95.8±12	125.1±14	69.5±4	55.5±30	7.1±1	1.0±0.3
	F6	794.0±271	147.0±16	0.2±0.3	292.5±28	0.3±0.5	103.0±21	285.5±124	63.0±0	100.5±67	5.4±2	1.1±0.3
GR	M	1571.4±498	107.5±17	0.5±0.4	209.4±46.	0.5±0.4	99.9±11	274.1±287	67.7±3	96.0±45	3.4±1.2	2.1±0.8
	F1	1593.3±556	137.0±24	0.4±0.5	261.8±57	0.5±0.4	83.3±3	161.8±71	69.8±4	56.2±9	5.8±1.1	1.5±0.3
	F2	2026.0±1260	120.8±15	0.4±0.5	289.7±45	0.7±0.4	87.8±9	156.3±94	66.2±5	62.4±30	5.1±1.5	1.4±0.3
	F3	1838.0±1269	123.5±22	0.6±0.4	247.0±96	1.0±0.1	95.7±8	195±55	195.7±55	84.5±30	3.8±1.2	1.5±0.6
HM	M	1916.0±597	129.6±16	0.7±0.3	246.4±30	0.7±0.3	101.0±19	171.8±76	67.5±7	58.9±20	5.5±1.1	1.4±0.5
	F1	1958.3±1020	150.9±41	0.5±0.4	324.2±68	0.6±0.3	82.7±7	144.1±59	66.3±2	56.4±20	6.8±1.2	1.4±0.4
	F4	1626.0±498	129.3±15	0.3±0.2	289.3±45	0.2±0.0	96.8±30	222.3±102	65.0±2	72.7±46	5.7±1.1	1.3±0.2
	F6	2306.4±699	112.4±10	0.8±0.4	245.6±91	0.8±0.4	94.0±8	205±106	64.6±2	56.0±19	5.1±1.0	1.3±0.2
HT	M	168.7±39	216.0±28	0.4±0.2	282.5±82	0.5±0.3	214.0±29	274.7±346	190.7±25	292.6±448	2.0±0.9	7.8±9.1
	F1	235.0±221	355.9±52	0.5±0.2	475.3±174	0.5±0.3	347.3±55	391.2±271	312.8±60	347.3±55	2.0±0.8	8.6±10.6
	F2	194.4±177	374.3±51	0.3±0.2	477.9±128	0.5±0.3	350.6±53	399.5±53	297.4±79	350.6±53	2.4±0.8	4.8±3.2

CALL	***ID***	***fp1mean***	***fp1max***	***fp1amean***	***ranmean***	***pfmean***	***pfmax***	***pfmin***	***noise***	***tonality***
SC	F1	1141.9±450	1799.9±154.4	549.7±306	3017.6±1242	1072.4±382	1827.7±188	268.1±234	85.3±35	13.1±34
	F3	912.0±334	1199.6±429	935.8±468	4297.8±3688	833.6±292	1268.8±398	448.8±343	83.8±16	6.0±7
TG	M	139.1±88	196.8±131	263.4±124	989.3±369	178.6±110	242.7±155	111.9±73	54.1±37	19.9±31
	F1	175.2±101	218.5±114	276.1±119	843.4±305	199.5±105	230.2±119	141.9±103	66.8±33	14.8±24
	F3	200.2±138	249.5±170	261.6±122	832.2±406	217.0±120	259.8±122	182.2±118	59.4±33	10.0±20
	F4	175.4±149	269.6±275	152.7±86	1309.2±320	444.5±321	547.7±86	380.1±340	80.9±35	8.1±21
CG	M	173.0±50	198.8±60	615.9±283	545.8±158	172.7±55	218.6±86	132.0±53	81.6±28	5.4±18
	F1	178.1±62	227.8±59	297.3±115	671.2±200	183.8±60	234.3±115	135.5±66	76.4±33	14.4±25
	F4	257.3±84	288.8±97	324.1±58	592.1±144	285.0±61	310.6±58	202.1±79	84.4±16	4.5±10
	F5	258.3±37	271.3±34	497.9±219	371.3±110	269.1±38	278.5±219	259.7±47	24.0±32	31.8±37
SG	M	114.5±32	162.3±39	605.5±267	380.4±122	118.8±25	190.1±70	73.2±19	91.2±10	2.7±4
	F1	92.6±20	157.2±58	210.0±58	607.7±201	109.6±35	187.0±58	71.6±36	94.8±13	1.9±7
	F2	71.6±14	136.0±88	253.5±119	510.1±187	89.7±12	161.3±119	65.4±9	89.6±19	5.9±15
	F4	147.01±37	233.7±55	283.5±75	631.1±273	159.3±51	285.3±75	68.7±16	98.6±4	0.2±0
DG	M	150.3±34	207.5±47	784.7±251	453±194	156.2±33	235.9±94	82.4±22	93.1±8.2	1.9±4
	F1	108.5±44	202.5±113	216.8±67	592.8±296	121.9±40	253.1±67	62.2±6	94.5±10	3.6±8
	F4	154.3±36	236.3±41	228.6±81	457.8±82	141.1±30	245.5±81	81.1±19	98.9±2	0.0±0
	F6	87.0±35	206±105	149.3±95	358.5±91	104.0±37	214.3±95	49.0±2.3	92.3±11	5.5±8
GR	M	78.2±25	135.8±66	203.7±84	269.6±87	93.8±22	175.8±94	58.9±8.9	65.3±28	22.1±24
	F1	115.8±66	426.7±447	329.2±153	367.0±48	114.0±40	337.8±153	66.5±5.7	51.8±12	40.8±11
	F2	65.3±10	170.1±104	150.1±64	306.3±134	86.2±13	273.9±64	58.9±10	41.0±19	52.3±21
	F3	89.7±29	212.7±117	74.8±34	292.3±32	113.8±37	235.5±34	59.5±12	81.7±10	5.7±6
HM	M	104.8±28	204.2±92	331.0±215	431.1±107	120.3±20	283.3±117	64.3±13	90.3±16	4.9±11
	F1	94.3±54	247.9±188	228.8±64	480.7±136	101.2±46	194.5±64	64.3±4.7	36.4±14	56.9±14
	F4	74.3±17	216.5±156	235.3±115	475.0±94	96.0±16	390.5±115	57.0±10	65.3±20	29.0±21
	F6	64.6±13	125.2±64	128.6±67	368.2±117	79.4±16	168.8±67	49.4±3.6	81.0±10	14.2±9
HT	M	170.3±62	217.4±95	733.4±346	427.2±130	215.8±33	246.5±77	192.3±25	16.7±20	63.8±28
	F1	366.6±86	398.3±94	619.3±257	587.7±376	368.8±83	404.3±257	327.2±85	17.7±23	57.4±33
	F2	368.5±57	408.5±70	368.5±305	624.9±214	370.4±56	424.6±305	335.9±58	17.0±20	59.7±28