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A Functional Analysis of Vocalisations of Black  
Howler Monkeys (*Alouatta caraya*)

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



September 2004

E756

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To Pedro Henrique, my nephew, who is already vocalising loudly and frequently.

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## ABSTRACT

Vocal behaviour represents a fundamental aspect of a mammal's behavioural repertoire. In this thesis I present a functional study of the vocal repertoire of black howler monkeys (*Alouatta caraya*). I collected observational data on behavioural states and circumstances surrounding the emission of low amplitude calls of a habituated group in the wild. Loud calls were studied both observationally and experimentally through the use of playbacks.

I present a call never described before, the *moo*, arguing that it possesses a contact role, and suggest possible specific functions: maintenance of contact, co-ordination of group travel, and regaining lost contact. In infants *moos* are related to stressful situations. I suggest three non-exclusive hypotheses for the proximate function: indication of emotion; indication of physical needs; and manipulation. The ultimate function for infants seems to be elicitation of a care-giving response, and possibly indication of retaliation/disagreement as well.

I describe three structurally and functionally related calls, *screeches*, *cries*, and *screech-cries*. All were related to stressful situations, but seemed to have some degree of specificity regarding the level of presumed stress of a situation, although contextual specificity cannot be ruled out. *Screech-cries* appeared to relate to lower stress levels, *cries* to the highest, and *screeches* to medium and high stress. I propose that *screeches* serve to elicit help/care-giving, but also to signal submissive status, while *cries* present the same functions, but with inverse priority. *Screeches-cries* would mostly announce disagreement and submission, but could also elicit care.

I propose that roars (a loud call) function in the inter-group spacing system. The group had exclusive access to a large area, with a small overlap at the borders. I hypothesise that roars provide a mechanism for advertisement of occupancy, and an aggressive display during encounters to reinforce occupancy and provide a way of settling disputes without chases and fights. A series of alternative proposals are discussed, most of which could be dismissed. In particular, roars do *not* function in a system of mutual avoidance nor operate in regular reinforcement of border locations.

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*“One of a group signals with his hand and the others gather around, and as soon as they are seated he begins an “oration.” When he has finished, he signals the rest to answer him and they cry together until he again causes them to be silent by a motion of his hand.”* Abridged edition by Marcgrave of M. de Buffon accounts (1791) quoted in Carpenter (1934).

*“the most remarkable of the American monkeys are the howlers, whose tremendous roaring exceeds that of a lion or bull, and is to be heard frequently at morning and evening in the primeval forests. The sound is produced by means of a large, thick boney vessel in the throat, into which the air is forced; and it is remarkable that this one group of monkeys should possess an organ not found in any other monkey or even any other mammal, apparently for no other purpose than to be able to make a louder noise than the rest.”* Wallace (1878) quoted in Carpenter (1934)

## CHAPTER 1: INTRODUCTION

*“The monkeys that are in these Parts are the ugliest I ever saw. They are much bigger than a Hare, and have great Tails about two Foot and a half long. The under-side of their Tails is all bare, with a black hard Skin; but the upper-side, and all the Body is covered with coarse, long, black, straight Hair. These Creatures keep together 20 or 30 in a Company, and ramble over the Woods; leaping from Tree to Tree. If they meet with a single Person they will threaten to devour him. When I have been alone I have been afraid to shoot them, especially the first Time I met them. They were a large Company dancing from Tree to Tree, over my Head; chattering and making a terrible Noise; and a great many grim Faces, and shewing antick Gestures.”* Dampier, W. (1700) quoted in Carpenter (1934).

### 1.1 The study of vocal communication

#### 1.1.1 Introduction

Communication, in its many modes (chemical, visual, auditory, etc.), is a phenomenon that has long attracted the attention of researchers. As with every field of research, a definition of terms and concepts is necessary. However, everyone attempting to study animal communication is initially befuddled with a plethora of definitions and theoretical discussions revolving around the concepts of communication, information and signal (see Hauser, 1997 p. 7 for a review of some definitions). Nonetheless, nearly all definitions seem to agree that communication involves the transmission of information between a sender and a receiver through the environment, and that a change in the behaviour of the receiver occurs in response to that (see Hauser, 1997; Bradbury & Vehrencamp, 1998). Many definitions also include the notion that the transmission of information must be beneficial to the sender. Most of the discussion revolves around the question if one should consider that a benefit to the receiver should be included in the definition as well. This particular standpoint has been constantly challenged since the early days of sociobiology and evolutionary game theory. The most controversial proposal was the one by Dawkins & Krebs (1978), who viewed communication as a way for an individual to manipulate the behaviour of others to the sender’s benefit, dropping out completely the concept of information transfer from their definition. Due to many criticisms of their

original proposal, the authors later provided a review of their ideas, exploring more the side of the receiver, and allowing for the possibility of co-operation (Krebs & Dawkins, 1984). Whichever the definition one follows, few people would dispute that most animal vocal utterances (and also many non-vocal acoustic emissions) *are* instances of communication, no matter how we choose to define it.

Among the wide spectra of signals employed by animals, the study of sounds has been particularly prolific, in part because hearing is an important sense for our own species, but mainly due to technical facilities for its study and because one can often be confident of their communicative role (Bradbury & Vehrencamp, 1998). However, there are also further reasons for the study of vocal communication, in particular of primates. It is now widely accepted that the study of primate vocal behaviour (and also of animal vocalisations in general) can help to shed light on many problems related to the evolution of communication in our own species. Furthermore, primate vocal behaviour can also be an important way of assessing primate cognitive capacities (Cheney & Seyfarth, 1990). Within the arena of these two inter-related themes, evolution of human language and cognitive abilities behind call production and perception, one can discern some topics upon which the research on mammal vocalisations has concentrated its focus. Besides, there are also other major topics of the study on non-human calls which have evolutionary or ecologically relevance and do not fit into these two areas. In the sections that follow, I will briefly outline some of the themes belonging to the first group. Being a very broad overview, many interesting topics with a vast literature were left aside for the sake of space. These include, for example, the study of individuality in call production (and also group, and sub-specific distinctiveness), of honest signalling, of the relation between design of calls, environmental characteristics and functionality, of vocal ontogeny and the role of learning, etc.

### *1.1.2 Informational content of vocalisations: affective or referential?*

Until quite recently, it was believed that animal signals, differently from human language, were merely affective, being an expression of a particular emotion, with no external referents. However, the study of vervet monkey

(*Cercopithecus aethiops*) alarm calls started to challenge this notion definitely (Cheney & Seyfarth, 1990; Seyfarth et al., 1980a,b). Using carefully designed playback experiments, Dorothy Cheney and Robert Seyfarth were able to discard alternative hypotheses, and confirm that vervet monkeys possessed at least three acoustically distinct alarm calls, labelling referentially three different types of predators (eagles, leopards and snakes). As the authors clearly point out, this conclusion does not mean that the calls do not have an additional emotional content, which can provide extra information. In fact, they probably do, but the same thing happens with human language. Since these groundbreaking findings, other researchers have widened them, providing additional examples of referential labelling in primate communication. Thus, vervet monkeys use different grunts in different social situations, and referring to events and objects external to the emitter (Cheney & Seyfarth, 1982). Diana and Campbell's monkeys (*Cercopithecus diana* and *Cercopithecus campbelli*) use different alarm calls to refer to distinct kinds of predators (Zuberbühler, 1999; Zuberbühler, 2000; Zuberbühler, 2001). Rhesus monkeys produce five different scream types in agonistic situations, depending on the type of opponent and the level of aggression (Gouzoules et al., 1984). Finally, chimpanzees produce two acoustically different screams if they are the aggressor or the victim in an agonistic interaction (Katie Slocombe, pers. com.).

### 1.1.3 Intentionality in call production

Another debated issue is the one of intentionality behind call production in animals. The problem here is to know if a given vocalisation is produced with the intent of informing others or not. This issue becomes particularly salient in the study of contact and alarm calls. In the first case, there seems to be a system of vocal exchange in place in many instances, and in the case of alarm calls, the callers seems to be informing others of the presence of the predator. For the contact calls, it has been argued that the supposed responses are actually a consequence of the state of separation of the respondent itself, not an answer to the first caller (Cheney & Seyfarth, 1999; Cheney et al., 1996; Rendall et al., 2000; Seyfarth & Cheney, 2003). There would be no intention of informing the location of the group or the caller to the individual that is astray. The argument is

that such intentional behaviour would imply an understanding of the state of the separated animal or, in other words, theory of mind, something not shown in monkeys so far. However, Byrne (2000) defends that contact calls may possess first-order intentionality, which does not need theory of mind to work. In this case “...both signallers and hearers *want* to reunite... and *know* that they should call in order to do so swiftly. It is not necessary that they be able to understand what others know...contact calling may be a goal-directed tactic, learned or even perhaps hard-wired, employed flexibly and selectively, but without insight into its mechanism” (Byrne, 2000, p. 507). The original critics of the intentionality idea also conceded some alternative explanations. They suggested that other mechanisms could produce vocal exchanges or that there might be some degree of perception of the other’s perspective (Rendall et al., 2000), a proposal which is somewhat vague though. Therefore, as one can see, this is still an unresolved issue, depending both on clear data, and also on theoretical debates.

#### *1.1.4 Syntax, grammar and conversation rules*

Syntax and grammar are other characteristics that are usually considered unique to human language and speech. Here, studies of animal vocal behaviour also provided some challenging, although not as profound as in the referentiality case. By highlighting the similarities and differences between human vocal behaviour and animal communication systems, these challenges can help to shed light on the evolution of language and speech. Understanding the conditions under which syntax (or different kinds of syntax) can emerge or can be adaptive is crucial to our understanding of the evolution of human traits, and can also help to test hypotheses about the evolution of such traits.

The first clearer example of syntax within primates came from the work of John Robinson (1984) with wedge-capped capuchins. The author worked under a paradigm that distinguished two kinds of syntax, phonological and lexical. The first would be composed of rules that specify the order of calls within a sequence, and such order is important for the meaning, but there is no relation between the meaning of the elements and the final sequence. In lexical syntax, the meaning of the sequence is the sum of individual meanings. The author argued that titi monkeys seemed to possess the first, but not the second,

while capuchins showed evidence of lexical syntax, a position that did not remain unchallenged (Cheney & Seyfarth, 1990). However, the author made clear that there was nothing in the vocal system of the studied species that resembled human grammar. Looking at the problem under a different perspective, Fitch and Hauser (2004) showed that cotton-top tamarins (*Saguinus oedipus*) can understand simple grammars characterised merely by transitional probabilities between the elements (which is reminiscent of some of Robinson's, 1984 results). However, when they tested the animals with more complex grammars, involving for example hierarchical structures, the monkeys failed to master them.

Snowdon and Cleveland (1984), studying vocal emissions by three pigmy marmosets reported a different sort of finding. The authors found out what was described as “conversational rules”, apparently similar to the turn-taking behaviour of human conversation. Thus, the individuals had an order in sequences of calling that was significantly different from chance. One animal had a much higher probability of starting a bout, and the order of animals that followed was not random either. The description of the loud call duet sessions of white-cheeked gibbons (Deputte, 1982) seems to indicate that the sessions had organisational rules. Also, the structure of the calls of males and females could be interpreted as having a phonological syntax, but the author did not analyse the results in neither way.

#### *1.1.5 Graded and discrete vocal repertoires*

Among the many contributions of Peter Marler to the field of vocal communication is his distinction between graded and discrete repertoires or signals (quoted in Hauser, 1997). Thus, clearly defined call types would compose discrete repertoires, with no transitional types. On the other hand, graded signals would lie along a continuum, with no clear limits between types. This continuity, however, could be perceived in a categorical way by the receiver. Despite the recognition that Marler did not view his classification as a static dichotomy, the division of repertoires and calls into discrete or graded has been criticised on several grounds (Hauser, 1997). Nonetheless, “it may be heuristically useful in

the initial stages of research to divide nonhuman primate vocal repertoires into graded and discrete classes ...” (Cheney and Seyfarth, 1990, p. 128).

Whichever one’s position in this debate, the important point here is the study of how a species perceive a given set of stimuli, and ultimately to compare the results to the way we perceive speech sounds ourselves. The most exciting discoveries related to this topic are of two kinds. The first is the observation that some vocalisations, perceived as unitary types by human observers, are actually composed of a set of distinct calls, which can be reliably separated by acoustic analyses, and have clearly different meanings (Cheney & Seyfarth, 1982; Cheney & Seyfarth, 1990). The second is that some call types, produced in a graded way, are actually perceived by the animals as discrete, as humans do with speech sounds (Snowdon, 1989; Snowdon, 1997; Snowdon & Pola, 1978).

#### *1.1.6 Basic approaches to the study of vocal communication*

Despite the importance and relevance of the topics of study described above, all of them depend on basic studies of vocal behaviour. As Snowdon (1989, p. 612) puts it: “Before any analyses of complex vocal communication can be made, it is essential to have a good natural history of vocal communication”.

When studying vocal communication there are two basic approaches that can be taken, structural and functional, which are non-exclusive. Basic structural or repertoire studies aim at describing the different vocal types emitted by members of a given species, generally providing spectrograms and a description of the physical parameters of the calls. Usually there is also a description of the context and situations in which the calls are emitted, and sometimes a consideration of their function, based on *ad libitum* observations. Such studies, although largely descriptive in nature, constitute a fundamental source of basic information upon which more detailed work can be done. Functional studies, on the other hand, usually focus on a single call type, or on a group of related vocalisations, trying to understand the role it plays in the lives of the animals. In a variant of this, a researcher might choose to study a functional group (e.g. alarm or food calls) which can be composed of one or more call types. Within the broad category of functional studies, theoretical and methodological approaches

are incredibly varied, mostly due to the level at which function is considered, something frequently not stated in an explicit way. The researcher might be interested in investigating the function at a proximate level, that is, which kind of information is encoded in the vocal signal (e.g. age, dominance status, size, physical condition, willingness to engage in a contest, etc.). Other studies focus on the effects of the calls on the behaviour of other animals of the same or of different species (i.e. mechanisms to achieve an ultimate function). Yet another version is the study of the effect of different environmental and social variables on call production, which can give important clues in all those levels. For example, a male loud call may be found to encode information on the size of the animal (proximal level). Other males either display submissive behaviour or challenge (mechanism), and the call regulates dominance relationships (ultimate level). The vocalisation might be produced around food patches, or when females are in oestrus (influence of social variables). Finally, there is the possibility of combining structural and functional approaches, which happens in studies aiming at understanding the relation between form and function.

## 1.2 Study genus and study species

### 1.2.1 General characterisation

Howler monkeys are diurnal Neotropical primates (infraorder Platyrrhini) that belong to the genus *Alouatta* of the Atelinae sub-family (family Atelidae), which also includes the spider monkeys, the miqui and the woolly monkeys. They are among the largest of Neotropical primates, with weights ranging from 4 to 10 kg (*A. caraya* females 3.8-5.4 kg; males 5.0-8.3 kg). Howler monkeys are also the most sexually dimorphic of the Platyrrhini, with inter-specific variation in the degree of dimorphism. Differences occur in body size (males are larger), canine and hyoid size, and, in at least two species, in body coloration as well (*A. caraya* and one subspecies of *A. fusca*). In weight, *A. caraya* females are 68% lighter than males; in coloration, the males are completely black while females are pale yellow or straw coloured. As with all members of the sub-family Atelinae, they possess a prehensile tail, which is frequently used in suspended feeding and playing postures. (Kinzey, 1997; Neville et al., 1988, Rowe, 1996)

The genus contains at least eight species, and a very wide geographical distribution, extending from Mexico in the North to the southern extremity of Brazil and northern areas of Argentina. Correspondingly, *Alouatta* occurs in an extensive range of environments, from gallery forests inside semi-arid and savannah environments, through Amazonian forests to Andean cloud forests and many others. *A. caraya* occurs in the central regions of South America, south of the Amazon basin, occupying the mid-western regions of Brazil, the Chaco regions of Bolivia and Paraguay, and the north of Argentina, also reaching the caatinga region of north-eastern Brazil. It occupies a range of forested environments, many of those within more open and dry environments such as the Brazilian cerrado and caatinga biomes, and the chaco.

Howlers are arboreal, quadrupedal, slow-moving monkeys, usually confined to the middle and upper canopy and emergent layers of the forest, and rarely coming to the ground (more frequent at some sites). (Kinzey, 1997; Neville et al., 1988; Rowe, 1996). The most striking characteristic of the genus is their modified vocal apparatus (Schön, 1971; Schön Ybarra, 1988), especially the

highly enlarged hyoid bone, which, however, has considerable inter-specific variability in its volume (Crockett & Eisenberg, 1987). This structure is thought to play a key role in the production of the loud vocalisations (Schön-Ybarra, 1988), the feature by which howler monkeys are most well-known. Popular names in many languages refer to their loud calls, and the genus name also probably originated from Native Americans' words related to throat or neck (Schön Ybarra, 1986). It has even been suggested that this anatomical commitment might affect other aspects of howlers' lives, such as positional behaviour (Schön Ybarra, 1984).

Howler monkeys are also notorious for their energy-saving lifestyle, with a large amount of time spent resting and a low level of intra-group activity. This behavioural pattern is generally interpreted as a response to a low quality diet, which usually includes large amount of leaves (especially mature ones), coupled with an absence of anatomical specialisation of the digestive system, as possessed by the colobines (Crockett & Eisenberg 1987, Kinzey 1997, Neville et al. 1988). The production of howler monkeys' spectacular sound utterances, which are time consuming and maybe energy consuming as well, contrasts sharply with their general lifestyle. This fact, associated with the presence of unique anatomical adaptations of the vocal apparatus, raises the suspicion that the loud calls may play an important role in howler monkeys' lives.

Howler monkeys are still regarded by many as uniform in their ecology and behaviour, and references are commonly made to "howler" diet, behaviour, etc. (this is partially due to the concentration of studies on two species, *A. palliata* and *A. seniculus*). This simple notion does not stand closer scrutiny. Although there are strong similarities between the species, the range of variation in different aspects of their ecology and behaviour is impressive. The situation somehow parallels the one in macaques: once regarded as a unitary group, nobody would seriously argue that case nowadays. Concerning diet, howlers are usually considered as prototypical folivores, but, in fact, they are better viewed as "folivore-frugivores or frugivore-folivores, depending on the population and the season" (Kinzey, 1997, p. 179). Their social behaviour is equally variable. For example, there is a wide range of group sizes, from the small troops of *A. pigra* with 4-10 individuals to the larger groups of *A. palliata* and occasionally *A. seniculus* with up to 45 and 26 monkeys respectively (Kinzey, 1997; Neville,

1972). Groups of *A. caraya* vary from 2 to 16 individuals, with an average size between 6 and 9 (Calegaro-Marques & Bicca-Marques, 1995; Pope, 1966; Pope, 1968; Rumiz, 1990; Thorington et al., 1984).

Howler groups can contain one or more males but, in the latter case, only one has exclusive access to oestrous females or during peak oestrus (Neville et al., 1988). Again this is a matter for variation, with some species having characteristically multi-male/multi-female groups (*A. palliata* and *A. seniculus*), and others possessing one-male groups more often (*A. pigra*). Isolated males and females also occur. Both sexes migrate and can either establish a new group or join a new one (Kinzey, 1997). Males may attempt to displace the resident alpha male and females to incorporate into the group, but resistance from group females was reported (Kinzey, 1997; Sekulic, 1983). Variation in aspects of their ecology and socio-ecology also occurs intra-specifically, and even in the same population, which can be clearly seen in the series of studies conducted on *A. palliata* in Barro Colorado Island (Panama) since the 1930s (Altmann, 1959; Carpenter, 1934; Carpenter, 1964; Chivers, 1969; Collias & Southwick, 1952; see also Crockett & Eisenberg, 1987).

Another common misconception about howler monkeys concerns their agonistic behaviour. They were once considered as very peaceful animals with aggression restricted to display behaviours. However, depending on the situation, overt physical aggression does occur, and some sites present high levels of agonism (particularly true of *A. seniculus*). The main aggressive interactions are male-male chases and fights during take-over attempts, and infanticides, which usually occurs after successful invasions (Clarke, 1983; Crockett & Eisenberg, 1987; Sekulic, 1983). However, it remains true that aggression, though serious, is confined to certain events and not a daily occurrence as in other primate societies. Evidence for male-male aggression and infanticide has been found in *A. caraya* (Rumiz, 1990).

Regarding ranging behaviour, home- and day-range values are quite variable between and within howler monkey species. Nonetheless, home ranges are usually small. The breadth of recorded variation is from 3 to 125 ha, but values are usually lower than 25 ha. Day ranges are also small, values varying between 20m and slightly more than 1200m, “but usually it [the average day range] is less than 600m” (Kinzey, 1997). Variation within a site is considerable,

commonly covering almost all the range of values of a species. (Crockett & Eisenberg, 1987; Kinzey, 1997; Neville, 1972)

Concerning predators, the best documented cases are instances of predation by the harpy eagle (*Harpia harpija*) (Eason, 1989; Gil-da-Costa et al., 2003; Peres, 1990; Sherman, 1991). Crested eagles (*Morphnus guianensis*) have been observed to prey on young spider monkeys (Julliot, 1994), so howlers could be a potential prey item as well. Among felids, jaguars (*Panthera onca*) have been reported to kill howlers (Peetz et al., 1992), and Carpenter (1934) witnessed an attack attempt from an ocelot (*Felis pardalis*). Pumas (*Felis concolor*), with an intermediate size between the last two species, presumably lie within the range of potential predators, and tayras (*Eira barbara*) are among other potential predators (Asensio and Gómez-Marín, 2002). Snakes have also been cited as possible predators (Neville et al., 1988), and have been observed to attack other platyrrhines (Ferrari et al., 2004), but no instance has been reported with respect to howlers.

Howlers are the most studied Neotropical primates (Kinzey, 1997). In fact they are also the ones studied for the longest time, with Carpenter's (1934) research on *A. palliata* being the first field study ever of a non-hominoid primate. However, there is a great imbalance in research effort: the majority of studies were conducted on *A. palliata* and *A. seniculus*, with the other species lagging behind (Kinzey, 1997), including *A. caraya*.

### 1.2.2 Vocal behaviour

As howler monkeys are notorious for their extremely conspicuous loud calls, not surprisingly these vocalisations are the aspect of their vocal behaviour most intensively studied. As the central theme of this thesis, I postpone the review of studies on loud calls to the chapter dealing specifically with them.

Moving focus to other kinds of calls, the situation changes dramatically. The amount of studies (mainly descriptive) is small, and *A. palliata* is again the most studied species. On Table 1.1 I summarise the scarce information on soft calls of different species of howler monkeys. Of the works considered, Baldwin and Baldwin (1976), conducted the most complete research on the repertoire of a howler species, and there we can find a description of a great number of calls,

with spectrograms for the majority, and an indication of their possible function. However, even in this study, the spectrograms are small and not very clear, and there is extremely limited description of physical parameters. These limitations impose serious restrictions on comparative work. Apart from these researches, the only additional sources are casual references to soft calls in articles focusing on other socio-ecological aspects.

Table 1.1 Information about small amplitude call types of howler monkeys described in the literature.

| Species                         | Call type   | Age-sex of caller   | Context/situation of use  | Function/Other remarks   |
|---------------------------------|---|---|---|--|
| <i>A. palliata</i> <sup>1</sup> | Deep metallic cluck   | Adult male  | Before and during group travel  | Initiation and control of group travel; co-ordination of animals in the clan                             |
| <i>A. palliata</i> <sup>1</sup> | Gurgling grunts and crackling sounds  | Adult male  | “Mildly disturbing and “apprehensive” situation”  | Preparation and co-ordination of defensive action by males   |
| <i>A. palliata</i> <sup>1</sup> | Wail ending with a grunt and a groan  | Adult females with infants  | When a young felt on the ground   | Aid in location and retrieval of fallen infants  |
| <i>A. palliata</i> <sup>1</sup> | Cries   | Infants   | When they felt on the ground  | Location and retrieval of fallen infants   |
| <i>A. palliata</i> <sup>1</sup> | Purr  | Infants/Juveniles   | “Contact with mother”   | Facilitation of mother-infant relationship   |
| <i>A. palliata</i> <sup>1</sup> | Little chirping squeal  | Infants/Juveniles   | During invitation to play   | Facilitation and co-ordination of play activity  |
| <i>A. palliata</i> <sup>1</sup> | Grunting sound  | Adult male  | When immatures are play-fighting and an individual is crying  | Control of activity of young by an adult male  |
| <i>A. palliata</i> <sup>1</sup> | Grunting similar to who! who! <sup>1</sup>  | Males   | Presence of strange or new stimuli  | Directing behaviour of the group. Altmann, 1959 considers this call and male barks to be the same.       |
| <i>A. palliata</i> <sup>2</sup> |   |   |   | “A locator signal and perhaps an indication that the infant is close to the mother and not in distress”  |
| <i>A. palliata</i> <sup>3</sup> | Eh  | Infants   | When exploring the surroundings, and when re-approaching mother   | In addition to the above, also involved in eliciting embracing. Suggested to reflect mild alarm/anxiety. |
| <i>A. palliata</i> <sup>2</sup> | Whimper   | Immatures   |   | Apparently in frustrating situations   |
| <i>A. palliata</i> <sup>3</sup> | Basic <i>whimper</i> calls (1), male emphatic <i>whimpers</i> (2), and chirping <i>whimper</i> (3) <sup>3</sup> | (1) All classes; (2) adult males; (3) juveniles and adult females | During group progression (1, 2, 3); when spotting a troop with which there was no mixing (1, 2, 3); juveniles “when mildly startled, surprised, threatened or pestered” (1); in active play; in adult greeting; and during mother-infant interactions (after falls, when infant was lost) |  |
| <i>A. palliata</i> <sup>2</sup> | Grunt   | Adult male  | During group travel   | May be the same call as the “deep metallic cluck”  |

|                                 |                       |   |  |
|---------------------------------|-----------------------|---|--|
| <i>A. palliata</i> <sup>3</sup> | Cackle-laugh or heh   | All                                     | During agonistic interactions, particularly the threatened animal  |
| <i>A. palliata</i> <sup>3</sup> | Caw                   | infant                                  | Separation from the mother and when the mother refuses contact   |
| <i>A. palliata</i> <sup>3</sup> | Wrah-has              | Mothers of dependent infants            | When they were astray  |
| <i>A. palliata</i> <sup>3</sup> | Yelps/screeches       | Infants, juveniles, adult females       | “Sudden fright situations”   |
| <i>A. palliata</i> <sup>3</sup> | Hiccup                | Adult males                             | During pauses in roar sessions   |
| <i>A. palliata</i> <sup>3</sup> | Squeaks               | Infants                                 | Mild distress situations (mother leaving, and when attempting to leave rough play)   |
| <i>A. palliata</i> <sup>3</sup> | Barks                 | Infants                                 | Rough play, when startled, when access to the nipple was hindered  |
| <i>A. caraya</i> <sup>4</sup>   | <i>Stress screams</i> | young and sub-adult females and infants | During aggressive interactions, play, and attempts of allomaternal care of newborns  |
| <i>A. caraya</i> <sup>4</sup>   | <i>Snarl</i>          | All except juvenile male                | Stress contexts, play  |
| <i>A. caraya</i> <sup>4</sup>   | <i>Cry</i>            | Infants/Juveniles                       | During stress situations (e.g. separation from group)  |
| <i>A. caraya</i> <sup>4</sup>   | <i>Quack</i>          | Sub-adult male                          | Aggressive behaviours of the adult male and a sub-adult female that occurred during and after copulation attempts by the sub-adult |
| <i>A. caraya</i> <sup>4</sup>   | <i>Mutter</i>         | All                                     | During feeding and attempts of allomaternal care   |
| <i>A. caraya</i> <sup>4</sup>   | <i>Lullaby</i>        | Female infant                           |  |
| <i>A. caraya</i> <sup>4</sup>   | <i>Cough</i>          | Adult male                              | Pre-copulatory behaviour   |

<sup>1</sup>Carpenter (1934); <sup>2</sup>Altmann (1959); <sup>3</sup>Baldwin and Baldwin (1976); <sup>4</sup>Calegari-Marques & Bicca-Marques (1995) – this work is in Portuguese, and the names of the calls and the information were translated by me.

When one moves away from the most studied howler species (*A. palliata*), the scenario is one of sparse mentions and no systematic research. The single exception is the study of Calegario-Marques & Bicca-Marques (1996), with an onomatopoeic description of some *A. caraya* calls, plus a few words on the situations of use. The authors also made a list of possible homologies of their set of calls with ones previously described, as follows. *Stress screams* could be similar to *hehs* or *cackle-laughs*, or to the *screeches* described in Neville (1972), while *cries* were possibly related to the *whimpers* described in Altmann (1959) or the *cries* mentioned by Carpenter (1934). But, it must be said that the situation of this research is rather peculiar with a single group living on a very small patch of forest. Also, no spectrograms of the vocalisations are provided.

Given this situation, the study of the vocal behaviour of *A. caraya* with the perspective adopted here is interesting under many perspectives. First, the functional study of loud calls of howler monkeys is already fascinating in itself, given their unique anatomical specialisations, and the likely relevance for their way of life. Second, although the loud calls of the genus have been reasonably well investigated, it still is a very challenging theme and an open topic. As we shall see in more detail in chapter 5, a variety of functions have been proposed for the loud calls of the species studied, and there is the disagreement both inter and intra-specifically with respect to the functions of the loud calls (another possible example of howlers' variation in behaviour). In other words, different functions have been proposed for the functions of similar loud call types in different species, and different authors reached somewhat different conclusions with respect to the functions of a given call type even within a single species (*A. palliata*). The issue is far from being resolved. Furthermore, *A. caraya* loud calls have not been studied before with respect to their function, and the only spectrographic description is based on captive recordings (Whitehead, 1995). Third, a more detailed description of soft amplitude calls is something that also has not been done before for this species, and which is actually lacking for the majority of howler species. Finally, a functional investigation of the smaller amplitude calls, attempting to substantiate impressions and *ad libitum* observations and back up functional claims with detailed behavioural data, would be unique for the whole genus, as far as I am aware.

### 1.3 Objectives and organisation of the thesis

My Ph.D. research had the general aim of studying the structure and functions of the vocalisations of black howler monkeys (*Alouatta caraya* – Primates – Atelidae), especially the loud calls, but also the less studied softer types. Obviously with such a broad goal one has to restrict the focus to feasible objectives. Thus, within this thesis, I confined my analysis of the small amplitude calls to the ones that seemed most promising in terms of results (*moo* calls and vocalisations of the *screech* complex). With respect to structure, a detailed acoustic analysis is outside the scope of the thesis. I am going to restrict myself here to the presentation of spectrograms and brief descriptions of the studied calls, but the recordings obtained will be used for a more thorough analysis in the future.

In the functional side of the study, the approach and objectives were different for calls of different amplitude. For low amplitude calls, I intend to go a step further from typical repertoire studies, and substantiate claims about their function or contexts of use. My intentions are to soundly fit the chosen calls into a functional group, to suggest hypotheses about their function(s), and provide a reliable basis for future studies. For the loud calls, I focused both on observational and experimental data in order to get a deeper understanding of their function, at least on an ultimate level. The first provides information on the circumstances of loud call emission, and the influence of environmental and social variables on the production. I complement this information with the results of playback experiments designed to understand the regulation of use of space and the role of loud calls in it. My overall intention was on one side to enrich the discussion about the functions of the loud calls of howler monkeys, and on the other provide a model for a more detailed study of the soft calls, and a foundation for future studies.

My general approach that was taken was to see vocalisations as behavioural traits used by the monkeys to solve problems in their lives. Although this study has a purposely basic nature from the start, I also intend later on to discuss potential links to some of the major themes outlined above, and propose avenues of investigation that might prove fruitful in their study.

After this broad introduction, the following chapter will outline general characteristics of the study area and the study group, as well as introduce the basic methods used in data collection and analyses of the soft calls, including the ethogram in which the observations were based. Chapter 3 discusses the data on one soft call type, labelled *moo* call, for which I defend a contact role and also offer evidence of its association with stressful situations. In Chapter 4 I consider a group of related calls (*screeches*, *cries* and *screech-cries*), which comprise the *screech* complex. I will show data of the relation of the calls of this complex to anxiety/distress situations, as well as propose some proximal functional hypotheses for each of the call types. Both chapters on soft calls follow a similar structure. I start with a review of the evidence of primate calls with similar functions, as well as the available evidence for howler monkeys, followed by the description of more specific methods of data collection/analysis not introduced in Chapter 2. After the discussion, I propose a detailed study design to be used in more focal studies of the specific calls concerned. Chapter 4 also contains an attempt to relate the study of *moos* with the one on the *screech* complex, given the similar contexts, in which they occur. Loud calls are considered in Chapter 5. I start with a specific review of the topic, and describe the particular methods used in the study of these vocalisations, including the experimental procedures. Several sources of data are presented (regular observational data, experimental results and *ad libitum* observations) and I discuss both the most likely function of the roars in light of the available evidence, and also discard many possible functions not supported by the data. Chapter 6 attempts to summarise the main findings of the data chapters into a cohesive framework considering the role each call plays on the natural history of the species. I then attempt to develop relations between my findings and conclusions to some of the major themes in the study of mammal vocal research. Appendixes 1 and 2 contain supplementary information.

## CHAPTER 2: STUDY SITE AND GENERAL METHODS

“... alarm calls in general occurred unpredictably, and, following Murphy's law, were given at the highest rates when our recording equipment was turned off.” (Cheney and Seyfarth, 1990, p. 129)

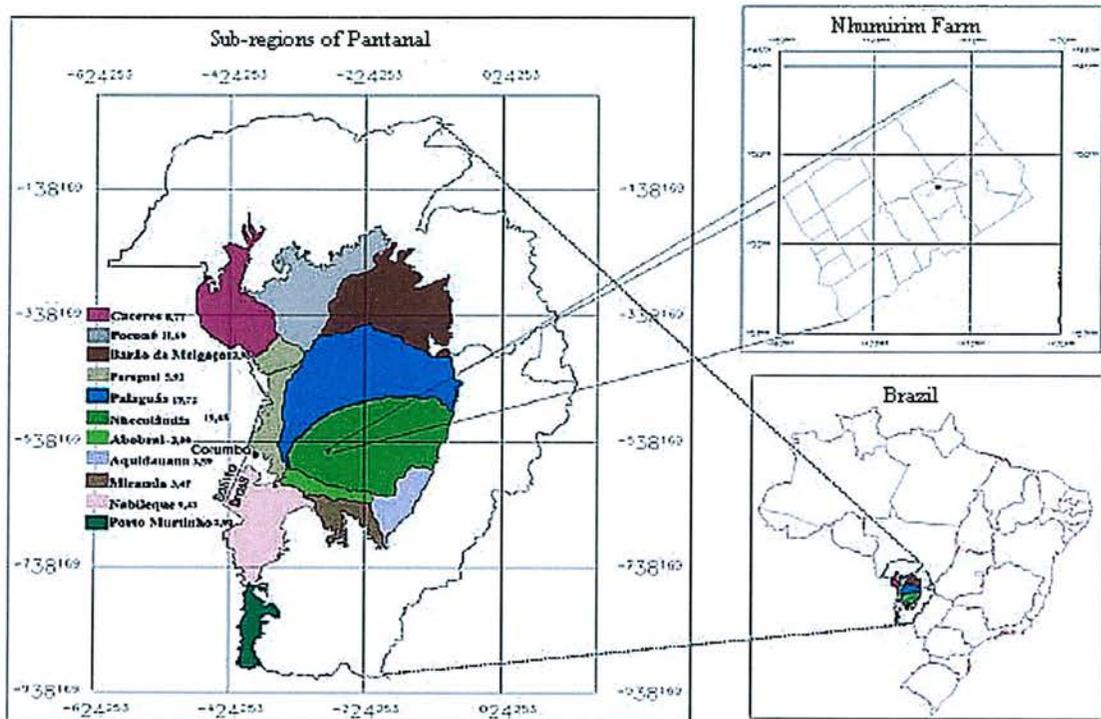
### 2.1 Study site

The research was conducted in Nhumirim Farm, a 4390ha research area located in the Mato Grosso do Sul state on the mid-western region of Brazil (18° 59' S and 56° 39' W) (EMBRAPA, 1997), see Figure 2.1. EMBRAPA, a body of the Ministry of Agriculture and Supplying of Brazil devoted mainly to farming related research, owns the area. The farm is located in Pantanal, a complex biome whose main feature is the seasonal flooding of its vast plains. The inundation presents strong spatial and annual variability.

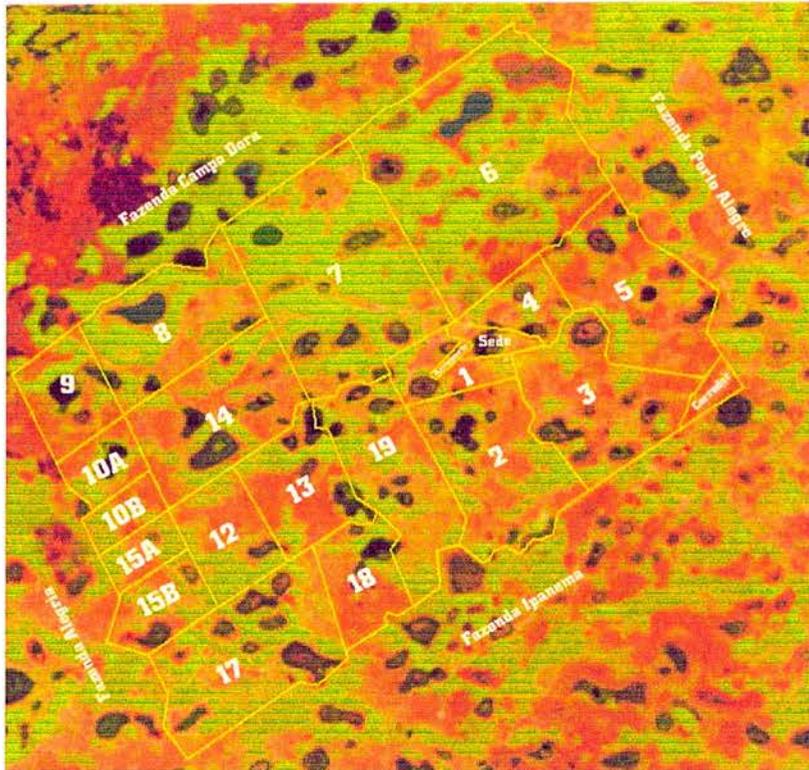
The vegetation of the farm follows the general pattern of the Pantanal region, that is, it is a mosaic of different habitats (see Figure 2.2). In the area occur grassfields, scrubland savannah, wooded savannah, tall woodland savannah, and semi deciduous forest (EMBRAPA 1997), with all sorts of transitional types. Temporary watercourses and numerous small ponds, a few of them brackish, also occur, a characteristic of the Nhecolândia sub-region of Pantanal, where the ranch is located (EMBRAPA 1997). I conducted the research in a plot of semi-deciduous forest interspersed with wooded savannah patches, located near a brackish pond (see Figure 2.3). The canopy in the semi-deciduous forest type in the area is around 12m, although emergent trees may occur (pers. obs.) and the crowns may or may not touch each other (vertical discontinuity is also high, pers. obs.) (EMBRAPA 1997). For details of forest composition see EMBRAPA (1997). The mammalian and avian fauna in the farm include possible predators (pumas *Felis concolor*, ocelots *F. pardalis*, tayras *Eira barbara*, boas *Boa constrictor*, and anacondas *Eunectes notaeus*, jaguars *Panthera onca* are extremely rare in the area) and partial competitors (the most common being coatis *Nasua nasua*, toucans *Ramphastus toco*, and other birds such as *Pipile pipile* and *Ortalis canicollis*). No other primate species occur in the area, and none of the

two raptors (harpy eagles *Harpia harpyja* and crested eagle *Morphnus guianensis*) reported to attack Neotropical primates occur in the area.

The farm has some environmental disturbance primarily due to cattle-ranching activities and the presence of the herds themselves. Logging is minimal and hunting at the farm is generally restricted to feral pigs as quarry. The cattle and the horses occasionally use the forest patches for grazing and also for travelling. The situation on the neighbouring, privately owned farms is not as good: hunting and especially logging are somewhat more common, and man-induced fires are very frequent. However, monkeys are seldom hunted; rather, targets are game meat animals and the large cats which prey on calves.



**Figure 2.1** Location of Nhumirim Farm within Pantanal. Modified from Soriano, 2003.

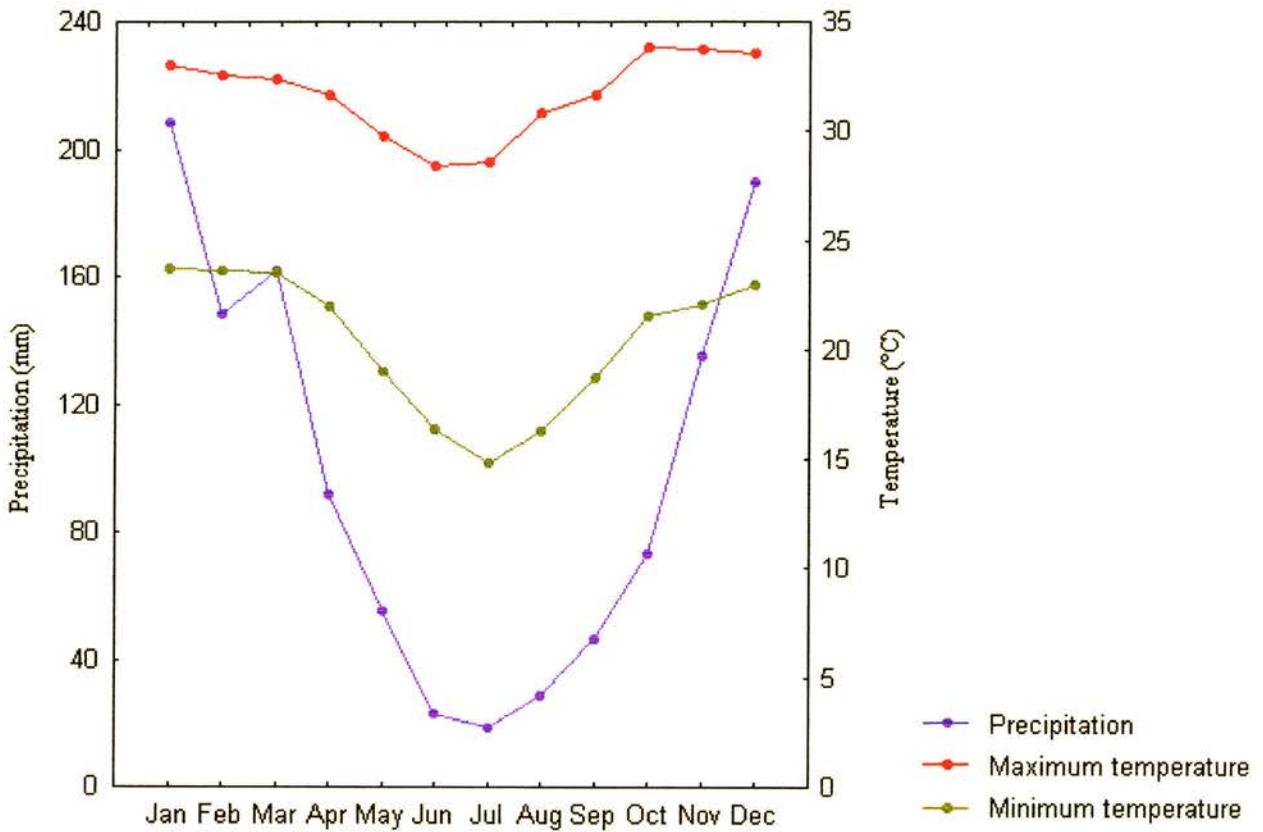


**Figure 2.2** Satellite image of the regional surroundings of the study area to which a map of the farm was super-imposed. Water bodies in black, wooded habitats in green and open areas in red. The study was conducted on the forest tract on the area number 8. Picture reproduced with permission from CPAP-EMBRAPA.

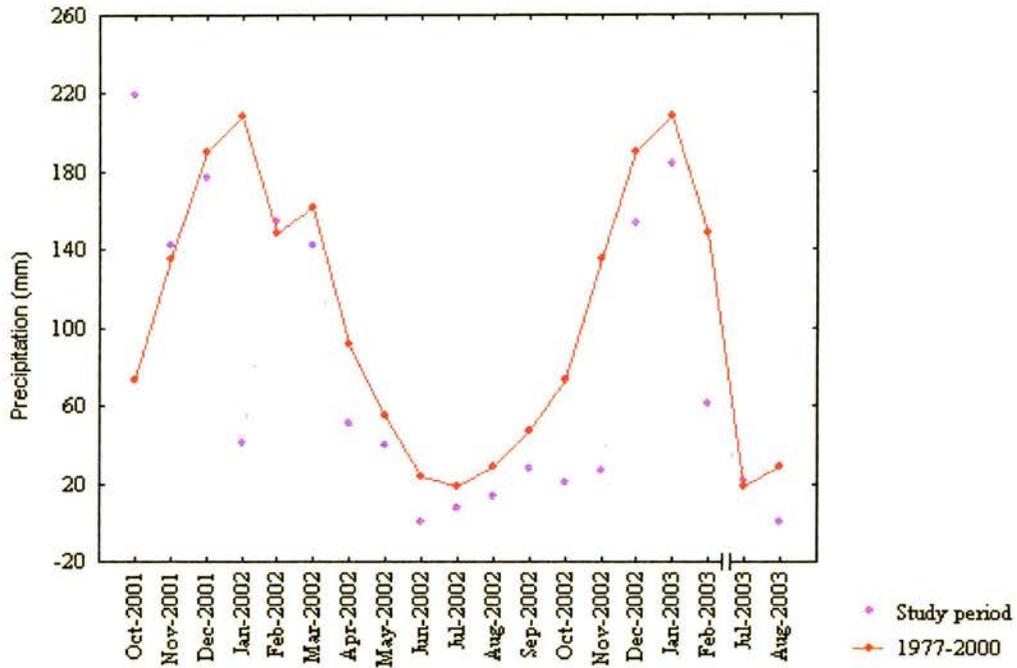


**Figure 2.3** Aerial photograph of the study area, showing the brackish water pond on the first plane. The forest tract on which I conducted the observations is the one located at the bottom of the picture. Photograph taken with the camera facing on an approximately northern direction. Picture reproduced with permission from CPAP-EMBRAPA.

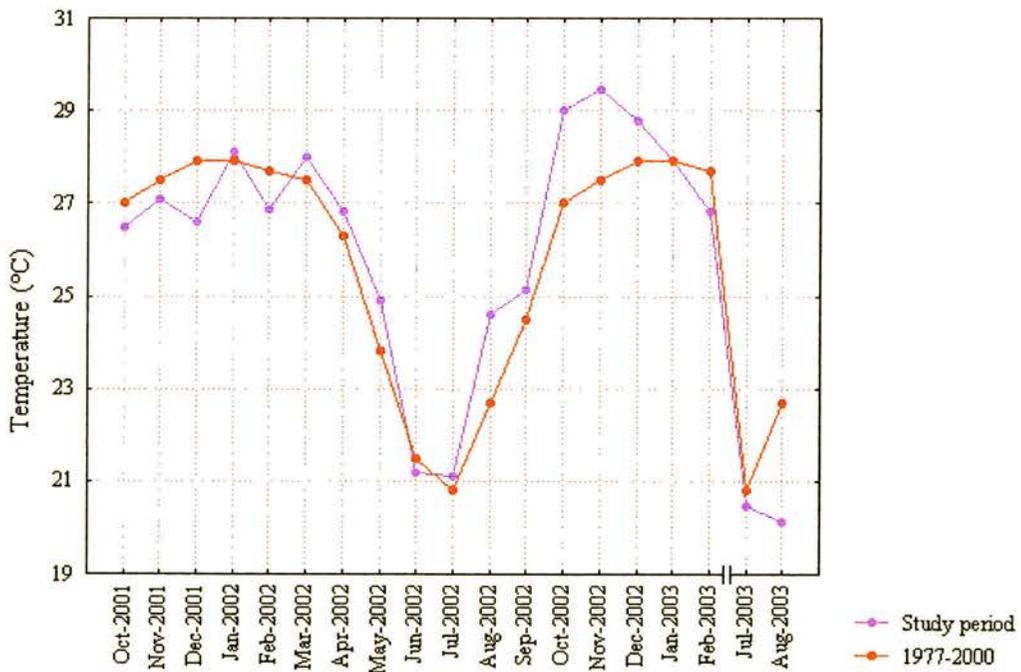
The climate in the region is tropical with seasonally (November-March) concentrated rainfall. The mean annual temperature (1977-2000) in the farm is 25.4°C (absolute minimum close to 0°C and absolute maximum above 40°C) and the average annual rainfall is 1179.8 mm, of which approximately 70% concentrated on the rainy months (EMBRAPA 1997, Soriano and Alves, 2003 see Figure 2.4). There is also marked inter-annual variation on the amount of rainfall. For data referring to the study periods see Figure 2.5 and Figure 2.6.



**Figure 2.4 Average precipitation, minimum and maximum temperature per month on the period 1977-2000. Graph built from the data on Soriano and Alves, 2003.**



**Figure 2.5 Total monthly rainfall during the study period compared with average data from the period 1977-2000. Graph built using data from Soriano and Alves, 2003 and Soriano, pers. comm.**



**Figure 2.6 Average monthly temperatures during the study period compared with average data from the period 1977-2000. Graph built using data from Soriano and Alves, 2003 and Soriano, pers. comm.**

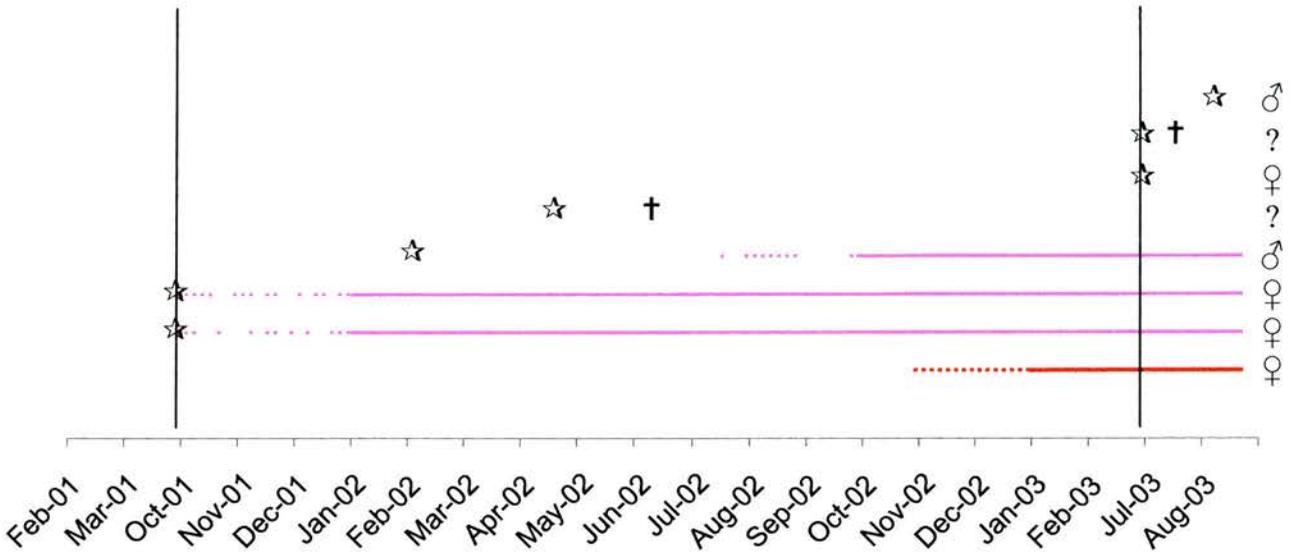
## 2.2 Study group

Before the start of the data collection in the first field season (see topic 2.3), I visited some forest patches in the area in search of the most suitable conditions for the study. I required that the chosen forest plot should contain at least 2 groups, preferably more, with the aim of not excluding possible effects of intergroup relations on vocal behaviour. The group chosen contained, at the start of the pilot study, one adult male, one sub-adult male, 2 adult females, 2 juvenile males, 1 sub-adult female and 2 female infants. At the start of the main study, the sub-adult male had become adult, the juvenile males were now sub-adults, the female infants had become juveniles, and two new female infants had been born while I was away. During the course of the main study further changes occurred, depicted in Figure 2.7. At the end of the extra season the group had two adult males, three adult females, two sub-adult males, five juveniles (4 females and 1 male) and 2 infants (1 female and 1 male). However, behavioural data collection was restricted to the 13 individuals present during the main study.

For the sake of simplicity, in the following chapters individuals will be represented by numbers and an age-sex acronym. In Table 2.1 I present the correspondence between the numbers and codes and the individuals, alongside relevant information concerning their affiliation.

Although I did not collect regular data that could allow establishing rank relations precisely, during the course of the study I could have a fair idea of these relations. Thus, adult male number 1 was dominant over all other animals. This was based on his clearly larger body size, exclusive mating access to females, initiation of all roaring sessions, and displacements at a distance (larger than the 0.5m criteria used) or submissive behaviour of all other individuals. Male number 2 was dominant to all individuals except 1. The observations that led me to this conclusion include: his larger body size than the others; larger participation in roaring sessions after male 1; a few displacements, particular during access to food sources. Sub-adults 3 and 4 were dominant over females and immatures (relations with female 5 were not clear). Conclusions with respect to their dominance over females were based on: a few displacement episodes and also access to food sources; no retaliation whatsoever during insistent harassing

attempts to copulate; Female 5 was dominant over the other females and immatures. Dominance with respect to female 5 was concluded given: the higher proximity of female 5 to male 1; the apparent suppression of loud calling of female 6 by female 5; and the somewhat more peripheral behaviour of female 6. Female 5 constantly chased and displaced at a distance female 9 for a considerable part of the study, and was therefore clearly dominant. The offspring of female 5 was also dominant with respect to individual number 9 (based on the clear approach-avoidance and ambiguous behaviour of 9 towards the offspring of 5 after 9 was re-accepted in the group, and the sometimes aggressive behaviour of them towards 9, which generated prompt retreat). Relations of females 9 and 6 were unclear (6 accepted the proximity of 9 during the chase period, and nothing indicative of a direction of dominance could be detected). Relations between juveniles and infants were also not clear, although individuals at those classes preferred to interact with similar sized animals. Smaller infants sometimes avoided rougher play with the older juveniles, which is an indication of dominance by the later. Relations of female 6 with the offspring of female 5 were also not clear (during highly insistent attempts of juvenile 7 and infant 10 to interact with female's 6 newborn infants, she resorted first to avoidance and leaving, and only after some time to mock bites and attacks).



**Figure 2.7** Changes in composition of the study group (☆ – births; † – disappearances; ..... - transition to adulthood; - · - transition from infant to juvenile stage). A continuous line signals the completion of a transition. Timing of changes is a rough estimate. The sex of the individual concerned is indicated on the right. Vertical lines separate the three different study periods. Stars on top of these lines indicate that the births occurred while I was away. Eight individuals whose status remained unchanged from the start of the main study were not depicted (2 adult males, 2 adult females, 2 sub-adult males, and 2 juvenile females, individuals 1, 2, 3, 4, 5, 6, 7, 8, see table below).

**Table 2.1** Numeric codes of the individuals in the study group that will be used on the analysis chapters. Also data on the putative mother.<sup>a</sup>

| Age-sex                | Number | Acronym | Affiliation <sup>b</sup> |
|------------------------|--------|---------|--------------------------|
| Adult male             | 1      | AM      |                          |
| Adult male             | 2      | AM      |                          |
| Sub-adult male         | 3      | SAM     |                          |
| Sub-adult male         | 4      | SAM     |                          |
| Adult female           | 5      | AF      |                          |
| Adult female           | 6      | AF      |                          |
| Juvenile female        | 7      | JF      | 5                        |
| Juvenile female        | 8      | JF      | 6                        |
| Sub-adult/adult female | 9      | SA/A F  |                          |
| Infant/juvenile female | 10     | I/J F   | 5                        |
| Infant/juvenile female | 11     | I/J F   | 6                        |
| Infant/juvenile male   | 12     | I/J M   | 5                        |
| Infant female          | 13     | IF      | 6                        |

<sup>a</sup> I did not register data on the infants born between the main and the extra study, and the one born during the extra season.

<sup>b</sup> Affiliative relations based on the individual responsible for breast feeding and for the bulk of carrying. Delivery of infant 13 was observed, and infant 12 was seen a couple of days after birth, still on the phase of ventral hanging.

## 2.3 Data collection

The field study comprised 3 field seasons: a pilot study in February/March 2001, a main study from October 2001 to February 2003, and an extra season in July/August 2003. Approximate fieldwork hours were 250, 1935 and 305 respectively. I maintained contact with the study group for at least 95% of this time.

During each of these seasons, I collected different kinds of data (alongside playback experiments) for varying amounts of time. Below I specify the general methods used in the main and the extra study, and the period over which I collected particular kinds of data. (During the pilot study I used other methods to gather data; as these data were discarded, the methods will not be described here.)

I used additional, more specific methods for the study of particular calls, the description of which will be delayed to the respective chapters. Also, I will postpone the description of data collection methods relevant to the functional study of roars and barks to the chapter dealing with loud calls.

### *2.3.1 Behavioural data*

Upon finding the group, I collected data continuously on a given animal (Altmann, 1974) over fixed periods of time (40 min. for the first month, and then 50 min.), followed by a time-out period (20 or 10 min. respectively), after which I turned attention to another individual. The order of animals sampled during the day was pseudo-randomly<sup>1</sup> determined and all age-sex classes were included.

I registered the data with the aid of specialised software (Observer 3.1, Noldus Information Technology), whose data collecting module was installed on a handheld device (Psion Organizer LZ64). Every night I downloaded the focal samples onto a laptop computer.

On each focal sample I kept a continuous record of mutually exclusive behavioural states (Box1) performed by the focal animal. On top of those, I registered instantaneous behavioural events (Box2) performed by the same

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<sup>1</sup> Random procedures in computers are, theoretically speaking, not purely random but produced by algorithms which derive a number from a given seed in a way that approaches randomness, thus the expression pseudo-random.

animal, which, by definition, had negligible duration (or the duration did not matter), and could occur concurrently with the ongoing behavioural state. I also attempted to register the maximum possible number of calls emitted by other animals that were not the focal. Some behavioural categories (states and events) accepted modifiers, which included the animal towards which a given behaviour was being performed, and food items. In the case of calls emitted by animals other than the focal the modifier indicated the emitter, when known. *Ad libitum* notes on the context or eliciting situation of calls were typed directly in the data logger, as the Observer software had a facility for writing more extensive notes, which possessed a time tag.

The specific behavioural categories used did not vary during the study (see Boxes 1 and 2 for the full list), except for deletions of rare or unobserved behaviours and a few additions of potentially interesting ones. These slight modifications occurred three times. Moreover, in the case of rare behaviours that were potentially interesting, I registered their occurrence with the software facility of including written notes that were time-tagged. The core list was kept intact and, with just a very few adjustments, all data files were combined for joint analysis.

I collected data for 8-9 hours a day and, in order to assure equal sampling time over different hours, I devised a 3-day alternation scheme. According to this plan, a 12-13 hour activity period, encompassing all sunlight hours (plus some time before dawn), was divided in 3 roughly equal periods (period 1: early morning; period 2: late-morning/early afternoon; period 3: late afternoon). Then, I established a 3-day rota, registering data on two different periods on each day (first day – periods 2 and 3, second day – periods 1 and 3, third day – periods 1 and 2). This assured that, after 3 days, 2 “full” days of data had been collected. When I stayed until late afternoon (period 3), I waited for the animals to settle on a sleeping tree and, on the next morning, I tried to arrive before they left it. Locating the group when the sleeping place was not known was fairly fast, normally taking less than 30 minutes.

Box 1: List of behavioural states

Feeding: inspection, manipulation, mastication or ingestion of food item. I also noted the food item consumed (young leaf, old leaf, leaf unspecified, bud, fruit, flower, stem, other).

Resting: general inactivity for more than 5 seconds.

Travelling: movement between trees. Infants had a separate category, 'riding', when they were travelling on the back of a carrier.

Grooming (active and passive)<sup>a</sup>.

Drinking water<sup>\*b</sup>.

Manipulate lesion (active and passive): Manipulate, lick or suckle skin lesions<sup>c</sup>.

Play: operationally defined through its modalities, that is, manipulating or biting twigs, leaves, bark, etc. (auto-play), wrestling or chasing\*.

Invitation to play (active and passive): operationally defined when an animal bites or pulls a part of another one's body in a non-aggressive context (for some time it was collected as an event).

Roar: very loud call emitted continuously, both during inhalation and exhalation (each cycle roughly 2-3 seconds)<sup>d</sup>.

Bark: very loud call, more pulsatile in nature than the roar. It might also be emitted during inhalation and exhalation, although not necessarily. When this occurs, there seems to be a slight pause between the phases, and the cycle is much shorter (less than one second).

Interaction with infant (active and passive): attempt to play, touch, pull or otherwise interact with a newborn or a highly dependent infant;

Other: behaviour not included in the categories above (e.g. defecation);

Not visible.

<sup>a</sup> When the behaviour is labelled "active and passive" it means that there were two codes for the data collection, so it was registered when the focal animal was performing a given behaviour or being the recipient or target of it. When a description is provided it is always of the active behaviour. For these behaviours, note was taken of the partner of the focal on the interaction. When the behaviour is self-explanatory or present a category widely employed in the literature, the description will be omitted.

<sup>b</sup> Behaviours marked by an asterisk are those for which a detailed or further description can be found in (Neville et al., 1988).

<sup>c</sup> All the animals in the group presented at some point in the study one or more hairless swellings of the skin with an opening in the middle, possibly larvae infestation. These will be henceforth referred to as "lesion".

<sup>d</sup> Appropriate description of call types will be deferred to their respective chapters.

## Box 2: List of behavioural events

Approach (active and passive): animal gets closer than 0.5m of another one.  
Leave (active and passive): animal moves more than 0.5m apart from another one.  
Follow (active and passive): animal follows another one closely, after being left.  
Present back (active and passive): animal turns its back to another one.  
Displace (active and passive): animal approaches other and is left by it.  
Cry: a very high-pitched sound, seemingly tonal, frequency modulated in an irregular manner.  
Screech: high-pitched sound, seemingly tonal, frequency modulated in a cyclical way with up- and down-sweeps.  
Screech-cry: noisy sounds, husky in nature, frequently occurring after the down-sweep of a screech. Lower frequency than the previous categories. Later divided in 'moo' and 'aah' sub-categories, if it resembled more a *u* or *a* vowel respectively.  
Oodle: blowing sound, produced by a sequence of rapid inhalation and exhalations.  
Short grunt: low pitched, noisy sound of short duration.  
Incipient roar: a short bout of roaring-like vocalisations.  
Sneeze.  
Muttering: a short, low-pitched call, composed of a series of syllables (more than 3), resembling a snarl in slow motion. Commonly emitted with the mouth shut, it has a muffled quality.  
Mutter-roar: sound similar to the mutter but emitted in the build-up to a roar session.  
Hum: call similar to the muttering but being composed of only 1 or 2 syllables.  
Moo: a short (~ 1 s), low pitched call, louder than mutters, presenting a more tonal aspect and being slightly frequency modulated.  
Hunf: call sounding like a voiced blow of air at a medium frequency.  
Snarl: call similar to a dog snarl, but emitted in short pulses (less than 1s), usually uttered in long sequences composed of trains of such pulses. Each pulse might be of different sound quality in relation to the adjacent ones, apparently depending on the degree of mouth opening.  
Staccato: Vocalisation composed of individual pulses of sound emitted at apparently regular intervals. Each pulse could vary from a sound similar to a short grunt to a higher pitched sound.  
Growl: sound resembling a snarl in very slow motion, where the "rough" nature of the sound is clearly visible through individualisation of notes. Emitted with the mouth wide opened.  
Manual prevention (active and passive): animal prevents access of other to a part of its body or actively interrupts such access (includes taking an infant that is riding one's back).  
Self-manipulation: divided in touching and scratching.  
Chase (active and passive)\*.  
Yawn\*.  
Rub throat/beard: repeatedly rub the muzzle, beard and throat against a substrate.  
Piloerection.  
Fight.  
Bite.  
Shake branch.  
Break branch.  
Bite branch: sometimes accompanied by nodding (see below).  
Pivoting\*.  
Slapping.  
Extending leg\*.  
Quick attack: animal rapidly turns its head towards another and effects an (apparently) mock bite.  
Look at: animal turns its head in the direction of a sound.  
Copulation\*.  
Sniffing: animal inspects and sniffs at another one's genitalia.  
Dispersion: many animals suddenly run in random directions.  
Bridge (active and passive): animal grasps the terminal branches bordering both sides of a gap between branches and makes a bridge over it with its body.  
Bare teeth\*.  
O-mouth display: animal protrudes and rounds the lips, shaping them into a 0, hiding the teeth.  
Touch with mouth (active and passive).  
Touch with mouth and screech (active and passive): combined behaviour whereby the animal (invariably an infant) touches another with the mouth and emits a prolonged series of screeches.  
Nodding: the movement resembles more a figure of 8 made with the head.  
Embracing: passing the arm round another animal's neck.

Besides the behavioural data, at the beginning of a data collection period, I noted the distances of each visible animal in relation to the focal one. I registered both focal animal behavioural data and distance data during the main field season only.

From September 2002 until the end of the main study and also during the extra season, I also registered data on group diameter, defined as the maximum distance between two group members (in 5m categories). I registered the group diameter every 30 minutes (instantaneous time sampling Altmann, 1974) to build up baseline data on typical group spreads, and also focally, during emissions of a small amplitude call, the *moo*.

### *2.3.2 Intensity of use*

During the initial months of the main study, a quadrat system was superimposed on the home range of the study group. I cut north-south and east-west trails spaced 50m apart, which generated quadrats of 50 x 50m. A row (east-west) number and a column (north-south) letter individually identified each quadrat. Once the system was close to completion, I started collecting data on the intensity of use of the different areas of the home range. Thus, at every 10 minutes (with respect to full hours) I registered the quadrat where the majority of the group was. I collected such data during the main study from May 2002, and also during the extra field season.

### *2.3.3 Recording and digitalisation of calls*

Call recording was done in all 3 field seasons. I recorded calls in an opportunistic fashion on chrome or metal tapes with a Marantz CP-430 professional recorder (frequency range 40 Hz-15 kHz with chrome tape and up to 17 kHz with metal ones) (or a Sony WM-D6 professional Walkman, frequency response 30 Hz to 15 kHz) and a Sennheiser ME 88 directional microphone with K3-U power module (frequency range 50 Hz to 15 kHz). Relevant information (when available) was dictated onto the tape immediately after the recording, including the identity of the caller(s), the call type as recognised in the field (using the same categories of the behavioural data collection), environmental

circumstances that might interfere with the quality, and also *ad libitum* contextual notes. More than 25 hours of tapes were recorded, although with varying quality and blank stretches corresponding to unsuccessful attempts.

Calls were digitised through a Sound Blaster 16 PCI sound card using CoolEdit Pro 2.0 (Syntrillium Software Corporation, 2002) at 44100 Hz and 16-bit resolution. The choice of such a high sample rate given the usually low pitch of the majority of howler calls is an over precaution to prevent aliasing, as the sounds were not filtered. This phenomenon occurs when a sound contains energy above the Nyquist frequency, which is half of the sampling rate. In this case, if such frequencies are not filtered, the digitisation process generates spurious frequencies on the sound file (Fry, 1979). The use of a high sampling rate decreases considerably the chances that significant energy will be present above the Nyquist frequency .

## 2.4 Data analysis

### 2.4.1 Behavioural data

Data analysis was both exploratory and confirmatory. For the soft amplitude calls analysed in this thesis, I had some hypotheses, from the observations of my pilot study, of the general category of functions that they belong to (e.g. alarm, contact, distress, etc.). Thus, I used the data in the search for confirmatory evidence of these preliminary ideas. Besides, I also searched for further evidence that could allow narrowing the range of possible functions.

In each case, the first approach was a comparison of call rate between individuals, to verify if a given call is associated with particular age-sex classes. Following, I compared call rate between behavioural states, to test if the call is positively or negatively associated to specific state(s). As some categories of functions also present positive or negative association with particular states, this analysis can provide support or lessen the case of the working hypotheses.

I calculated individual rates of calling for two sets of data. One comprising the calls emitted by an individual during its focal data collection periods only ('focal calls'), and another comprising all calls registered for an individual during

the whole study ('all calls'), that is, during its own focal samples plus the calls emitted in other animals' samples. Call rates on each behavioural state could only be calculated using the focal data, as I did not know the behavioural state associated to emissions during focal periods of other animals.

To investigate if the individuals had different rates of emission of a given call type, I had to resort to a goodness-of-fit comparison between the observed number of calls produced by each animal and the expected values. I had to employ different methods for the calculation of expected number of 'focal calls' and 'all calls' of an individual. To calculate the expected number of 'focal calls' of an individual I multiplied the focal call rate of the group as a whole by the number of hours of data collected for that individual. The focal call rate of the group was obtained by adding up the number of 'focal calls' of all animals together and then dividing this value by the sum of focal hours of each individual (excluding periods of non-visibility for each animal). To calculate the expected number of calls produced by an individual during all sampling periods ('all calls'), I first divided the total number of accounted calls (emissions for which the caller could be identified) by the sum of the times each individual was present in the group. This produced a measure of calling rate/hour/animal present. Then, for each animal, I multiplied this rate by the amount of time it was present in the group.

The next general step on the analysis of a soft call was the inspection of association of the call with other behavioural events. For each small amplitude call, I first selected for analysis a few behavioural events from the list presented on Box 2. The choices were informed either by the working hypotheses or by *ad libitum* observations during the other phases of the study. The rationale for the choices will be given on the appropriate chapters. For each selected event, I had either a hypothesis of the period during which the animals were expected to call more often (before or after the event), or a hypothesis of which of two latencies should be smaller (between the last preceding call and the event or between the event and the first succeeding call).

In the case of *moos*, the first approach described above (comparison of call rates between individuals and states) was done firstly considering all occurrences of the call, and secondly reducing the data set by considering bouts of calls as the data points. To define the bouts, it is necessary first to establish a time criterion for independence, in order to know which call emissions are non-independent and

should be joined into a bout. To determine this interval, I first compiled for each individual a list of the time differences between consecutive emissions of *moos*. Then, I built histograms of cumulative frequency of progressively larger inter-call intervals. Upon inspecting visually the histograms, I selected a value of two minutes, which is higher than the third quartile (of the distribution of inter-call values) for almost all animals. The histograms and calculations are presented in Appendix 1. Having selected the independence criterion, I had to combine non-independent *moos* into volleys. To extract bouts from the data files, a small program was written in Ruby environment by Ken Munro from School of Psychology, which deals with the behavioural data files in the following way. First one specifies which behavioural code the program is going to look at (in this case *moos* from a predetermined individual) and the time interval (criterion chosen for independence). Then, the program scans the data files (each 50 minute period of data collection is one file) looking for the codes of the behaviour in question. Subsequently, it deletes all events that are separated from a previous occurrence by less than the time criterion established, leaving only the first one of a sequence. Each call left by the program is considered to be representative of the volley. This method of extraction of bouts has implications for the analysis of call rates according to the behavioural state. Deleted ‘moos’ did not necessarily occur in the same behavioural context than the undeleted one, but one has to assume that there is no particular bias in favour or against any behavioural state. The smallness of the sample sizes once the data is divided by states calls for care in the interpretation of the results.

Explanation of the analysis of group diameter data will be delayed to the chapter on *moo* calls.

#### 2.4.2 Acoustic analysis

It is clear that any thorough study of the vocal repertoire of a species, and also any advanced research on a particular call or a set of related calls, must involve detailed acoustic analyses at some step. The applications of such analyses are immensely varied, including: the description of call types in precise acoustic parameters; the distinction of variants of a given type (particularly interesting if these correlate with specific contexts); the investigation of individual, group, local

and sub-specific variation; the matching of acoustic parameters between individuals (long or short term); the study of learning versus innate components on the ontogenetic trajectory of a call, etc. However, I focused my research on the behavioural analyses of the call types, attempting to unravel the contexts in which calls were emitted, and their meaning and function(s). The lack of detailed acoustic analyses is clearly a limitation of this study, but the research described here was conceived as the first step within a long-term plan to study the vocal behaviour of this and, if possible, related species. The recordings conducted were made with the main objective of obtaining an overall picture of the vocal repertoire. Detailed acoustic analyses will be carried up in follow-up studies. In the following chapters, I will draw attention to specific aspects which would particularly benefit from acoustic analysis, and also outline the particular analyses that could be carried out.

Given that in some species the vocal repertoire is highly graded, criticism could be made to the fact that the classification of call types in the field was made by ear all the way through the behavioural data collection. However, most of the vocal repertoire of the black howler monkeys seemed to be easily categorised in more or less discrete types. Furthermore, based on preliminary recordings done on the pilot study, I could confirm before the main study that some of the call types really did present clearly distinct spectrograms. After the main study, further checks were made, and I pointed out the possible sources of ambiguity (the calls belonging to the screech complex might graduate into each other, see Chapter 4).

To produce spectrograms for illustrative purposes I used Praat version 4.2 (Boersma & Weenink, 2003). Window type was Gaussian, recommended due to its superior results over the alternatives. Window length varied from case to case and was chosen in order to depict the prominent features of the call most clearly, especially with respect to the frequency features.

### *2.4.3 Statistical analysis*

Data amenable to analysis was retrieved from the data files either manually or with the analysis modules of Observer 3.1 and then stored and analysed in Excel 97, SPSS (v. 11.0) or Statistica ('99 edition). Specific tests used along the study included a variety of parametric and non-parametric tests, and the

options are described in the following chapters. All statistical tests were calculated after Sokal and Rohlf (1995) or Siegel and Castellan (1988). Unless otherwise stated tests were two-tailed. I used the following symbols for significance levels, throughout the text: \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; \*\*\* =  $p < 0.001$ ; ns = non-significant ( $p > 0.05$ ). Trends are reported for significance values between 0.05 and 0.1. Power analysis was carried out using the software GPOWER (Faul & Erdfelder, 1992). The purpose of conducting a power analysis is, in lay terms, to estimate how good your test is in detecting a difference of a given magnitude between your samples or to detect a relationship (or association). In statistical terms it is the inverse of  $\beta$  (the probability of falsely accepting the null hypothesis or failing to reject it when the alternative hypothesis is true). Thus, in studies with high power, one can be confident when rejecting the null hypothesis of having taken the right decision. (see Cohen, 1988 for information on the topic). To do it properly, one should specify the alternative hypothesis, and then, based on the distance between the null and alternative hypothesis, calculate the effect size, which is then entered in the calculation of power. However, most of the time in behavioural research, we are not used in specifying a particular alternative hypothesis. Cohen (1988) proposes some conventions of small, medium and large effect sizes, and suggests standard values for a couple of most used statistical tests. The use of these conventions amounts to verifying the discriminatory power of an analysis to discern a small, medium or large difference between the null hypothesis and an alternative one (not specified). In this study, power analysis was not used in a very strict way, but just as a means of conveying a general feeling of the discriminatory power of a give analysis. The proper way to use this important statistical tool, is to define *before* collecting the data what is the desired effect size, and then calculate what is the sample size required to obtain a powerful analysis.

## CHAPTER 3: MOO CALL

### Abstract

Many primate species possess calls that function in preventing group fission, maintaining contact between individuals/sub-groups, and facilitating reunion of isolated individuals, labelled as contact or isolation calls. Anecdotal observations indicated that the moo call of black howler monkeys seemed to have such a ‘contact/isolation’ function, but was also—in infants only—related to anxiety and distress. Here I present data to further investigate those possibilities. Feeding was the behavioural context with a significantly smaller call rate than other states, and travelling had the highest rates among individuals (non significant). Group diameter during emission of moos was significantly larger than baseline levels, and decreased significantly after a moo or a volley of moos, although it did not return to baseline levels. After moo calling, decreases in group spread were much more likely than increases. These results strongly support a contact function for moos. Infants presented a significantly higher call rate, and evidence for an anxiety/distress function was also found. When infants met a large arboreal gap, they mooed more frequently before than after crossing it (crossing was usually done with help from an older individual, at least for smaller infants). They also called more often before riding the back of a carrier than after. In conflicts of interest with older individuals (e.g. prevention of dorsal riding or of interaction with a newborn) infants mooed more frequently after the conflict than before it. However, such a result was not found when the mother left their infants. On a large number of instances of these events no call was heard, so these results must be viewed with caution.

### 3.1 Introduction

In the primate literature ‘contact call’ and ‘cohesion call’ are expressions that have been typically employed to refer to vocalisations used to maintain or re-establish auditory and/or visual contact between individuals. The terms ‘isolation’ and ‘lost’ call are also applied for utterances with those functions, but more specifically for calls emitted by individuals with no visual contact with others and/or separated by large distances. However, there is a lack of nomenclatural and conceptual standardisation. The labels mentioned are used somewhat interchangeably, and the implied function or described contexts of emission vary from case to case. In a few cases, the expression contact call is even used to refer to vocalisations belonging to a different functional domain (see below). In an attempt to clarify the situation, I devised a classification framework that aims to disentangle the functions most commonly ascribed to contact calls, as suggested by the author(s) or inferred from the context(s) wherein they are emitted. Thus, a given vocalisation, labelled as a contact call, can have one or more of the following functions (Table 3.1 presents a non-exhaustive review of works in which a vocalisation could be assigned to one of the categories below):

1. Gain or maintain access/proximity/physical contact to an individual

Calls emitted before physical contact is established or during bodily contact do not fit easily into the notion of ‘contact calls’ as commonly used. They more appropriately belong to the realm of vocalisations related to close affiliative social activities (e.g. play calls, pre-groom calls, etc.). It is likely that they possess a submissive or appeasing function, or even establishing a friendly intent on the part of the approaching or approached individual. Proposals in this direction are not common.

2. Maintain contact at close (visual) range

Calls given by animals at close (presumably visual) range that are not travelling. Apart from stating a contact function, nothing more specific is said in connection with the suggestions included in this category. In fact, it is difficult to

imagine a pure contact function, in the sense of “keeping in touch with others”, for these vocalisations. Some of them might in fact be distance-increasing calls, as suggested for the common *kra* calls of long-tailed macaques (Palombit, 1992), or the *heh* calls of wedge-capped capuchins (Robinson, 1982). However, some of the studies grouped here were conducted in captivity, which might alter the behaviour of the species considered.

3. Maintain contact at intermediate ranges and/or in situations likely to lead to separation:

This functional group encompasses calls given by animals that are separated by intermediate ranges, that is, when visibility between them is likely to be poor. It also includes travelling and spread foraging situations, and calls said to be emitted by dispersed animals, but with no indication of unusually large distances involved. The common ground here is that there is a potential for animals to get unintentionally separated from others but, as Palombit (1992) puts it, their “general whereabouts are more or less known”. The likely function is to maintain the cohesiveness of the group under the above circumstances and avoid separation. Examples for this class are much more common and cover a wide range of species. Obviously, within such a broad definition one will find many differences, such as with respect to the specific context of emission or regarding species typical characteristics. This ultimately might influence finer functional considerations. For example, Oda (1996) mentions that *meow* calls are emitted by ring-tailed lemurs more often during travelling and resting, while squirrel monkeys (*Saimiri oerstedii*) increase their calling rate with increasing distance or before initiation of group travel, but regardless of context (Boinski, 1991), and long-tailed macaques apparently use different calls in feeding and resting situations (Palombit, 1992). Many species and habitat characteristics are likely to play a role in these distinctions such as the pattern of movement (single line x dispersed); the existence or not of a foraging (“feeding on the move”) habit in the species behavioural repertoire; the size and distribution of the food patches; the dispersion pattern of the animals, etc.

#### 4. Maintain contact at a distance

This category comprises calls emitted by individuals separated by intermediate to large distances, with definite absence of visual contact. It includes cases where animals normally separate for variable periods of time (dispersed foraging, fission-fusion) and either keep constant vocal contact or call at some point in an apparent effort to reunite individuals/sub-groups. I also grouped here cases in which an animal gets accidentally separated from others, usually described as “lost” or isolated (something contentious and hard to prove). Obviously there is a continuum between this and the previous functional group. However, longer distances pose problems for the acoustic structure of the sound (localizability, degradation, minimising conspicuousness to predators, etc.) which are either not present or are less critical at shorter ranges. The likely function for this category is again to maintain the cohesiveness of the group or to reunite individuals.

In a few cases, a species’ vocal repertoire is described with no mention of a call subserving a contact function, *sensu* groups 2 to 4 (Chalmers, 1968; Chivers, 1975; Hohmann & Herzog, 1985). Possibly, these studies were not of adequate extent. A species without a contact mechanism is perhaps difficult to imagine, as cases when an animal gets separated must happen in all species. Situations in which it is necessary to maintain contact with others are presumably also universal. Nonetheless, regaining contact may still be achieved through different means.

Table 3.1 – review of studies in which a given call could be described as contact, cohesion, isolation or lost by its explicit labelling, the description of the contexts in which it is emitted and/or the proposed function. Also repertoire studies in which it was noted the lack of such call.

| Species                                      | Call name                                 | Context   | Function   | Group |
|--|---|---|--|-------|
| <sup>a</sup> <i>Indri indri</i>              | Song                                      | Independent ranging or pairs separated by over 100m                 | Cohesive (reaggregation)   | 3-4   |
| <sup>b</sup> <i>Lemur catta</i> <sup>1</sup> | Clicks                                    | Periods of restless locomotion                                      |  | 2     |
| <sup>c</sup> <i>Lemur catta</i>              | Clicks; click-grunt                       | “Fast normal locomotion”  |  | 3     |
|  | Mew, meow                                 | Isolation, excited locomotion                                       |  | 3-4   |
| <sup>d</sup> <i>Lemur catta</i>              | Meow call; cohesion call; cohesion miaouw |   | “Contact function by providing an auditory cue for the location of group members who are dispersed”  | 2-4   |
| <sup>e</sup> <i>Lemur catta</i>              | Moan <sup>2</sup>                         |   | “Group cohesion in low-to-moderate arousal...”   | 3     |
|  | Wail, variant 1                           |   | “Group cohesion; indicates moderate-to-high arousal of caller”   | 2-3   |
|  | Wail, variant 2                           | By “lost” animals, among other contexts                             | “Group cohesion under ... extreme arousal”   | 4     |
|  | Hmm, Huh                                  | “During and just prior to group relocation”                         | “Indicates that slow group relocation is imminent and promotes group cohesion under the same ... reflects a caller’s desire to maintain contact” | 2     |
|  | Chirp                                     |   | Possibly group cohesion in rapid group movement  |       |
| <sup>f</sup> <i>Lemur catta</i>              | Meow call                                 | Loss of contact with fellows  | contact  | 2-3   |
| <sup>b</sup> <i>L. fulvus</i>                | Long-click grunts                         | When a lemur is put alone   |  | 3-4   |
|  | Cough                                     | “...separation from social companions.                              |  | 4     |
|  | Moan and wail                             | Wails replace moans ... as time or degree of separation increases.” |  | 4     |

|  |   |   |     |
|--|---|---|-----|
| <sup>s</sup> <i>L. fulvus</i>                                | 'Mm' call   | Serves as a cohesion signal (refers to another paper)                                     | 2-3 |
|  | Spring call, 'mm' call; low short modulate call; multi-note calls | "These four calls could serve to maintain group contact"                                  | 2-3 |
| <sup>b</sup> <i>Propithecus verreauxi</i>                    | Click grunts  | Excited locomotion  | 2-3 |
| <sup>h</sup> <i>Eooticus elegantulus</i>                     | Tsic  | Reciprocal calling at the end of the night before regrouping and going to sleeping site   | 3-4 |
| <sup>h</sup> <i>Galago alleni</i>                            | Click   | "When an animal is seeking to establish contact"  | 3-4 |
|  | Croaking call   | Establish contact between males and females for meeting; maintain contact between females | 3-4 |
| <sup>b</sup> <i>G. crassicaudatus</i>                        | Loud click  | When seeking contact with absent fellows  | 3-4 |
| <sup>h</sup> <i>G. demidovii</i>                             | Gathering call  | Mainly "before dawn ... when re-assembling"   | 3-4 |
|  | Chips   | "Signalling the respective positions of the animals concerned"                            | 3-4 |
| <sup>i</sup> <i>Callimico goeldii</i>                        | Rhythmical calls  | Isolation   | 4   |
|  | Monosyllabic calls  | Disturbances, but "may serve as contact calls"  | 2-3 |
| <sup>i</sup> <i>Callithrix argentata</i> ; <i>C. jacchus</i> | Faint phee  | "Undisturbed and in close visual contact"   | 2   |
|  | Heterotypical faint high-pitched notes                            | "When huddling together"  | 1   |
|  | Longer phee calls   | "When losing visual contact with each other   | 3   |
|  | Loud phee cries   | Isolated animals  | 4   |
|  | Twitters  | Loose visual contact and isolation  | 3-4 |
| <sup>j</sup> <i>C. argentata</i>                             | Contact calls   | Intra-group cohesion; coordinate group activities; loose contact                          | 2-4 |

|  |  |   |                              |
|--|--|---|------------------------------|
| <sup>i</sup> <i>C. jacchus</i>   | Short whirr; whirr, short broken whirr, broken whirr   | Contact calls ranging from short visual contact to isolation  | 2-4                          |
| <sup>k</sup> <i>C. pygmaea</i>   | Shrill<br>Closed mouth trill   | Isolation<br>Moving through the environment and sometimes when able to see each other   | 4<br>2-3                     |
| <sup>l</sup> <i>Saguinus fuscicollis</i>   | Quiet trill<br>J-call<br>Short calls   | Cohesion or contact over short distances<br>Dispersion/visually isolated<br>General activity; before congregating in groups   | 2-3<br>3-4<br>2-4            |
| <sup>m</sup> <i>S. fuscicollis</i>   | Soft long calls<br>Chee, chip, chee-chip, multiple   | Same contexts but higher arousals<br>Contact calls ranging from short visual contact to isolation   | 2-4                          |
| <sup>i</sup> <i>S. geoffroyi</i> ; <i>S. oedipus</i>   | Shrill<br>Te calls<br>Variations on te<br>Monosyllabic calls given in isolation, trills  | Isolation<br>Undisturbed and in close visual contact<br>Loose visual contact and disturbance<br>Isolation   | 4<br>2<br>3<br>4             |
| <sup>n</sup> <i>S. labiatus</i><br><sup>o</sup> <i>S. mystax</i><br><sup>p</sup> <i>S. oedipus</i><br><sup>i</sup> <i>Leontopithecus rosalia</i> | Contact call<br>Long call<br>Combination long calls<br>Pe calls<br>Whee calls<br>Heterotypical sequences culminated in pü pü pü<br>Titters | Reduced or prevented visual contact<br>Isolated animals, responded by its troop.<br>Socially isolated animals<br>Close visual contact<br>When animals lose visual contact<br>Isolated animals | 3-4<br>4<br>4<br>2<br>2<br>3 |
| <sup>q</sup> <i>L. rosalia</i> <sup>4</sup>  | Whines<br>Contact chatter  | When losing visual contact<br>Contact contexts (approach, touch, huddle, wrestle, grooming, sniffing)<br>Contact contexts (huddle, wrestle, grooming, mount)                                  | 3<br>1<br>1                  |

Contact at larger distances  
“spatially locating an individual ... stray from the group”, and also aids group cohesion

|   |                                  |  |     |
|---|----------------------------------|--|-----|
| <sup>r</sup> <i>Callicebus moloch</i>             | Whistles and trills              | "May be uttered by individuals ... "lost" or isolated"   | 4   |
| <sup>s</sup> <i>C. moloch</i>                     | Chirrup                          | Captive animals when isolated  | 4   |
|   | Chirrup                          | "Contexts in which locating and recognising group members foster group cohesion  | 2-3 |
| <sup>b</sup> <i>Cebus albifrons</i>               | Caw                              | Probably serves as a contact call  | 3-4 |
|   | Racuous squawk                   | Distant contact call   | 4   |
| <sup>t</sup> <i>C. capucinus</i>                  | Arrawh                           | "Exclusively produced by individuals separated by great distances from other group members"  | 3-4 |
| <sup>u</sup> <i>C. capucinus</i>                  | Contact and lost call            | It is not clear if the presence of contact and lost calls is a reality or a hypothesis in this abstract.                                 | 3-4 |
| <sup>v</sup> <i>C. nigrivittatus</i> <sup>3</sup> | Arrawh                           | "Single individual moving about"   | 3-4 |
|   | Huh                              | "Movement ... was blocked or ... the individual acted as if it did not know where to go"   | 2-3 |
| <sup>w</sup> <i>C. nigrivittatus</i>              | Arrawh                           | Isolated animals; animals lagging during group progression or moving in different direction  | 3-4 |
|   | Huh                              | Intermediate distances and many contexts – often within visual contact   | 2-3 |
| <sup>x</sup> <i>C. olivaceus</i>                  | Heh                              | When animals are crowded   | 2   |
|   | Squaws, chirps, trills, whistles | Associated with contact-seeking and maintenance or ambivalent social situations. Foraging/moving contexts associated mainly with chirps. | 1-3 |
| <sup>y</sup> <i>Saimiri oerstedii</i>             | Peeps, call rate                 | Increasing distance; guiding group travel  | 3-4 |
|   | Isolation peep                   | Lost of visual contact/large separation from the group   | 4   |
| <sup>z</sup> <i>S. sciureus</i>                   |                                  | "Seeking" function   | 2-3 |

|   |  |  |              |
|---|--|--|--------------|
|   | Peep   | “...Associated with contact and attention”   | 2-3          |
|   | Chirp  |  |              |
| <sup>aa</sup> <i>Alouatta palliata</i>  | Deep metallic cluck  | “Contact call for short to medium distances”<br>“Initiates progression, controls its direction and rate and coordinates the animals of the clan”<br>“Maintain auditory contact between the individuals of the clan”  | 2-3          |
| <sup>bb</sup> <i>A. palliata</i>  | Notes similar to clucking  |  |              |
| <sup>cc</sup> <i>A. palliata</i>  | Whimper<br>Wrah-ha calls   | Troop progression<br>Mothers of dependent infants when separated from the troop  | 2-3<br>4     |
| <sup>dd</sup> <i>A. palliata</i><br><sup>ee</sup> <i>Ateles geoffroyi</i>   | Broad band contact call<br>Whinny  | Group movements and sexual activity<br>In some circumstances elicit vocal response and/or approach from distant individuals  | 2-3?<br>3-4? |
| <sup>ff</sup> <i>Brachyteles arachnoides</i>  | Staccatos and neighs with large proportion of short elements<br>Neighs with more long elements | Short-range vocal exchanges<br>Long-range vocal exchanges  | 2-3<br>4     |
| <sup>gg</sup> <i>Cercocebus torquatus</i><br><sup>hh</sup> <i>Cercopithecus diana</i><br><sup>ii</sup> <i>C. wolffi</i> | Twitter<br>Clear calls   | Special type of twitter produced when split into sub-groups to forage  | 2-3          |
|   | Contact calls<br>Moving calls  | Avoid predation “in a mutualistic system of co-ordinated vigilance”<br>“Play a role in group cohesion”   | 2            |
| <sup>jj</sup> <i>Macaca fascicularis</i>  | Wraagh<br>LLM coos   | Frequently when moving or foraging for insects<br>Between subgroups when foraging for insects<br>Particularly by isolated animals  | 3-4<br>4     |
|   | HLM coos   | “Re-establishing social/spatial relations that have been severed”<br>“Mediate varying spatial relations with conspecifics which are not close but whose general whereabouts are more or less known”<br>“Routine maintenance of spatial relationships among adults” | 3<br>2-3     |

|  |                             |   |      |
|--|-----------------------------|---|------|
| <sup>kk</sup> <i>M. fuscata</i>                            | Contact call                | Before grooming contacts  | 1    |
| <sup>ll</sup> <i>M. mulatta</i>                            | Contact call                |   | 3-4  |
| <sup>mm</sup> <i>M. silenus</i>                            | Loud call                   |   | 4    |
| <sup>nn</sup> <i>M. sinica</i>                             | Hum and grunt contact calls | Emitted on a variety of situations always in close visual contact                   | 2    |
|  | Food calls                  | Discovery of an abundant food source  | 3-4  |
|  | Lost calls                  | Some degree of auditory and visual separation                                       | 3-4  |
| <sup>oo</sup> <i>P. cynocephalus</i>                       | Contact barks               | Emitted by separated/dispersed individuals  | 3-4  |
| <sup>ur</sup> <i>Papio papio</i>                           | Barks                       |   | 3-4  |
| <sup>qq</sup> <i>Theropithecus gelada</i>                  | Contact call                | “...Before or during socio-positive social interactions”                            | 1    |
| <sup>rr</sup> <i>Cercocebus albigena</i>                   |                             | No sound that could have a contact function was mentioned in this repertoire paper. |      |
| <sup>ss</sup> <i>Cercocebus albigena</i>                   | Whoopgobbles                |   | 3-4? |
| <sup>tt</sup> <i>Cercopithecus nictitans and C. cephus</i> | Type 2 cohesion call        | “Anticipates and accompanies troop movements”;                                      | 3    |
|  | Lost call                   | “Among individuals who most often are not in view of another”                       | 4    |
| <sup>uu</sup> <i>Colobus guereza</i>                       |                             | No adult sounds mentioned in connection with contact.                               |      |
| <sup>vv</sup> <i>Hylobates klossii</i>                     | Whistles                    | Foraging and travelling   | 2-3  |
| <sup>ww</sup> <i>H. lar</i>                                | Contact calls               |   | 4    |
| <sup>xx</sup> <i>Symphalangus syndactylus</i>              |                             | No contact sound mentioned. Paucity of repertoire emphasised.                       |      |

|                                       |  |  |   |                    |
|---------------------------------------|--|--|---|--------------------|
| <sup>yy</sup> <i>Gorilla gorilla</i>  | Close calls  | “Commonly given in situations of potential separation”                         | “Facilitate cohesion of the group...” among other proposed functions  | 2-3                |
| <sup>zz</sup> <i>Pan paniscus</i>     | Peeps<br>Soft mixed series   |  | Contact during slow progression<br>maintain contact when they lose visual<br>Contact when feeding on the ground | 2<br>3             |
| <sup>aaa</sup> <i>Pan paniscus</i>    | Hooting (uuuuwa, uwa)<br>Hooting (uwáou)<br>Bark (hjáú, pjáu)<br>Pant-hoot | “Contact calls in the distance”<br>“Lost call”<br>“Contact calls within sight” |   | 3-4<br>4<br>2<br>3 |
| <sup>bbb</sup> <i>Pan troglodytes</i> |  |  | Maintain contact with specific individuals and recruit them   | 3                  |

<sup>a</sup>Pollock (1986); <sup>b</sup>Andrew (1963); <sup>c</sup>Jolly (1966); <sup>d</sup>Macedonia (1986); <sup>e</sup>Macedonia (1993); <sup>f</sup>Oda (1996; 1999); <sup>g</sup>Paillette and Petter (1978);

<sup>h</sup>Charles-Dominique (1977); <sup>i</sup>Epple (1968) for *C. jacchus* see also Pook (1977), Schrader & Todt (1993), Norcross and Newmann (1997; 1999), Norcross et al. (1999); <sup>j</sup>Veracini (2002); <sup>k</sup>Pola & Snowdon (1975), Snowdon & Pola (1978), Snowdon & Cleveland (1980), Snowdon & Hodun (1981); <sup>l</sup>Moody & Menzel (1976); <sup>m</sup>Pook (1977); <sup>n</sup>Stevens & Caine (1986); <sup>o</sup>Snowdon & Hodun (1985); <sup>p</sup>Cleveland and Snowdon (1982); <sup>q</sup>McLanahan & Green (1977); <sup>r</sup>Moynihan (1966); <sup>s</sup>Robinson (1979); <sup>t</sup>Boinski (1993); <sup>u</sup>Digweed & Fedigan (2003); <sup>v</sup>Oppenheimer & Oppenheimer (1973); <sup>w</sup>Robinson (1982); <sup>x</sup>Robinson (1984); <sup>y</sup>Boinski (1991); <sup>z</sup>Winter et al. (1966), see also Masataka & Symmes (1986); <sup>aa</sup>Carpenter (1934); <sup>bb</sup>Collias & Southwick (1952); <sup>cc</sup>Baldwin and Baldwin (1976); <sup>dd</sup>Jones (1998); <sup>ee</sup>Teixidor & Byrne (1999); <sup>ff</sup>Mendes & Ades (2004); <sup>gg</sup>Range & Fischer (2004); <sup>hh</sup>Uster and Zuberbühler (2001); <sup>ii</sup>Mulavva (1990); <sup>jj</sup>Palombit (1992a,b); <sup>kk</sup>Sugiura (1993), Masataka (1989); <sup>ll</sup>Rendall et al. (1996); <sup>mm</sup>Herzog & Hohmann (1984); <sup>nn</sup>Dittus (1988); <sup>oo</sup>Cheney et al. (1996); <sup>pp</sup>Byrne (1981); <sup>qq</sup>Aich et al. (1987); <sup>rr</sup>Chalmers (1968); <sup>ss</sup>Waser (1976); <sup>tt</sup>Gautier & Gautier-Hion (1988); <sup>uu</sup>Marler (1972); <sup>vv</sup>Tenaza (1976); <sup>ww</sup>Raemaekers and Raemaekers (1985); <sup>xx</sup>Chivers (1975); <sup>yy</sup>Harcourt et al. (1993); <sup>zz</sup>Bermejo & Omedes (1999); <sup>aaa</sup>Okayasu (1990); <sup>bbb</sup>Mitani and Nishida (1993)

<sup>1</sup> In bold captivity/experimental studies and in plain font naturalistic ones. If the species was studied by the same author/group both in captivity and in the wild, with similar findings, the font was left plain.

<sup>2</sup> based on cross-referencing, this call is synonym with the ones above.

<sup>3</sup> *C. nigrivittatus* is a synonym for *C. olivaceus* not in use anymore.

<sup>4</sup> In this study of *L. rosalia*, they provide also a synonymy with Andrew (1963) and Epple (1968), but their whole approach makes somewhat difficult the categorisation as done in other studies.

In some of the examples above, the same call was included in more than one category, which can have three possible explanations. Firstly there might be undetected acoustic distinction and the author lumped different call types or sub-types. A second possibility is that information about the distances or visual contact is not precise or wrong, and I misclassified a given call. Lastly, a given vocalisation could genuinely perform both functions, since the categories described here are somewhat arbitrary, as outlined above.

Looking at the functions above, it is possible to see that labelling a call as a contact one clearly depends on what the author means by contact, if physical contact (category 1) or a connection between individuals (categories 2-4). The most common usage has been the last one, while calls emitted in the situations described for category 1 have usually been labelled differently. Furthermore, it is not clear if the examples included within category 2 are calls related to establishing/maintaining connection between individuals, or if they possess an alternative function, given that visual contact is clear and unambiguous. So, to avoid unnecessary confusion, I suggest that the label 'contact' should be restricted to calls belonging to the categories 3 and 4 above, and those are the functions that I considered in this study.

Pervading the discussion on the possible functions of contact calls is the underlying idea of a more ultimate function of maintaining the cohesiveness of the group or a more proximate one of establishing/maintaining connection between individuals. From the point of view of the emitter, it is probably true that a contact call reflects its state of separation from the group, and thus its "desire" to reunite. It has been argued that when there seems to be a system of vocal exchange in place, the supposed responses are actually a consequence of the state of separation of the respondent, not an answer to the first caller (Cheney & Seyfarth, 1999; Cheney et al., 1996; Rendall et al., 2000; Seyfarth & Cheney, 2003). That is, the calls are not emitted with the intent of maintaining contact or informing the whereabouts of the group to the separated animal(s). This would imply intentionality and an understanding of another animal's state or, in other words, theory of mind, something not shown in monkeys so far. However, (Byrne, 2000) argues that even without comprehension of mental states contact calling may still involve intentionality, but of first-order. In this case "...both signallers and hearers *want* to reunite... and *know* that they should call in order to do so swiftly. It is not necessary that they be able to understand what others know...contact calling may be a goal-directed tactic, learned or even perhaps hard-wired, employed flexibly and selectively, but without insight into its mechanism" (Byrne, 2000, p. 507). Even among the original critics of the intentionality idea the position is sometimes softer (Rendall et al., 2000), through the recognition that other mechanisms could produce vocal exchanges or that

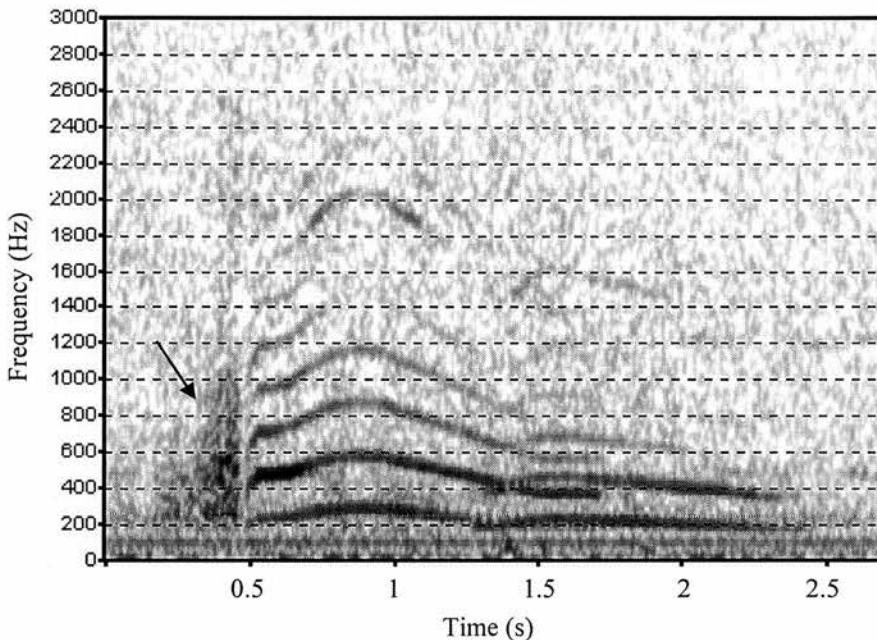
there might be some degree of perception of the other's perspective, although the topic is not developed more than this vague proposal.

Uster and Zuberbühler (2001) argue for a different ultimate function of Diana monkeys' clear calls. The authors suggest that these calls, while being useful to maintain proximity and contact to other group members, ultimately work as a mechanism to avoid predation. The idea is that, through these calls, individuals share information on the "watchfulness and location of other out-of-sight group members". One should note however that: (1) the predation avoidance function would be in addition to or at another level with respect to the 'maintaining cohesiveness function', and not in conflict with it; and (2) Once again, as so often in the literature involving contact, the problem might be more a semantic one than an actual incompatibility. In other words, if the ultimate function of the call is to avoid or decrease predation risk, labelling the call as 'contact call' or with another name is more a matter of taste. Nonetheless, this paper is interesting in pointing that a given call that might be perceived as merely functioning to maintain contact between out-of-sight group members might actually have further functions.

To date there are very few studies in which small amplitude vocalisations of howler monkeys have been described, and evidence for a contact call is scant. Jones (1998) briefly analyses a so-called "broad band contact call" of female mantled howler monkeys (*Alouatta palliata*), said to be emitted more during group movements, but also during sexual activity. She suggests that the call is associated with food in both contexts, but may also incite male-male competition, a somewhat broad and not well characterised proposal. In the only extensive repertoire analysis of a howler species published to date (Baldwin & Baldwin, 1976), no unambiguous and specific adult contact call is described. Thus, individuals of *A. palliata* emitted *whimpers* on a variety of situations, including troop progressions; infants produced *caws* when they were lost from their mothers, but also in other situations; and mothers of dependent infants produced *wrah-ha* calls when separated from the troop. Finally, in a very brief report on *A. caraya* calls, the authors mention a vocalisation (*cry*) emitted in stressful situations, and cite as an example circumstances in which the caller was away from the group (Calegario-Marques & Bicca-Marques, 1995). From the

written description it is not possible to compare the sounds with those recorded in my study.

In this chapter, I report a study made on a small amplitude vocalisation of black howler monkeys, onomatopoeically labelled *moo* call. These are relatively long vocalisations (around 1s), tonal, with a low fundamental, presenting just a few clear overtones, and in general with a typical convex frequency modulation but spanning a small frequency range (see Figure 3.1). A broad noisy segment precedes some emissions, especially from infants. Fundamental frequency varies among individuals between 100 and 200 Hz. Frequency modulation can take other forms or even be absent, but the one depicted is the most common.



**Figure 3.1 Spectrogram of two overlapping *moo* calls. Gaussian window. Time window: 0.04s. Bandwidth = 32.5 Hz. Note the noisy component of the first call (arrow)**

According to my preliminary results (pilot data revealed an association of *moos* with travelling) and anecdotal observations (impression of emission during situations of large group spread and when others were out of sight of the caller; emissions under bad weather conditions; an apparent response system in place), the *moo* call seemed to have a contact or lost function. This vocalisation also seemed to be related to anxiety or stressful situations, but only for infants (see also chapter on Screech Complex calls). The anecdotal data that lead to this

hypothesis were the apparent association to circumstances which could be interpreted as stressful (e.g. when an infant was having difficulties in crossing a wide gap, when it was taken from the back of a carrier, when access to the nipple was refused, when the mother left the infant alone, among others). Here I describe attempts to carry these observations a step further by collecting data that would substantiate those impressions and provide the basis for more detailed studies.

## 3.2 Methods

### 3.2.1 Data analysis

Apart from the general analytical approaches described in the previous chapter, I also used group diameter data to explore the possible contact function for this call. The first step was to compare the distribution of values of group diameter registered focally during emission of *moos* (either single calls or volleys)<sup>1</sup> with the baseline distribution of such values (registered with instantaneous samples at every 30 min.). The prediction to be examined is that, if *moos* possess some contact related function, then they should be associated with group diameters larger than usual. The reason is that larger group spreads are situations in which maintaining contact is presumably more necessary or in which it is more likely for animals to get separated from the group or to be, in fact, already isolated.

However, the proposed relationship between a possible contact call and larger group spreads is not necessarily a simple one. Even if a given call is not emitted in situations of larger group spread, the call could still function to maintain contact. For example, they could be emitted during fast travel through a low visibility habitat, when the group diameter is maintained within normal values, but the animals must maintain contact to avoid losing track of others. On the other hand, a given call can be emitted in situations in which the group is quite spread and yet not have a contact function, but one related to situations of larger group spread for some other reason. As an example, we can imagine a call with some strictly foraging function on a species in which the group members forage quite separated. So, larger values of group diameter are neither necessary nor sufficient to define a given call as having a contact function. The relationship is better defined as: if a given call is associated with a group spread larger than the baseline values, then it could present a contact function, depending on other sources of supporting evidence.

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<sup>1</sup> As it was a common occurrence not to have the data on group diameter collected focally during emission of *moos* due to the taxing observation scheme that was conducted, I devised a way of obtaining additional data points from the data files. I retrieved baseline values of diameter that happened to fall less than 3 minutes before or after a given *moo*, and added this data to the focally collected sample.

If this result is found, then one can make the following prediction: if the call has a contact function, then after the emission of a call (or a bout), the values of group diameter should return to the average values. To test this prediction, I needed a sample of group diameter values taken after call emissions. To obtain this sample, I retrieved from the baseline data set the first data point after each vocal emission (or the last one in a volley), given the diameter data point was more than 5 minutes and less than 45 minutes after the call. I then compared the distribution of those values to the remaining baseline sample.

A similar prediction is: if the call has a contact function, it is likely that after the emission of a call one will observe significantly more reductions than increases in group diameter. To test this prediction, I simply compared the diameter values **after** the call (retrieved as above) to the values during the emissions, and noted if there was an increase, a decrease or no change. If nothing was influencing the grouping pattern, one would expect to observe the same number of increases and decreases.

For the analysis of diameter data, besides the independence problem referring to the call emissions (calls emitted within a bout and thus non-independent with respect to the immediate context or motivation), I had to consider also the independence of the group diameter values themselves. Two calls emitted independently and separated by more than two minutes (or even produced by different individuals) could refer to the same value of group diameter and the same spread situation. So, I decided to consider a focal observation of group diameter during a *moo* emission to be an independent data point only if no call had occurred in the previous ten minutes. Calls separated by intervals smaller than ten minutes were grouped for analysis. This criterion is more conservative than the one used to group the calls in bouts, in a further attempt to guarantee contextual independence.

To study the possible relation of the *moo* call to anxiety in infants, I made two predictions. If the call is associated with high anxiety levels, then infants should (1) call more before than after the cessation of a potentially stressful situation, and also (2) call more *after* a stressful event than before it.

To test the first prediction, I chose to study the events ‘gap crossing’, and ‘riding’. With respect to the first one, the rationale is that, for infants, gaps too wide to be easily crossed are likely to represent a stressful situation because of

the separation from the mother or the group. During the whole course of the study, I noticed that infants were very reluctant to cross gaps between trees, especially during the first weeks of independent travelling, calling intensively in these situations (not only *moos*, see also Chapter 4). Since it was not always possible to discern exactly when an animal came across a gap (the stressful event), particularly a non-focal one, I analysed the cessation of the condition. The data included both *ad libitum* notes stating that a youngster had crossed a wide gap, by whichever means employed (e.g. using another as a bridge, riding the back of another animal, jumping) or had either given up or taken a detour. I also used the regularly collected behavioural category 'bridge' (an animal uses the body of another as a bridge between terminal branches), which by necessity meant that a large gap was crossed. This is obviously a far from exhaustive sample and it might not be unbiased, as infant calling usually drove my attention to the *ad libitum* cases (silent crossings could only be observed in focal samples). However, as my primary interest is in the calls themselves, the sample do allow testing the prediction above, which concerns relative rates of calling before and after the termination of the stressful condition.

Concerning the event 'riding' (travelling on the back of another individual), the point in time when an infant rides the back of a carrier was imagined to represent, in some cases, the termination of a stressful situation. For example, when infants are in the stage when they are already leaving the body of the mother to play and explore, but are not capable of independent travelling yet, they might fear being left behind (e.g. if the mother starts moving). Or when the carriers are refusing to allow riding or actively taking the infant out of the back, the infants can be under distress to cope with their developing motor abilities, which terminates if the carrier allows riding back. Again, it is much easier studying these contexts from the point of the cessation of the stress.

I studied two other events from the point of the start of the supposed stress, 'conflicts' and 'be left'. The first one includes the following events (all regularly collected): carrier removing the infant from its back or preventing access to it; mother preventing other infants from interacting with a newborn; and mock or real bites. All these events represent a conflict of interest between the infant or juvenile and another animal. I considered as conflicts of interest both cases when an animal is prevented from continuing to perform an action,

and when it is prevented from obtaining access to something it apparently wants, either manually or by a bite. My justification for lumping the events is that they have the common feature of frustration, caused by an action of another animal (as opposed to a feature of the environment, like in the gap problem). I restricted the analysis of the event ‘be left’ (described in the Methods chapter) to the cases where the mother left the infant.

To compare call occurrence before and after selected events, I first excluded those instances with equal numbers of calls before and after the event, including the cases with no calls at all. For the remaining occurrences, I computed the number of cases when the animal called more before the target event than after (‘call before’) and the reverse (‘call after’). Depending on the event being analysed, I considered 5, 2 or 1-minute periods bordering the event for these calculations. Another procedure was to construct graphs of likelihood of calling in consecutive time bins of equal length both before and after the event, to check the profile of the calling behaviour surrounding the event of interest. For example, the instance depicted in Figure 3.2 below would be classified as ‘call before’ for a 5-minute analysis period, given that there were eight *moo* emissions before the target event within this time period, against only three *moos* in the 5-minute period following the event. On the other hand, for an analysis period of one minute, this example would be classified as a ‘call after’ since the individual produced two calls in the minute following the analysis event, against a single emission in the same period preceding it. To compute the graphs of likelihood of calling in successive time bins with respect to the target event, periods containing calls would contribute a “yes” to the probability of calling within a given time period with respect to the target event, while periods with no calls would contribute a no. In the example below, period 1 contributes a “yes” for the time period running from 5 to 4 minutes before the target event.

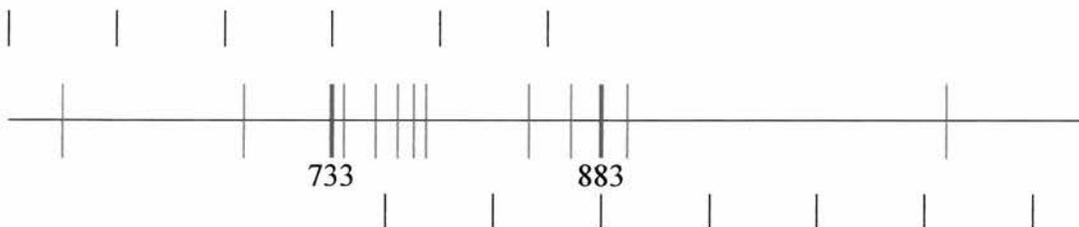


**Figure 3.2. Hypothetical example of a part of an Observer data file. The blue line represents the occurrence of the behaviour being analysed (gap crossing for example). The red lines are emissions of *moos* by the infant/juvenile involved in the target event. The grey lines separate 1-minute periods with respect to the target event.**

However, when computing the data to analyse the relation between calls and the selected events (gap crossing, riding, conflicts, and be left), one has to take into account the problem of multiple occurrences of the target event close in time to each other. Thus, calls occurring between two instances of the event being analysed could be classified both as calls after the first event and calls before the second event. These situations might interfere with the statistical analyses, as a given emission could appear in two different categories. Thus, suppose I am testing the prediction that the animals should call more after a stressful event, and they do so in reality. Then, occurrences of the analysis event close in time to each other could lead to a weakening of the significance: calls caused by the first instance of a pair of successive target events could be erroneously counted as emissions before the succeeding event. On the other hand, suppose that when testing the same prediction (animals should call more after a stressful event), that the animals actually do the opposite (they call more before the target event). In this case, calls emitted before an event could be erroneously counted as emissions after the preceding event of two closely related occurrences. As it is impossible to know which event a call relates to, I adopted some pragmatic criteria when I was retrieving the data from Observer files. The criteria varied according to the analysis being carried out, as detailed below.

1. For the events 'gap crossing', 'conflict', and 'be left', in order to compare call occurrence before/after an event, I included only those events that were separated by more than double the time period being used in a given analysis. Thus, for example, if I was using 1-minute analysis periods, only those events separated by more than 2 minutes would be included. In the example depicted in Figure 3.3, the two instances would be discarded for an analysis of periods of 5 minutes, but would be considered when using 1-minute analysis periods. This procedure ensured that the same call would never be included in two different categories (before and after) at the same time. However, it still does not ensure undue placement on a category, it just guarantees that, for the analysis period being used, a given call is not counted twice in different categories. Thus, for the events which are considered as the start point of the stress ('conflict' and 'be left'), if they have any influence on call emission, and if this influence persists longer than the time period being

considered, this is a conservative procedure, going against my hypothesis. The reason is that I can still end up incorporating some calls before a given event that were actually due to the preceding one. For ‘gap crossing’ the same argument applies, but in an inverted way, as this was studied from the cessation of the stressful condition. As an additional criterion, when the target events were separated by 5 s or less, I used the number of calls before the first event against the number of calls after the second, as if they formed a single occurrence. For the event ‘riding’, when a file contained multiple occurrences I applied a more pragmatic criterion. Given the excessive number of multiple occurrences involved, I decided to use only the first occurrence of an event on a given Observer data file, and discard the others. Similarly to what was argued above, this criterion is a conservative one. As ‘riding’ is considered the termination of a potentially stressful situation, the animals were predicted to call more before the event. Therefore, by using the first occurrence of a file, I risk incorporating calls after the event that were actually caused by a subsequent stress, which would be solved by the next riding event.



**Figure 3.3 Hypothetical example of a part of an Observer data file. The blue lines represent two occurrences of the target behaviour being analysed separated by 150s (number below the emissions indicate their respective time tags). The red lines are emissions of moos by the infant/juvenile involved in the target event. Black lines at the top separate 1-minute periods with respect to the first occurrence of the target event, and black lines at the bottom separate 1-minute periods with respect to the second occurrence of the target event.**

2. For building up graphs of likelihood of calling in consecutive time bins surrounding the event, I used a different set of criteria. If the events were separated by less than 10 seconds, I considered the calls of the second event only, and discarded the data from the first. For events separated by more than 10 s but less than the maximum time period used in the graphs, I considered

the calls of each event only until the occurrence of the next/previous one. In other words, for the first event of a pair, I never used the calls after the second, and for the second I never used the calls before the previous one. Then, only calls appearing between the events would be counted twice, and in this case, a given duplicated call will be a “call after” for the first event and a “call before” for the second event, thus falling in completely different regions of the graph. At the example depicted above (Figure 3.3), the calls occurring between the two blue lines would be considered as calls after the first event and as calls before the second event. Thus, the first instance of the target event would have calls on the first and second minute after the event, and the succeeding periods were discarded (incomplete periods and calls occurring after the succeeding target event were eliminated). The second instance of the target event would have calls on the first and second minute preceding the event, the preceding periods were discarded. For the analysis of stressful events, the possibility of subsequent occurrences of the event re-elevating a waning call rate is ruled out, as calls occurring after subsequent target events are never counted as calls after the preceding event. This criterion in general works against my hypotheses, as calls occurring after stressful events will end up falling before the subsequent ones, the opposite occurring with the analysis of “cessation” events.

### *3.2.2 Statistical analysis*

To verify if individuals had similar call rates, I used a goodness-of-fit chi-square test. To compare call rate between states, I first tested the data for normality and homoscedasticity (individual call rates were the data points). If the data were not normal, I attempted a transformation. For normal data (transformed or not), I compared the states with one-way ANOVAs, with the states being the different treatments and the individuals comprising the data points. For normal and heteroscedastic data, I used Welch Robust test of equality of means, which is preferable to the F-statistic when the data fail to meet the assumption of homogeneity of variance (SPSS 11.0 electronic manual). Post-hoc tests employed were Tukey’s Honest Significant Difference (HSD) after one-way ANOVAs and Tamhane’s test after Welch Robust test.

I also employed goodness-of-fit chi-square test to compare distributions of observed and expected group diameter values.

For all the analyses of relations between calling and selected events, I tested the number of cases with more calls before the event: with more calls after against a 1:1 hypothesis with a binomial test.

Power analysis was conducted whenever possible, given the limitations and the available options of software G-power.

### 3.3 Results

#### 3.3.1 Call rate according to state: analysis by individual calls

During the data collection periods in the main study, I registered a total of 11438 *moos*. Overall call rate was 8.47 calls/hour of observation or 0.7 calls/hour/animal (last value calculated using the sum of hours that each individual was present with the group). However, only 6075 calls could be assigned to a given individual (overall call rate of 4.5 calls/hour of observation or 0.38 calls/hour/animal). Infants were noted to produce calls at a much higher rate than older individuals (Table 3.2), despite the fact that they are more difficult to identify, and thus to be assigned to a given call when the emitter is not the focal. There was indeed a highly significant difference between the animals ( $\chi^2 = 18625$ ,  $p \ll 0.001$ ,  $df = 12$ , power approaches 1 for a medium difference to be detected, see Figure 3.4). Although the test does not indicate exactly who differs from whom, individuals 10 (Inf./Juv. ♀), 11 (Inf./Juv. ♀), 12 (Inf./Juv. ♂) and 13 (Inf. ♀) contributed more to the chi-square value, presenting rates much larger than expected. All other animals had call rates much smaller than expected and contributed more or less equally to the value of the statistic.

Considering all data periods together, that is, calls produced by an animal not only during its focal periods, but also in other animals' data periods, is a more reliable sample in terms of size. However, in reality this procedure underestimates the calling rate of each animal (note that nearly half of the calls were unaccounted for). Considering only the focal periods of each animal, the rates are considerably higher and the ranking (order of more frequent to less frequent callers) alters slightly (Table 3.2). Nevertheless, infants remain by far the most frequent callers, and the animals still differ significantly in their call rates ( $\chi^2 = 2782.6$ ,  $p \ll 0.001$ ,  $df = 12$ , power approaches 1 for a medium difference to be detected), with individuals 10, 11, 12 and 13 contributing the most to the value of the statistic.

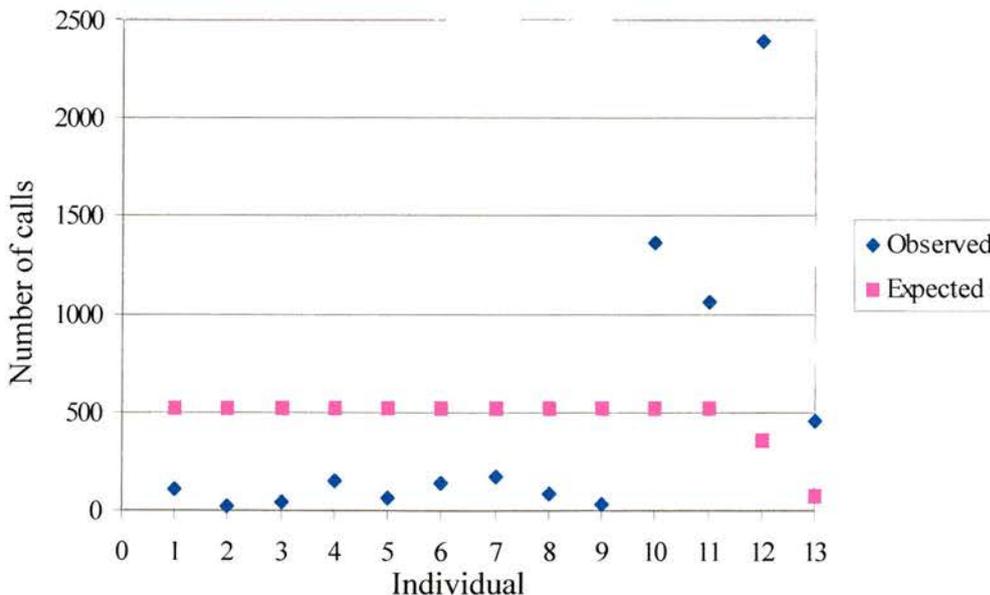
**Table 3.2 Frequency of moos and call rate per individual considering both the whole data set and only the focal periods.**

| Individual        | n (total) <sup>a</sup> | Call rate <sup>b</sup> | n (focal hours) | Call rate (focal hours) <sup>c</sup> |
|-------------------|------------------------|------------------------|-----------------|--------------------------------------|
| 1 (Ad. ♂)         | 104                    | 0.077                  | 51              | 0.461                                |
| 2 (Ad. ♂)         | 24                     | 0.018                  | 12              | 0.111                                |
| 3 (Sub-ad. ♂)     | 42                     | 0.031                  | 8               | 0.078                                |
| 4 (Sub-ad. ♂)     | 156                    | 0.115                  | 58              | 0.557                                |
| 5 (Ad. ♀)         | 61                     | 0.045                  | 10              | 0.096                                |
| 6 (Ad. ♀)         | 144                    | 0.107                  | 31              | 0.286                                |
| 7 (Juv. ♀)        | 177                    | 0.131                  | 36              | 0.390                                |
| 8 (Juv. ♀)        | 82                     | 0.061                  | 18              | 0.187                                |
| 9 (Sub-ad./Ad. ♀) | 28                     | 0.021                  | 13              | 0.131                                |
| 10 (Inf./Juv. ♀)  | 1367                   | 1.012                  | 309             | 3.407                                |
| 11 (Inf./Juv. ♀)  | 1063                   | 0.787                  | 283             | 2.928                                |
| 12 (Inf./Juv. ♂)  | 2395                   | 2.537                  | 355             | 5.754                                |
| 13 (Inf. ♀)       | 450                    | 2.310                  | 22              | 2.540                                |
| Unidentified      | 5371                   | 3.975                  |                 |                                      |
| Total             | 11464                  | 8.485                  |                 |                                      |

<sup>a</sup> n refer to the number of calls either considering all focal periods (total) or only those when the individual was the focal animal (focal)

<sup>b</sup> Call rate at this column was calculated as the total number of calls assigned to each individual (irrespective if they were emitted during focal or non-focal periods) divided by the total number of data collection hours (from all animals together).

<sup>c</sup> Call rate at this column was calculated considering only those calls emitted by a given animal during its focal data collection. This was then divided by the data collecting time of the individual concerned only (excluding periods of no visibility).

**Figure 3.4 Observed and expected values of number of calls per individual (considering all focal periods together).**

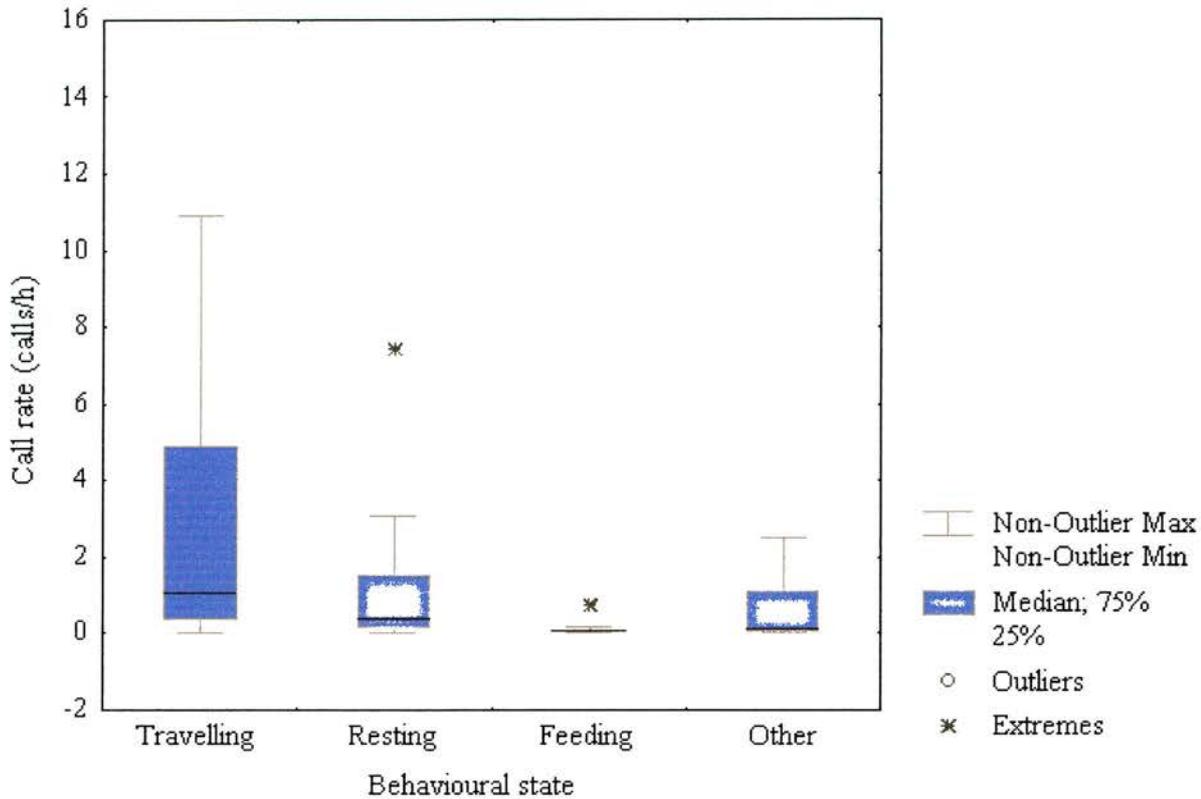
Comparing the call rates according to different activity states shows that travelling almost invariably possesses the highest rates, feeding the lowest, with resting lying intermediate (see Table 3.3 and Figure 3.5). However, these observations should be seen with caution, as I am splitting already small focal samples into four behavioural states.

The call rates on each of the four states did not distribute normally and variances were not homogeneous. Log-transforming the data restored normality for almost all groups: Shapiro-Wilk test statistics and significance values for travelling, feeding, resting and others are respectively 0.940 ( $p = 0.523$ ,  $df = 11$ ), 0.981 ( $p = 0.970$ ,  $df = 11$ ), 0.787 ( $p = 0.021$ ,  $df = 8$ ), and 0.858 ( $p = 0.181$ ,  $df = 6$ ). Homoscedasticity is also accrued: Levene's test  $F_{3,32} = 0.806$  ( $p = 0.5$ ). Comparing the transformed variable between states, demonstrates that there is indeed a difference (One-way ANOVA  $F_{3,32} = 6.365$ ,  $p < 0.01$ ). Given the smallness of the sample size, power for this analysis is quite low (power = 0.1919 for a medium effect to be detected). However, the constancy of the trends among the animals lends some support for the result. Post-hoc comparisons showed that feeding differed from all other states, with no other significant differences (Tukey's HSD travelling X feeding,  $p < 0.01$ ; resting X feeding,  $p < 0.05$ ; other X feeding,  $p < 0.05$ ; all other comparisons,  $p > 0.5$ ). Thus, animals called significantly less during feeding than in other behavioural activities. The seemingly higher call rate during travelling observed in the table is not confirmed, although the smallness of sample sizes may play a role. In the context of these results, it is relevant that the monkeys usually fed while in a compact group organisation (Figure 3.6).

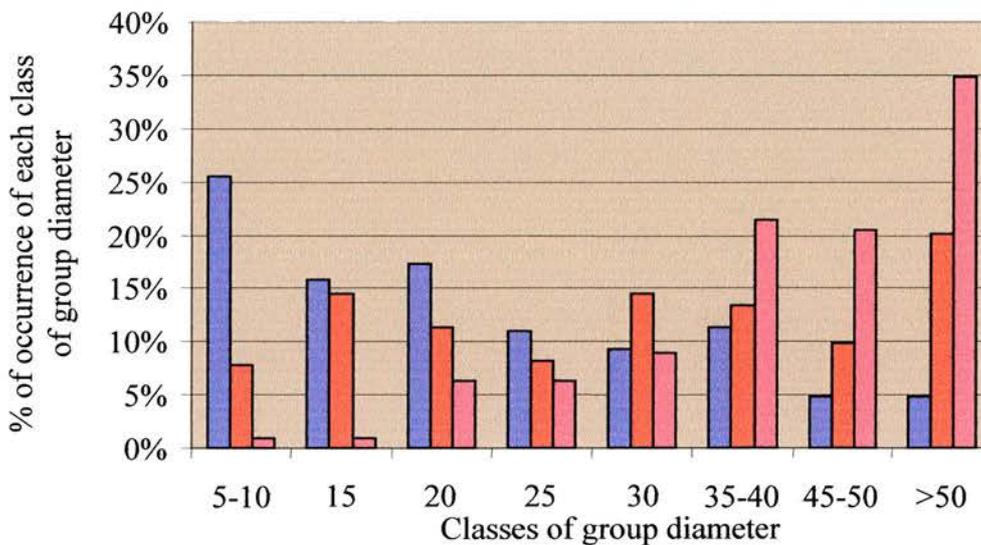
**Table 3.3 Number of moo emissions and call rates (moos/hour) according to the state of the caller**

| Individual        | Travelling  | Resting    | Feeding   | Other     |
|-------------------|-------------|------------|-----------|-----------|
| 1 (Ad. ♂)         | 6 (0.81)*   | 44 (0.50)  | 1 (0.09)  | 0 (0.00)  |
| 2 (Ad. ♂)         | 0 (0.00)    | 12 (0.15)  | 0 (0.00)  | 0 (0.00)  |
| 3 (Sub-ad. ♂)     | 1 (0.12)    | 7 (0.11)   | 0 (0.00)  | 0 (0.00)  |
| 4 (Sub-ad. ♂)     | 10 (1.30)   | 43 (0.62)  | 1 (0.05)  | 4 (0.52)  |
| 5 (Ad. ♀)         | 4 (0.41)    | 4 (0.06)   | 1 (0.06)  | 1 (0.20)  |
| 6 (Ad. ♀)         | 5 (0.48)    | 26 (0.33)  | 0 (0.00)  | 0 (0.00)  |
| 7 (Juv. ♀)        | 11 (1.32)   | 24 (0.43)  | 1 (0.05)  | 0 (0.00)  |
| 8 (Juv. ♀)        | 15 (1.68)   | 0 (0.00)   | 1 (0.04)  | 2 (0.26)  |
| 9 (Sub-ad./Ad. ♀) | 2 (0.25)    | 11 (0.17)  | 0 (0.00)  | 0 (0.00)  |
| 10 (Inf./Juv. ♀)  | 147 (13.76) | 125 (2.41) | 13 (0.71) | 24 (2.48) |
| 11 (Inf./Juv. ♀)  | 89 (8.15)   | 172 (3.05) | 1 (0.06)  | 21 (1.71) |
| 12 (Inf./Juv. ♂)  | 87 (10.92)  | 224 (7.42) | 1 (0.18)  | 43 (2.37) |
| 13 (Inf. ♀)       | 0 (0.00)    | 9 (1.38)   | 0 (0.00)  | 13 (7.56) |

\* Call rates (values within brackets) calculated dividing the number of calls emitted by a given animal (during its focal hours) when on a given behavioural context by the number of hours that the individual concerned performed the behaviour.



**Figure 3.5** Boxplot of call rates (non transformed data) according to the state of the caller.



**Figure 3.6.** Percentage of occurrence of each class of group diameter during: ■ resting; ■ feeding; ■ travelling.

However, stressful situations for infants (analysed below) usually occurred while resting, and they were normally accompanied by calling. As these situations can not be considered resting per se, this could artificially inflate rates

during resting and prevent the detection of differences with respect to travelling. Thus, I repeated the analysis but excluded the smaller infants, which possessed the bulk of stress-related calls. It was not necessary to transform the data, as excluding the infants restored normality for almost all behavioural states, although homoscedasticity was not accrued. Shapiro-Wilk test statistics and significance values for travelling, feeding, resting and others are respectively 0.917 ( $p = 0.366$ ,  $df = 9$ ), 0.932 ( $p = 0.501$ ,  $df = 9$ ), 0.847 ( $p = 0.069$ ,  $df = 9$ ) and 0.682 ( $p < 0.001$ ,  $df = 9$ ); Levene's test  $F = 16.728$  ( $p < 0.001$ ). There was still a difference between the states (Welch robust test for equality of means – test statistic = 6.855,  $p < 0.01$ ). Post-hoc comparisons showed marginally significant differences between feeding and the other states, with no other significant differences (Tamhane's test of the differences between groups: travelling X feeding,  $p = 0.056$ ; resting X feeding,  $p = 0.071$ ; other X feeding,  $p < 0.05$ ; all other comparisons,  $p > 0.1$ ). Thus, the hypothesised potential influence of stressful situations during resting on the statistical comparison between behavioural states does not seem to be substantial.

### 3.3.2 Call rate according to state: analysis by bouts

I next analyse bouts of calls, instead of using each occurrence, to test whether differences between individuals and states found above might be artefacts of variations (between individuals or states) in the number of calls per bout.

Infants possessed a much higher bout rate, particularly the smaller ones, with the other animals having roughly similar figures (see Table 3.4). Differences between individuals were indeed highly significant ( $\chi^2 = 2364$  for bouts overall, and  $\chi^2 = 3054.8$  for bouts in focal periods, in both cases  $p \ll 0.001$ ,  $df = 12$ , and power approaches 1 for a medium difference to be detected, see Figure 3.7). Infants and small juveniles also seemed to present a larger number of *moos* per bout, although this could not be tested. In connection with the proposal that infants use this call differently, two facts are relevant. Infants and juveniles can be ranked according to the volley rate in an ascendant fashion according to their age, but not so with respect to the number of *moos* per bout.

Infants 12 and 13 (similar sized<sup>2</sup>) present similar volley rate and *moos* per bout. Individuals 10 and 11 (older than 12 and 13), have comparable number of *moos* per volley with respect to 12 and 13, although a smaller bout rate, indicating that they were calling less frequently but with an equal mean number of calls on each occasion. For the remaining individuals, both volley rate and number of calls per bout were roughly similar, and smaller than the infants, indicating that they were both calling less frequently and with a smaller number of *moos* on each occasion. Another interesting feature from the data is that the offspring of female 6 (11 and 13) seem to have a smaller number of *moos* than the ones from female 5 (10 and 12). This is worth pursuing in the future in connection with mothering styles and rank, since female 5 was dominant over 6.

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<sup>2</sup> See methods section for a depiction of life histories.

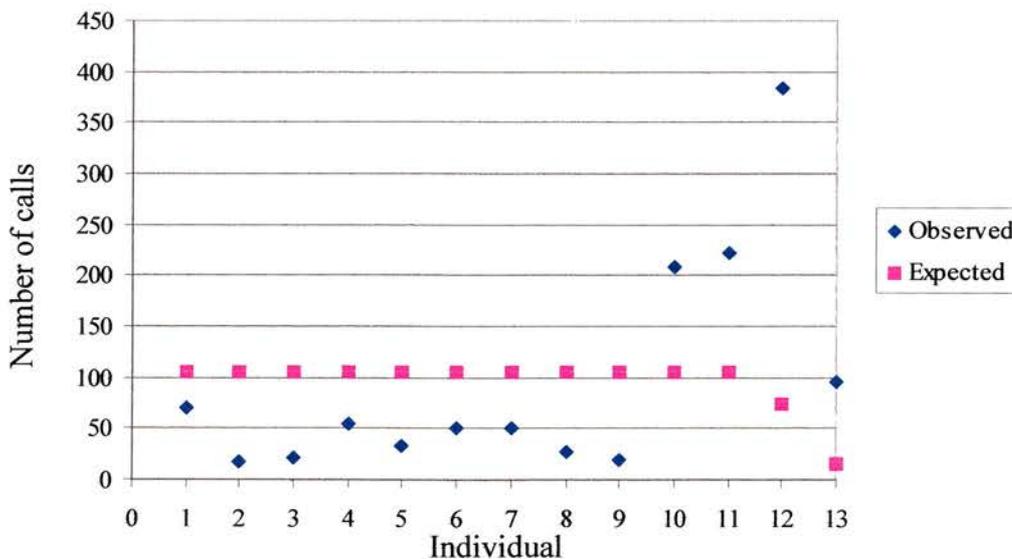
**Table 3.4 Number of bouts, mean rate (volleys/hour) and average number of calls per bout for each individual, considering both the whole data set and only the focal periods.**

| Individual        | n (total) | Bout rate (total) <sup>a</sup> | Moos/bout (total) <sup>b</sup> | n (focal) | Bout rate (focal) <sup>c</sup> | Moos/bout (focal) |
|-------------------|-----------|--------------------------------|--------------------------------|-----------|--------------------------------|-------------------|
| 1 (Ad. ♂)         | 70        | 0.052                          | 1.3                            | 41        | 0.371                          | 1.3               |
| 2 (Ad. ♂)         | 17        | 0.013                          | 1.4                            | 7         | 0.065                          | 1.7               |
| 3 (Sub-ad. ♂)     | 21        | 0.016                          | 2                              | 6         | 0.058                          | 1.3               |
| 4 (Sub-ad. ♂)     | 55        | 0.041                          | 2.8                            | 16        | 0.154                          | 3.8               |
| 5 (Ad. ♀)         | 33        | 0.024                          | 1.8                            | 6         | 0.058                          | 1.8               |
| 6 (Ad. ♀)         | 50        | 0.037                          | 2.9                            | 11        | 0.102                          | 2.9               |
| 7 (Juv. ♀)        | 51        | 0.038                          | 3.5                            | 19        | 0.206                          | 2.1               |
| 8 (Juv. ♀)        | 28        | 0.021                          | 2.9                            | 6         | 0.062                          | 3.2               |
| 9 (Sub-ad./Ad. ♀) | 20        | 0.015                          | 1.4                            | 11        | 0.111                          | 1.5               |
| 10 (Inf./Juv. ♀)  | 208       | 0.154                          | 6.6                            | 69        | 0.761                          | 5.3               |
| 11 (Inf./Juv. ♀)  | 222       | 0.164                          | 4.8                            | 74        | 0.766                          | 4.1               |
| 12 (Inf./Juv. ♂)  | 384       | 0.407                          | 6.2                            | 76        | 1.232                          | 4.9               |
| 13 (Inf. ♀)       | 96        | 0.493                          | 4.7                            | 10        | 1.155                          | 2.2               |
| Total             | 1255      | 0.929                          | 4.8                            | 352       | 0.298                          | 3.75              |

<sup>a</sup> Bout rate (total) is the total number of bouts assigned to each individual (emitted in focal and non-focal periods) divided by the overall number of data collection hours.

<sup>b</sup> Average value of *moos* per bout (number of *moos* as reported in table 2 divided by the number of volleys showed here).

<sup>c</sup> Bout rate (focal) is the rate calculated using only data from focal periods.



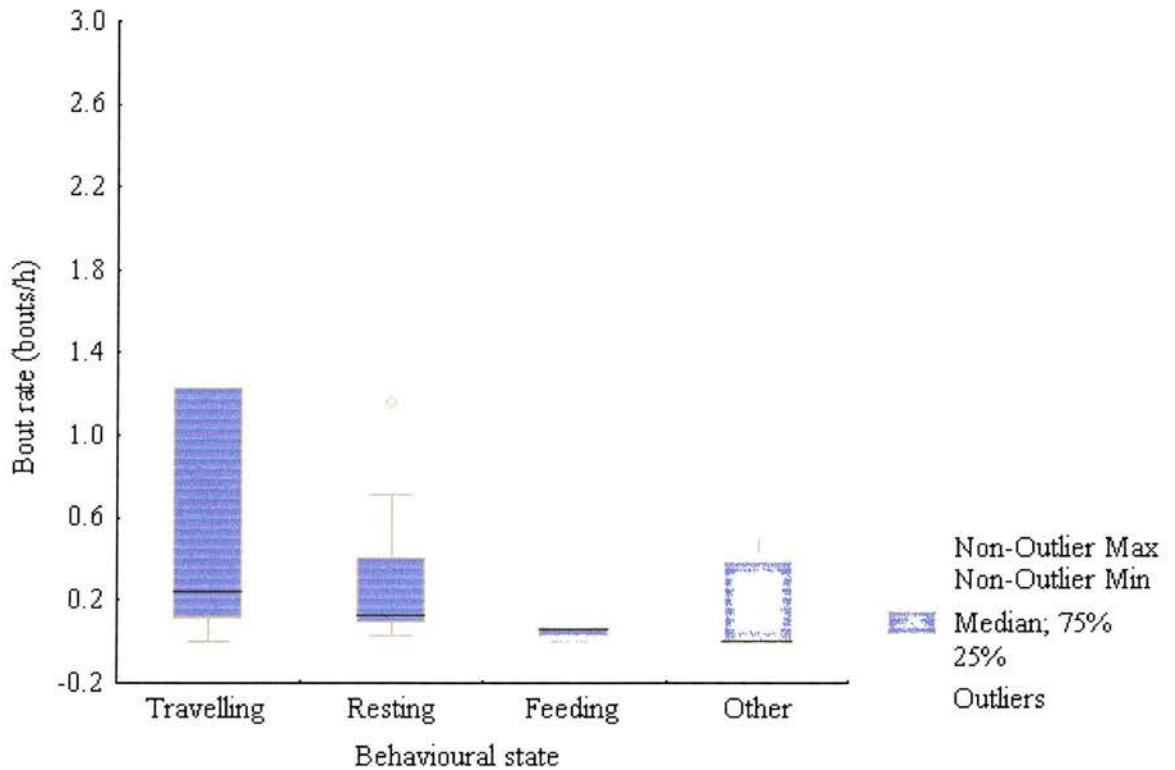
**Figure 3.7 Observed and expected values of number of bout calls per individual (considering all focal periods together).**

Despite the small sample sizes, bout rates during travelling normally had the highest rates, and feeding the smallest. Resting or other behaviours presented intermediate figures (see Table 3.5). Data on volley rates on all 4 states were not normally distributed and the variances were also not homogeneous. When inverse transforming the data, normality is restored for almost all groups: Shapiro-Wilk test statistics and significance values for travelling, feeding, resting and others are respectively 0.872 ( $p > 0.1$ ,  $df = 5$ ), 0.872 ( $p = >0.1$ ,  $df = 10$ ), 0.784 ( $p < 0.01$ ,  $df = 12$ ), and 0.915 ( $p > 0.1$ ,  $df = 9$ ). Homoscedasticity is also achieved: Levene's test  $F = 2.03$  ( $p > 0.1$ ). Analysing the transformed variable showed that there was indeed a difference between the bout rates on different states (One-way ANOVA  $F_{3,32} = 7.124$ ,  $p < 0.01$ , power is 0.1919 for a medium effect to be detected, see Figure 3.8). Post-hoc comparisons revealed the following differences: Tukey's HSD travelling X feeding,  $p < 0.01$ ; other X feeding,  $p < 0.01$ ; all other comparisons,  $p > 0.1$ ). Thus, feeding presented significantly lower rates (except in comparison to resting), while resting, travelling and other did not differ, despite the apparent trends in the data.

**Table 3.5 Number of bouts and bout rate according to the state of the caller<sup>a</sup>**

| Individual        | n (bout rate) |           |          |           |
|-------------------|---------------|-----------|----------|-----------|
|                   | Travelling    | Resting   | Feeding  | Other     |
| 1 (Ad. ♂)         | 6 (0.81)      | 33 (0.37) | 1 (0.09) | 0 (0)     |
| 2 (Ad. ♂)         | 0 (0)         | 7 (0.09)  | 0 (0)    | 0 (0)     |
| 3 (Sub-ad. ♂)     | 0 (0)         | 6 (0.09)  | 0 (0)    | 0 (0)     |
| 4 (Sub-ad. ♂)     | 3 (0.39)      | 9 (0.13)  | 1 (0.05) | 2 (0.26)  |
| 5 (Ad. ♀)         | 1 (0.10)      | 2 (0.03)  | 1 (0.06) | 1 (0.2)   |
| 6 (Ad. ♀)         | 2 (0.19)      | 8 (0.10)  | 1 (0.07) | 0 (0)     |
| 7 (Juv. ♀)        | 2 (0.24)      | 14 (0.25) | 1 (0.05) | 0 (0)     |
| 8 (Juv. ♀)        | 1 (0.11)      | 3 (0.05)  | 1 (0.04) | 0 (0)     |
| 9 (Sub-ad./Ad. ♀) | 2 (0.25)      | 8 (0.12)  | 0 (0)    | 0 (0)     |
| 10 (Inf./Juv. ♀)  | 28 (2.62)     | 23 (0.44) | 1 (0.05) | 5 (0.52)  |
| 11 (Inf./Juv. ♀)  | 18 (1.65)     | 40 (0.71) | 1 (0.06) | 11 (0.9)  |
| 12 (Inf./Juv. ♂)  | 18 (2.26)     | 35 (1.16) | 1 (0.18) | 15 (0.83) |
| 13 (Inf. ♀)       | 0 (0)         | 3 (0.46)  | 0 (0)    | 7 (4.07)  |

<sup>a</sup> Bout rates are the number of bouts emitted by a given animal (during its focal hours) when on a given behavioural context divided by the number of hours that the individual concerned performed the behaviour.



**Figure 3.8** Boxplot of bout rates (non transformed data) according to the state of the caller.

An interesting feature that emerges is that the mean number of calls on each volley seemed to be very different between states (see Table 3.6). While travel and resting present similar figures (with the odd value due probably to small sampling), feeding generally presents a smaller number of *moos* per volley.

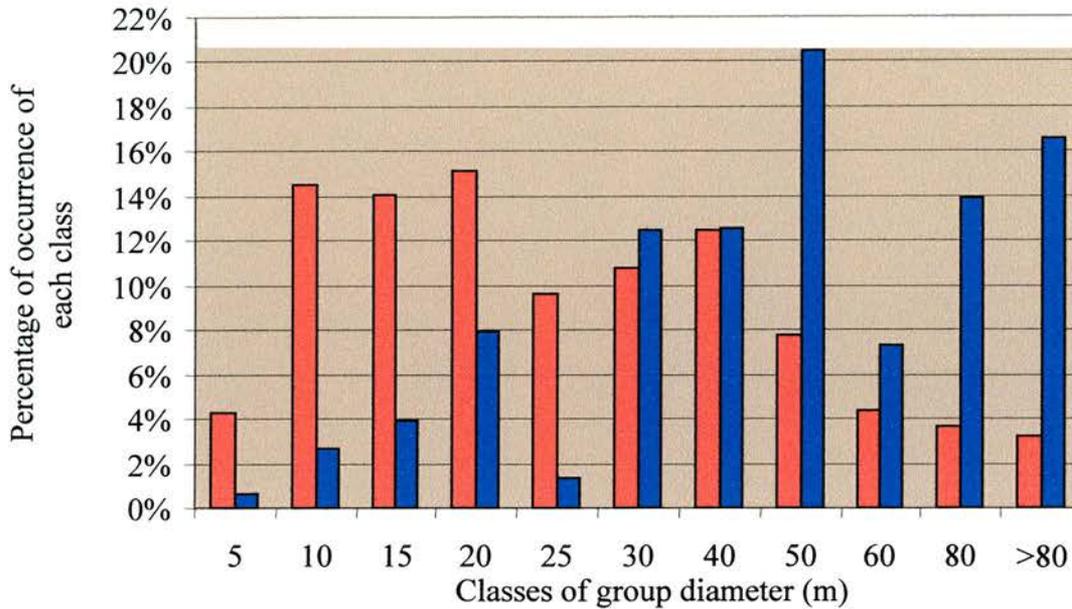
**Table 3.6 Number of moos per bout according to the state of the caller <sup>a</sup>.**

| Individual        | Calls per volley |         |         |       |
|-------------------|------------------|---------|---------|-------|
|                   | Travelling       | Resting | Feeding | Other |
| 1 (Ad. ♂)         | 1.00             | 1.33    | 1.00    | 0.00  |
| 2 (Ad. ♂)         | 0.00             | 1.71    | 0.00    | 0.00  |
| 3 (Sub-ad. ♂)     | 0.00             | 1.17    | 0.00    | 0.00  |
| 4 (Sub-ad. ♂)     | 3.33             | 4.78    | 1.00    | 2.00  |
| 5 (Ad. ♀)         | 4.00             | 2.00    | 1.00    | 1.00  |
| 6 (Ad. ♀)         | 2.50             | 3.25    | 0.00    | 0.00  |
| 7 (Juv. ♀)        | 5.50             | 1.71    | 1.00    | 0.00  |
| 8 (Juv. ♀)        | 15.0             | 0.00    | 1.00    | 0.00  |
| 9 (Sub-ad./Ad. ♀) | 1.00             | 1.38    | 0.00    | 0.00  |
| 10 (Inf./Juv. ♀)  | 5.25             | 5.43    | 13.0    | 4.80  |
| 11 (Inf./Juv. ♀)  | 4.94             | 4.30    | 1.00    | 1.91  |
| 12 (Inf./Juv. ♂)  | 4.83             | 6.40    | 1.00    | 2.87  |
| 13 (Inf. ♀)       | 0.00             | 3.00    | 0.00    | 1.86  |

<sup>a</sup> Average value of moos per bout (number of moos per state divided by the number of volleys on each state).

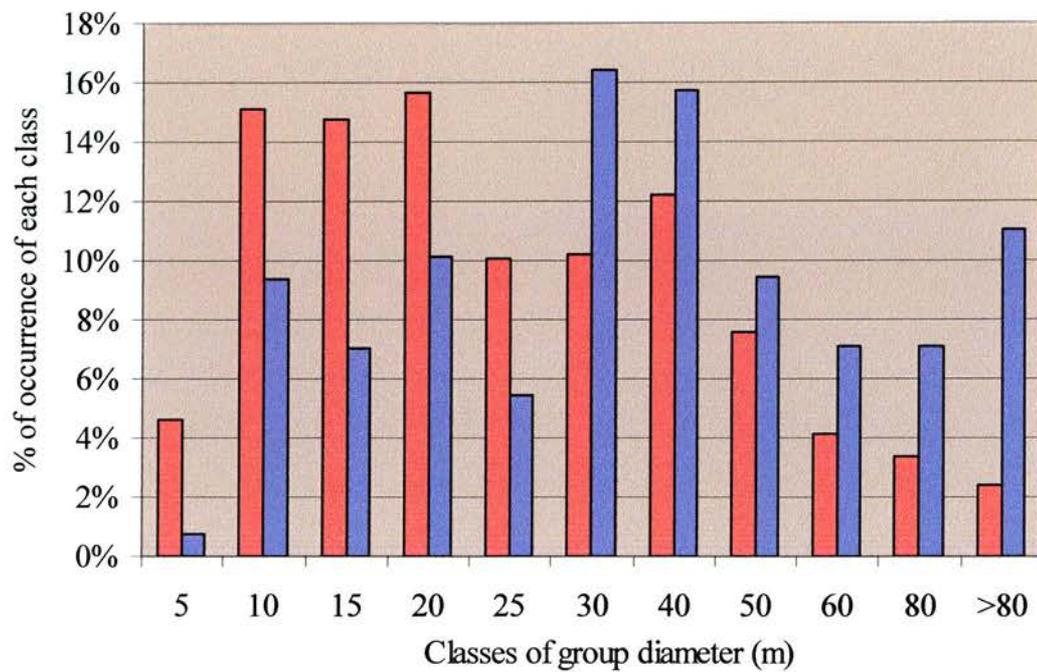
### 3.3.3 Group diameter data

Comparing the distribution of group diameter values recorded focally during *moo* emissions (*moo* diameters) with that expected if this distribution followed the baseline pattern shows a significant difference (Goodness-of-fit test  $\chi^2 = 208.4$ ,  $df = 10$ ,  $p < 0.001$ , Power = 0.71 for a medium effect to be detected see Figure 3.9). Percentage of occurrences of the five smaller diameter categories was lower for the *moo* diameter when compared to the baseline values, the opposite occurring with the last four classes. Categories 50, 80 and >80m contributed the most to the value of the statistic, especially the last one. These observations show that the statistically reliable deviation from the expected values was in the direction predicted under the hypothesis of a contact/isolation function.



**Figure 3.9 Percentage of occurrence of each class of group diameter: ■ baseline values; ■ , during emission of *moos*.**

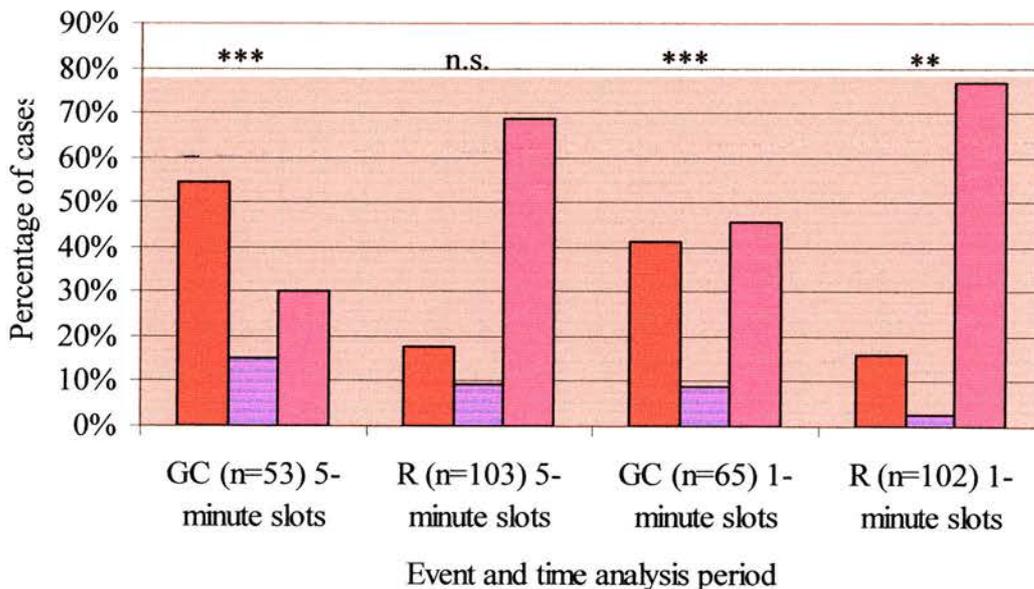
The data set composed of the first baseline points after calls/volleys was still significantly different from the expectation based on the remaining baseline values (Goodness-of-fit test  $\chi^2 = 70.35$ ,  $df = 10$ ,  $p < 0.001$ , Power = 0.6175 for a medium effect to be detected, see Figure 3.10). The category with the largest contribution to the value of the statistic is “>80m”, with the others contributing roughly equally. Percentage of occurrence of the five smaller diameter categories was lower for the set of first baseline points after *moos* when compared to the remaining baseline values, the opposite occurring with the last six classes. So, I could not validate the prediction that the values of the first baseline data points after calling should return to the average baseline values. In spite of this, comparing the figures of group diameter observed during calling with their matched values after the call, there were 36 increases and 76 decreases. Under normal circumstances, it is reasonable to expect an equal number of enlargements and reductions in a random set of consecutive diameter values, or otherwise the group is permanently shrinking or expanding. The probability of getting these values (36 increases and 76 decreases) by chance alone is very low (binomial test against a 1:1 proportion,  $p < 0.001$ ), leading one to conclude that group spread generally decreased, but not enough to restore the average baseline values.



**Figure 3.10.** Percentage of occurrence of each class of group diameter: ■, set of first baseline points after emission of *moos*; ■, remaining baseline values.

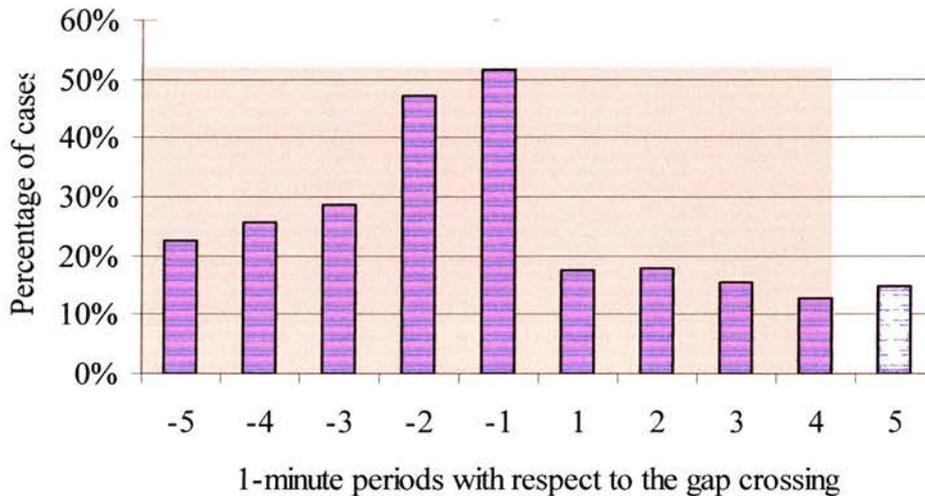
### 3.3.4 Moos as anxiety or distress calls

Starting with those behavioural events that can be considered as the cessation of stressful contexts (gap crossing and riding), I compared call occurrence in time periods of 5 and 1 minutes before and after the events. Recall that the prediction, under the hypothesis that the call is related to anxiety/distress, is that the animals should call more before than after the “cessation” event. In nearly all binomial tests carried out (see Methods) the null hypothesis was rejected (data for 5-min periods before/after, ‘gap crossing’  $n = 37$ ,  $P < 0.001$ ; ‘riding’  $n = 29$ ,  $P > 0.05$ ; data for 1-min periods before/after, ‘gap crossing’  $n = 34$ ,  $P < 0.001$ ; ‘riding’  $n = 29$ ,  $P < 0.01$ ) and the larger category was always the one representing the instances with more calls before than after the cessation (see Figure 3.11). The only exception was the riding behaviour when considering 5-minute periods. So, for the ‘gap crossing’ event, the prediction was upheld for both periods considered. For the ‘riding’ event the prediction was confirmed when considering 1-minute slots, but not when considering 5-minute ones. Therefore, for this behaviour the stress period seems to be smaller than for gap crossings. Another feature that is apparent on the figure is the large number of cases with no calls emitted both before and after riding events (discussed below).



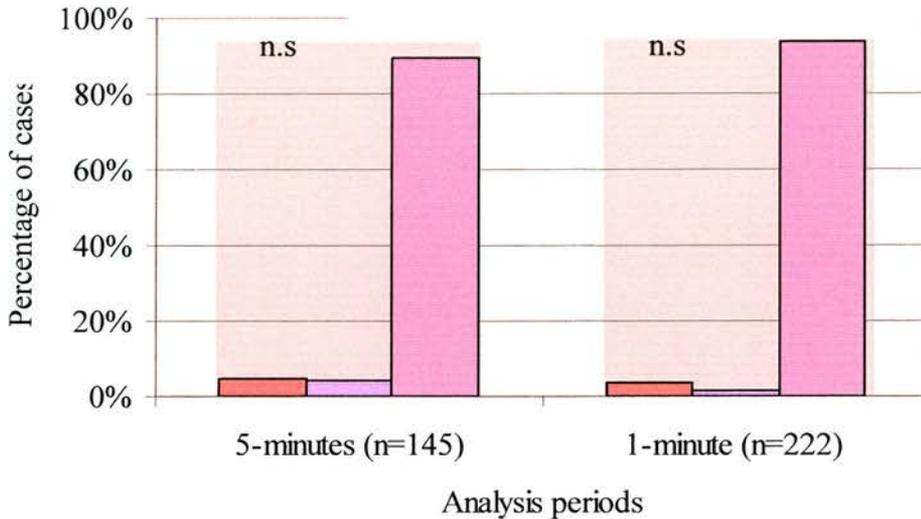
**Figure 3.11** Percentage of cases with: ■ more calls before than after the ‘cessation’ event; ■ more calls after than before; ■ no calls (with respect to equivalent time periods of 5 or 1 minutes as specified). GC – gap crossing; R – riding. In parentheses the total number of cases. Significance level symbols are for the binomial tests.

Looking at the call rates in successive time slots both before and after the gap crossing (Figure 3.12), there seems to be a trend of increased call rate in the minutes preceding the crossing of the gap. Furthermore, there is a drastic reduction in percentage of cases with calls after the cessation.



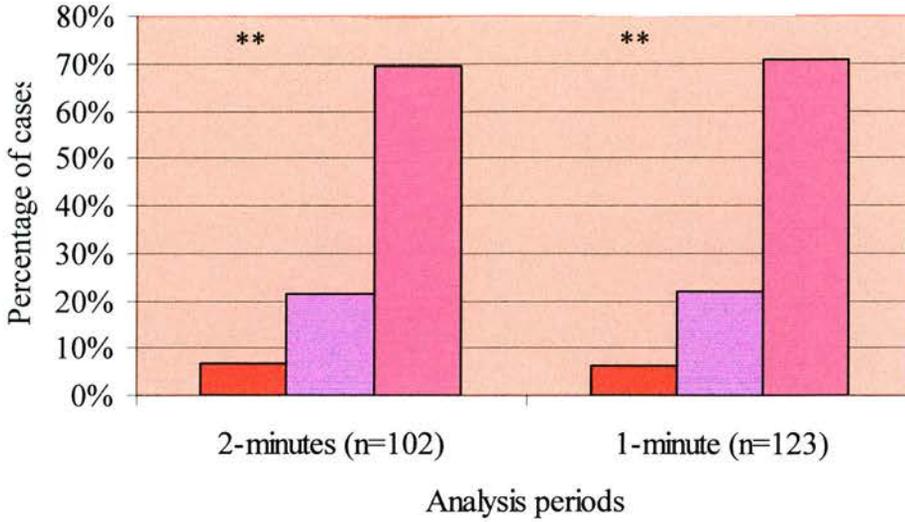
**Figure 3.12 Percentage of cases with at least one call in a given time bin. Percentages were calculated separately for the 10 consecutive 1-minute slots, symmetrically distributed before and after the crossing of the gap. Figures on the x-axis represent the 1-minute periods with respect to the “gap crossing” event.**

Turning to the behavioural events whose occurrence signals the start of the presumed stress, the prediction (under the anxiety/distress hypothesis for the function of the call) was that animals should call more after than before the event. Considering the ‘being left’ events (mother moves more than 0.5m apart from the infant), the null hypothesis could not be rejected for both analyses periods considered (data for 5-min periods before/after  $n = 13$ ,  $P > 0.05$ ; ‘data for 1-min periods before/after  $n = 12$ ,  $P > 0.05$ ). It is also striking the huge number of cases that did not involve any *moo* calling.

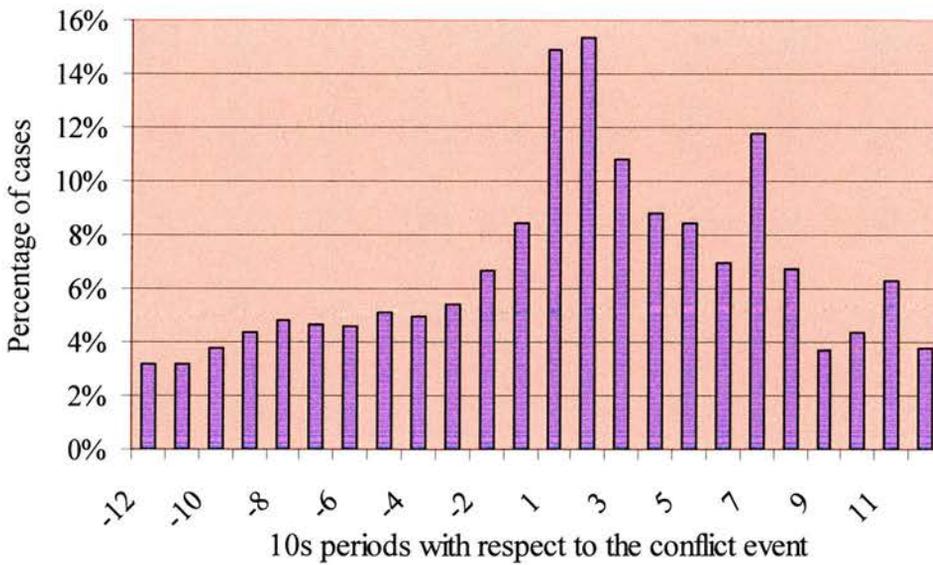


**Figure 3.13 Percentage of cases with: ■ more calls before than after ‘being left’ events; ■ more calls after than before; ■ no calls (always with respect to equivalent time periods of 5 or 1 minutes as specified). In parentheses the total number of cases. Significance level symbols are for the binomial tests, and as explained in the text.**

The behavioural category ‘conflict’ shows a different picture. Here, comparing ‘call before’ and ‘call after’ values with a binomial test against a 1:1 hypothesis produced significant results for both time periods considered (data for 2-min periods before/after  $n = 29$ ,  $P < 0.01$ ; ‘data for 1-min periods before/after  $n = 35$ ,  $P < 0.01$ ). In both cases the larger category was always the one representing the instances with more calls after than before the conflict (see Figure 3.14). I then looked at the pattern of calling in successive time periods, considering a fine-grained division of 10 seconds (see Figure 3.15). Calls were concentrated on the first 80 s, and particularly so on the 20 s following the ‘conflict’ event.



**Figure 3.14** Percentage of cases with: ■ more calls before than after ‘conflict’ events; ■ more calls after than before; ■ no calls (always with respect to equivalent time periods of 2 or 1 minutes as specified). In parentheses the total number of cases. Significance level symbols are for the binomial tests, and as explained in the text



**Figure 3.15** Percentage of cases with at least one call in a given time bin. 24 consecutive 10-seconds slots symmetrically distributed before and after the conflict were considered. Figures on the x-axis represent 10 second periods with respect to the conflict. Total sample size was different for each slot, varying from 156 to 201 cases.

## 3.4 Discussion

### 3.4.1 Role as a contact call

#### **Evidence for a general contact function**

When there was emission of *moos*, group diameter was significantly larger than usual. Also, after the calling, group spread decreased significantly more often than increased, although this was usually not enough to bring diameters back to baseline values. Call rate was significantly lower during feeding than in other activities. On the other hand, travelling had a larger call rate than the other categories. However, this was non-significant and has to await confirmation from studies with more power. Corroborating the result would be relevant for a contact role, since travelling is a situation with a higher chance of animals losing contact with each other, and travelling is the behavioural state with less group cohesiveness. Given that the monkeys usually fed while in a compact group organisation, the significantly lower call rate during feeding can be seen as providing extra support for a contact function, as this role is redundant in cohesive situations. In any case, it definitely allows us to exclude from consideration any functions strictly related to feeding (announcement of location of food sources, prevention of approaches, etc.). Concerning number of *moos* per volley of calls, while travel and resting generally presented similar figures, feeding generally presents a smaller number of *moos* per volley, which is an extra indication of the unimportance of *moos* during feeding. Considering all these pieces of evidence, it seems likely that the *moo* call does possess a contact role. Although much has to be studied with respect to this vocalisation, this is nonetheless the first clear demonstration of a contact call in a species of the genus *Alouatta*.

#### **Specific contact function(s)**

However, specifically which contact function(s) the *moo* call has is not clear. As I showed in the introduction to this chapter, there are many possible

roles that can be played by a contact call. Although my data are not sufficient to tackle this problem, I can offer anecdotal observations that present some clues. Later, I will propose a more specific observational design for a future study to try to unravel the specific function(s) of this call type.

The first question to be addressed is the relation between calling on one hand and travelling and group diameter on the other. Due to a positive relation between travelling and group spread (group diameter tends to be large during travel), if calling is associated with the first, it is bound to relate to the group diameter as well (but not the other way round, as the call may be specifically used in static contexts of large group spread). However, the proximal cue for calling might be either the travelling context itself, or a high dispersion. In the case of the large group spread, the specific function could be maintaining contact between dispersed members (not exclusively when travelling) or regaining lost contact. When travelling itself is the primary cause of calling, the function could be to avoid losing contact with other animals or be more specifically related to co-ordination of group travel.

*Ad libitum* observations point in the first direction (higher dispersion as the primary cause for calling, not travelling). First, animals did not call exclusively when travelling or about to start travelling. This situation contrasts with the calls studied in squirrel and capuchin monkeys for which a role in co-ordination of travel was advocated (Boinski, 1991, 1993). On a variety of occasions, animals (single, small sub-groups or even the “core” of the group when one or more individuals were missing) *mooed* when there was loss of visual contact between members of the group. The individual/party that would later join the others would normally be the calling one and the calls usually ceased after reunion. However, on at least one occasion, resting animals emitted a noticeably long sequence of calls in the absence of only the alpha male, which later reunited with the group, apparently without emitting calls himself. On a couple of cases the separated animal(s) stopped calling after hearing a *moo* from another individual, and started travelling on the direction of the sound. Another striking anecdotal observation was a situation whereby the alpha male was separated from the group by more than 150m (very large value considering the normal values of spread). He kept emitting *moos* for at least 40 minutes at regular intervals (and also *oodles* and one incipient *roar*). His erratic movements

and apparent indecision seemed as if he was trying to re-locate the group. I could not observe the reunion as these events took place towards dusk, but on the next dawn he was already with the group. All these observations point towards a function of regaining contact. However, there were also many instances wherein the animals were out of visual reach and regained contact without call emission.

There were also situations in which there was a high rate of calling involving adults, and every animal was within visual reach of a couple of others. Examples include cases when there were apparently conflicting tendencies (e.g. two animals leading in very different directions or part of the group start moving while others kept resting), and travelling sessions leading to a large group spread, with every individual in sight of some others but not of the whole group. The calls usually terminated when the group was more cohesive or when a clear travel session ensued. Those observations seem to indicate a function of maintaining contact at close or intermediate ranges or co-ordinating group travel, reinforced by the observation that travelling under very windy conditions, which impairs listening the natural sounds movements made by travelling animals, also seemed to trigger calling. However, if co-ordination is the role, it is definitely of a different nature from the one in squirrel and capuchin monkeys (Boinski, 1991, 1993), as initiators and leaders were not the main or exclusive callers. My observations are insufficient to propose a mechanism for the co-ordination, if this is the correct hypothesis.

A more puzzling set of observations was when animals were in close proximity (e.g. with a spread of 15m or less) and still called (see Figure 3.6). *Moos* or volleys emitted solely or predominantly by infants (not excluded from the group diameter analyses) might account for some of those instances. As *moos* might have additional roles for younger individuals, the contact role hypothesis would not be harmed by these observations. Also, I observed that protracted infant volleys, particularly when confronted with a wide gap between branches, seemed to exert a contagious effect on adults as well, which could account for some more cases. Finally, recall that I registered group diameter using the animals that my field assistant and me could locate, which means that some animals could be astray, and the group diameter would then be misleading. With the detailed study design proposed below, one will be able to check the circumstances surrounding the emission with (apparently) small group diameters,

and if they do occur independently of infant/juvenile influence. Another intriguing fact is that large group diameters were not necessarily followed by emission of *moos* (pers. obs.), which should be taken into account in further studies.

Thus, from these results and anecdotal observations, it seems that *moos* could be grouped under categories 3 (maintaining contact at intermediate ranges and/or in situations likely to lead to separation) and/or 4 (maintaining contact at distance), given alone the possibility that there could be more than one call type, subsumed here under one label. As is apparent from Table 1, there are few cases of *naturalistic* studies in which the *same* call could be placed under those two categories. In many cases there is a call which is used under a variety of circumstances with variable degrees of separation, and when the animals are “lost” there is another call type. Baboons are the clearer exception, although splitting in sub-groups is part of their routine, while this is not true of howlers. On the other hand, some species studied in more depth showed a complex picture of regulation of intragroup cohesion, with the same call(s) used in a variety of situations (e.g. Robinson, 1982). The possibility that *moos* might have a broader range of functions than other species’ contact calls makes them an interesting call for further research.

### **Intentionality**

Another issue of interest with contact or reunion calls is what is(are) the subjacent psychological mechanism(s) that allow the ultimate function. In other words, is there a call-response system (and which are the mechanisms behind it)? If so, is there intentionality in the emissions or not? Do animals call merely as a reflection of their own state or do they actively respond to others? Regarding this topic, my *ad libitum* observations seemed to indicate that this call exerts a mild contagion effect, especially in drawn out sessions. But, more interestingly, *moos* were at times apparently answered by other *moos* from distant individuals or by a volley of *mutterers*. Strangely enough, *mutterers* are rather quiet calls (emitted mostly during feeding), which almost certainly do not carry far in the forest. Therefore, it does not seem to present any locational cues for the isolated animal. Occasionally, when the *moo* session was very prolonged, the alpha male would

emit an *oodle*, which, although not being louder, could be an indication of a central focus, an acoustic beacon for the group. These observations indicate the potential to use this call type in studying the questions mentioned.

### 3.4.2 Relation with stressful situations

Either looking from the perspective of potentially stressful events or from their termination, it was possible to show an association of this call type to the time period when the anxiety was predicted to be higher, except for the event 'being left'. This is a first step in determining the function of the call in those situations.

Looking at the behaviours regarded as the cessation of (presumably) stressful situations, the event 'riding' (the point at which an infant mounted the back of its carrier) possessed a large number of cases with no calls emitted both before and after the event. There are two possible explanations for this result. First, the "objective" might have been attained without even building up anxiety (the infant can actively approach and ride before the carrier moves). Additionally, some cases might be more stressful than others, and calling could be restricted to these (for example when the carrier has already started moving, or the period when individuals are starting to refuse carrying). Conversely, "anxiety-free" cases are not possible in situations whereby the infant is facing a wide gap between trees, as an older individual is not always readily available for a bridge or a lift. This interpretation might explain the much smaller number of cases with no *moos* when analysing the event 'gap crossing'. The second explanation is that other calls, or even gestures, are also used in riding situations (particularly so when a carrier removes an infant from the back). Then, the present result (more calling before than after the termination of the stressful condition) should be replicated for those signals, but with a smaller number of cases with no calls at all. Those alternatives are not mutually exclusive, and one can also imagine that *moos* might have a syntactic role (Robinson, 1984; Snowdon, 1989), altering the meaning of other calls related to the anxiety situations, e.g. by informing higher degrees of stress.

Concerning the events 'conflict' (infant prevented of performing an action or having a comfortable situation interrupted) and 'be left' (mother leaving the infant), there were also a very large number of instances with no associated calls. The possibility that they were not in fact stressful events, although real, can not be called upon here, because it would be a post-hoc dismissal of our working hypothesis; stress can be properly assessed only

through hormonal studies. As in the case of ‘riding’, there may be heterogeneity on the stress levels on different instances of the selected events, and this can lie along two lines. The different behaviours included on the event ‘conflict’ might present different stress levels. The ‘being left’ event is more homogeneous on that respect, but one can conceive that under different circumstances the distress varies (e.g. mother leaving when there is a group travel session versus when the group is stationary). On the other hand, a given event could vary its stressful impact according to the age of the infant. One could also argue that other calls/gestures are commonly used in these contexts, as with the riding events, and again this is not mutually exclusive with respect to the previous alternative. In any case, the prediction was not upheld for the event ‘be left’, that is, the immatures did not call more after being left by their mother than before.

### 3.4.3 Possible functions in stressful contexts

When a given call is associated with a hypothetically stressful situation, determining its function will depend, among other factors, on the specific situation to which it is associated. But, in general terms, one can start with three possibilities for the proximate function: the call is an indicator of the emotional status of the animal, of its physical needs (e.g. hunger) or an attempt to manipulate other individuals. If the call is effective in overcoming the stressful situation, this ultimate result is usually equated with function (“call for help”), albeit probably erroneously as it implies a degree of intentionality that is, at best, doubtful. It also happens that the alternatives above are not mutually exclusive. For example, an infant can be hungry and also stressed by that. Or, having learned that a given vocalisation produces the cessation of the stress, an animal might call in later stages of its development, without a real need for that, or alter the threshold for calling. The results concerning the percentage of cases with *moos* in consecutive time periods before and after gap crossing events are not clear in this respect. The abrupt drop in the percentage of cases with *moos* after the events may at first be seen as indicative of a manipulative call. The reason, one would say, is that when the call is related to an emotional state or physical need, the endogenous responses generated by the situation do not vanish instantaneously with the cessation of the stressful condition itself. If these

endogenous reactions are the triggers of the call, then calling should wane in a smooth fashion. Alternatively, if the call is a mere manipulative manoeuvre, the individual could be expected to cease calling upon achieving its objective. But is this really the case? Even if a call is a display of an animal's emotional state, it does not necessarily follow that the rate has to decline slowly. Predation risks could have acted as a selective force to produce a suppression mechanism that prevents animals from calling once the "objective" is achieved, even if they are still motivated to do so. Or the termination of the situation might bring up another endogenous response that suppresses the urge to call. Finally, it has been shown before that there is an uncoupling of 'isolation' calls and the production of stress hormones (Norcross & Newman, 1999), which could account for faster drops in call rate after the "cessation" events without necessarily implying manipulation by the infant or juvenile.

Nonetheless, *ad libitum* observations seemed to indicate a developmental change in the way youngsters used *moos* in gap situations. Larger individuals usually quickly approach and helped small calling infants but, as the individuals grew older, they usually had to call for longer periods of time before getting help. On other occasions help was not given, so the calling individual had to give up, cross the gap by itself or take a detour. Eventually, the calls would not be answered at all. It is reasonable to suppose that an infant initially calls because it is in fact stressed. Having learned an association between calling and help, this opens the possibility for exploitation in later phases. By not attending to all instances of calling or taking longer to respond, other individuals might be protecting themselves against manipulative attempts. And the infant/juvenile probably has to adjust its threshold levels. Helping infants and adjusting the behaviour during their development does not need to be brought about by an understanding of the needs of the infant. A simpler explanation might be that as interest towards infants decrease as they grow, older animals are less prone to approach a calling infant.

Considering the ultimate function of the call, there seems to be at least three possible alternatives for a call produced in conflict or stressful situations (a more extensive discussion of this topic will be given in the screech-complex chapter):

- Call for help/ elicit care-giving response: the outcome is the approach of another animal and the termination of the stressful condition; or the production of a care-giving response;
- Announcement of disagreement or discomfort during an interaction, which can lead to retaliation: here one expects either a change/cessation in behaviour on the part of actor and a concomitant termination of calling, or escalation. Signalling a mild threat presents many similarities and can be included in this category;
- Signalling submissive status to prevent an agonistic interaction or terminate one in course.

In the case of *moos*, giving the situations to which it is most commonly associated, the first option seems the most likely function. The ‘conflict’ situations studied here also would point towards the care-giving function, since a great deal of cases involved the infant being taken from the back of the carrier. Being prevented to suckle, not included in the analysis (the animals can not call while suckling), was also very effective in eliciting calls. In those situations, other calls (belonging to the screech complex) were much more common, but *moos* were also present nonetheless. In some cases, the calling seemed to be effective in generating a caring response (infant allowed to ride or breast feed).

*Moos* were also heard during apparently unwanted interactions, such as prolonged and non-accepted invitations to play, although other call types were much more common. The function of the calling behaviour in these situations might be the announcement of disagreement/discomfort, as a warning of coming retaliations.

#### 3.4.4 Ontogenetic trajectory of the call

Although I could not follow an individual from birth to adulthood, and thus verify the development of the usage of the call for one single animal, during the main study I could observe large periods of development on individuals at different stages. As the periods overlapped, they provide a picture of the main developmental stages on the usage of the call when considered together. The first

point that merits attention is the strikingly different call rate between immatures and adults. Infants and juveniles called at a much higher rate than adults did. Furthermore, there seemed to be a clear trend of decrease in call rate during the immature stages, with infants calling much more than juveniles. As there does not seem a stage when *moos* are not emitted, as observed with the *wrr* calls of vervet monkeys (Hauser, 1989), we are left with three possible explanations (not mutually exclusive). The first possibility is that the kinds of situations/contexts that elicit the call wane or disappear as the animals grow. Although this explanation could apply for some events (riding for example), it is clearly not universal (gap crossing continues to be a problem throughout the whole life). The second alternative is that as the responsiveness of other animals to the calls decrease in an irreversible fashion, the threshold of anxiety levels necessary to elicit a call also increases. Then, with time, situations that previously elicited a call are progressively dropped out as stimulating contexts, and only the most stressful ones remain (capable of generating enough anxiety to stimulate a call). The third explanation is the reverse side of the previous one. That is, some situations might cease to be stressful as the animals grow. This can result from the progressive lack of response of older animals to the calls, which forces the infant to solve the problem by its own means and thus gain confidence. For example, when being refused to ride, the infant is forced to travel by itself and then at some point travelling is not a problem anymore. Additionally, one could argue that with the decrease and cessation on the attentiveness of other animals to the infant in a particular situation, neither the threshold nor the stress levels of the situation alter. The infant merely learns by association that on those contexts, it is not worth calling.

Whichever the case (or combination), the fact remains that the call is emitted continuously from infancy to adulthood (which has to be confirmed with detailed studies, particularly with animals in late juvenile/early sub-adult phases). Therefore, there could be some more specific common factor in the situations eliciting the calls in the various stages of development. Detecting this factor might help to determine the specific function(s) of the call, and to narrow down the general stress hypothesis. Gap crossings were the events to which the calls were more clearly associated. Therefore, there might be a similar motivation to call in gap situations by infants and during the circumstances that elicit calls by

adults, with the animals experiencing similar emotional states. I hypothesise here that when confronted with a wide gap, immatures might fear losing contact with other animals and, through calling, might be attempting to maintain or re-gain contact, which is exactly what adults seem to be doing. The association with the riding contexts can be also accommodated under this hypothesis. The animals might call before being allowed to ride because they fear losing the contact with the carrier, particularly if the later is already moving. However, this explanation still does not provide a full picture, since calls were also emitted in situations in which it is difficult to defend such contact role (e.g. after the conflict events analysed). An alternative, which relates to the emission of *moos* alongside calls of the screech complex, is that the *moo* might have some syntactic function within a bout of different calls. This topic is explored further in the next chapter.

### 3.5 Proposed study design

I now propose a more detailed study design, to be used by those attempting to elucidate the role of the *moo* call in more detail. The first aim would be to test the apparent trend of a higher calling rate during travelling, and to clarify the unexpected intermediate values during resting. Although my basic design (focal animal sampling of a continuum of states and superimposed behavioural events) still seems appropriate, some behavioural categories need sub-division to tackle these issues. Travelling should be divided in leading, following, or travelling alone; this partition can potentially generate information about the co-ordination of activities and the role of calling within it. The design should also record the position of the animal in the line of progression, divided in thirds, as done with baboons (Cheney et al., 1996). One should split resting into sleeping (long resting session involving closure of eyes), resting (intermediate sessions with eyes open), and pauses (momentary stops of an ongoing activity). To define a pause, the best option is a combination of operational criteria (e.g. stops preceded and followed by the same state) and behavioural data. From a histogram of duration of all pauses/resting sessions, one can verify if a clear pattern of peaks emerges which could guide the time criterion, or use some percentile criteria instead.

Concerning group diameter, although the way I collected data allowed a quantification of group spread, it did not measure the separation between individuals, and if they were within visual reach or not. Thus, one should also register the distances of every individual in relation to all others at regular time intervals, which would provide useful baseline figures about the average separation between each pair of animals. Then, when a *moo* is emitted, the researcher should collect focally these distances, noting especially which animals are likely to be in the visual field of the caller. The position of the animal within the “cloud” of group spread should also be noted: for stationary behaviours (resting/feeding), a centre/periphery criterion should suffice, whereas for travelling, the same criterion mentioned above could be applied (dividing the line of progression in thirds). The baseline could be analysed in a similar way as done by Palombit (1992b), using multiple regression, with the number of calls in a

given time period as the dependent variable and distances of interest as the independent ones. It would be particularly interesting to consider, besides group spread, the distances between the calling animal and (1) the nearest individual (in/out the visual field), (2) associates, (3) offspring/mother, (4) the alpha male and (5) the usual travel leaders. To measure group spread, apart from the maximum distance between animals, Palombit (1992b) registered the distance on an axis 90 degrees to the first one. The multiplication of the two provided an index of group spread, which might reflect more accurately a larger variety of situations than the mere maximum distances and is recommended for future studies. The focal data collected during calls should be compared to the baseline one, as I did in this research, but considering more specific interactants and as suggested for the regression.

The researcher should also make an effort to note the identities of all the callers in a volley, to see if there is a response system in place, if the answers are between specific pairs of individuals or generalised, and if there is a pattern or order in the volley. This kind of data, when analysed in parallel with information on patterns of association, can show if the exchanges, if they do exist, are mainly between preferred social partners (Oda, 1996). As this protocol can not be easily followed in conjunction with the focal animal scheme, I suggest that the two methods are alternated and this one could be used in conjunction with a focal behaviour data collection, including more details as specified below.

Co-ordination of group travel was one of the possible specific functions for this call (more related to situations of apparent indecision). Thus, to address this possibility, it is necessary both a better understanding of how travelling is organised and also a more rigorous sampling of the above mentioned *ad libitum* observations in connection with this proposal. As black howler groups are not very large and normally travel in single lines, probably the most important issue in travel co-ordination is the initiation of group movement. Accordingly, one should register all attempts to start a group travel session. A preliminary definition of an attempt could be: a situation whereby an animal starts travelling after a resting or feeding session, moving away from the nearest individual more than  $x$  meters ( $x$  being for example a proportion of the diameter of troop dispersion). Some of the criteria used by Sue Boinski in her studies of co-ordination of group travel (Boinski, 1991, 1993) could be useful as well. For

example, noting if the group started moving within 10 minutes of an attempt, the azimuth taken with respect to the initial alignment of the initiator with the rest of the troop, and so on. If all the animals in the group start moving in the same direction of an attempt, it is deemed successful, otherwise is a failure. In the successful cases it is interesting to note the time lag between the attempt and the last animal to start moving. A distribution of those latencies should provide a more objective evaluation of those cases in which there seems to be “resistance” to follow. One should pay special attention to conflicting initiation attempts, leading to real or potential group splitting and attempts to change group direction. A possible criterion is to register if an animal starts moving in a direction that deviates more than, say, 30 degrees from the current one.

To investigate if the younger animals are attempting to manipulate older animals with the calling behaviour, the study should look at the time that took for an animal to give up since it first started calling, and how this relates to the inferred seriousness of the stress, especially at the time they were not provided much help. For example, when analysing the event ‘gap crossing’, if the infants call only when stressed, they should call only in larger gaps (ones that they had to take a detour or give up completely if help is not provided). If trying to manipulate, an infant would call in all sorts of gap, but give up more easily *and* cross shorter ones, and keep calling for longer ones. Another possible test uses latencies to call and duration of the calling bout. If a call is related to anxiety levels, then the following prediction applies: the higher the anxiety (as measured by the time it spent calling before the termination of the stress or by another indicator such as frequency of self-directed behaviours), the shorter should be the latency to call after the event, and the longer should be the duration of the bout after the “cessation” event. Alternatively, if a call is manipulative, no difference should be found either in latency to call or in the duration of the bout after the cessation, with respect to different anxiety levels.

Also, given the potential of *moos* to be part of a response system, this call is also suitable for focusing on the psychological mechanisms behind call production and intentionality of vocal responses, especially with the use of playbacks (see Cheney et al., 1996; see Rendall et al., 2000).

As a discussion on observational designs that could help us to advance further steps in understanding calls connected to stressful situations will be made

in the chapter dealing with the *screech* complex of calls, the reader is referred to that chapter.

### 3.6 Summary

The functional significance of the *moo* call, a low amplitude vocalisation is analysed. In terms of its acoustic structure, the *moo* calls are tonal signals, which possesses their main acoustic energy at low frequency ranges, with no significant frequency modulation (only a convex ascent and descent in frequency spanning a small range), and with few harmonics.

During emissions of this call type group spread was shown to be high, being reduced after the emissions. The smallest call rates were associated with feeding, while the highest rates were linked to travelling. These results strongly support a contact function for *moos*. Anecdotal observations indicate several possible specific functions, such as maintenance of contact in situations likely to lead to separation or with dispersed group members, co-ordination of group travel, and regaining lost contact.

Infants present a significantly higher call rate. For this age class, *moos* are related to stressful situations. Proximate functions could not be determined and three non-exclusive hypotheses were suggested: indication of emotion; indication of physical needs; and manipulation. The ultimate function seems, in most cases, to be the elicitation of a care-giving response, although an indication of retaliation/disagreement could occur (alongside other calls) during unwanted interactions. A detailed design was proposed to both strengthen the findings reported here and to investigate the possible specific functions.

## CHAPTER 4: SCREECH COMPLEX

“Squeaks are also given in discomfort. They may be heard from hungry animals, and when on one occasion a pet lemur had drunk enough beer to feel a little ill, he continued to squeak at intervals for several hours sitting by himself.”  
Andrew (1963) p. 30

### Abstract

In virtually every primate species whose vocal behaviour has been studied in detail, infants and juveniles produce conspicuous and/or frequent vocalisations in situations that can be classified as distressful. The general interpretation is that these calls mainly work to elicit or adjust care-giving responses. In a preliminary study, a set of vocalisations of immature black howler monkeys (*screeches*, *cries* and *screech-cries*) seemed to be emitted in stressful contexts (due to the possible structural relatedness, in addition to the functional one, the calls were grouped under the name *screech* complex). Here I present data to investigate this possibility and to try to verify if they have different functions. In the contexts studies, all three call types were significantly associated with the period in which stress was presumed to be higher, but not uniformly so. Thus, they were uttered more often before than after crossing a gap, but only *screeches* occurred significantly more often after conflicts of interest. The latency from the start of an invitation to play to the first call after it was significantly shorter than the time since the previous call, for all three vocalisations. However, *screech-cries* were the calls emitted more often in this context. Along with anecdotal observations, it seems that each of the vocalisations relate to a slightly different set of circumstances, and performed a somewhat different role. *Screeches* seemed to be emitted in situations where the individual needed or wanted help or care, or in which access to a desired item was hindered; *cries* appeared to be particularly produced during more intense or prolonged stress; and *screech-cries* seem to represent mild or defensive threats or submissive signals. I propose a detailed design for future studies to test the ideas proposed and to tackle unresolved questions.

## 4.1 Introduction

Infant and juvenile primate calls have generated considerable attention among researchers interested in vocal behaviour. However, contrary to the case with some more typically adult calls (contact, alarm, etc.), there are few studies that concentrate on the function of the vocalisation(s) per se. Instead, the calls of young primates are often analysed as part of a study with some quite distinct aim. As examples one can cite the study of vocal development (Biben & Bernhards, 1995; Hauser, 1993; Lieblich et al., 1980; Newman, 1995; Newman & Symmes, 1982; Snowdon, 1997; Zimmermann, 1990; Zimmermann, 1995) or the issue of recognition (by peers, mother, etc.) of infant calls (Cheney & Seyfarth, 1980; Kaplan et al., 1978; Snowdon et al., 1985; Symmes & Biben, 1985). Although these research programmes have generated a wealth of interesting data, one is left with a less rich body of knowledge concerning the calls themselves.

Most of the available information on structure, function and contexts of infant and juvenile calls is found within repertoire studies, whose aim is often a description of the vocal behaviour of a species (Bermejo & Omedes, 1999; Daschbach et al., 1981; Epple, 1968; Harcourt et al., 1993; Hohmann & Herzog, 1985; Macedonia, 1993; Marler, 1972; Moody & Menzel, 1976; Moynihan, 1966; Palombit, 1992; Pola & Snowdon, 1975; Robinson, 1979; Winter et al., 1966). General socio-ecological studies or preliminary field studies are an additional source of information (e.g. Carpenter, 1934; Charles-Dominique, 1977; e.g. Oppenheimer & Oppenheimer, 1973).

### 4.1.1 Distress calls

In many studies, it is common to find descriptions of vocalisations produced by immatures in a variety of stressful situations, here labelled “distress calls”. Thus, for example, Macedonia (1993), in his section devoted to infant *Lemur catta*, describes various calls, emitted in a range of circumstances from discomfort to extreme fright. Similarly, Epple (1968), in a repertoire work involving several callitrichid species, also reports infantile distress calls for *Callithrix jacchus* and *Saguinus oedipus*. Immature lion-tailed macaques utter

calls when in isolation and during aggressive interactions (Hohmann & Herzog, 1985). To complete with an ape example, infant and juvenile bonobos emitted screams when isolated, while infants gave peep yelps and peeps when prevented from nursing (Hohmann & Fruth, 1994).

In some works there is only a generic mention of “disturbed” infants or “distress” contexts (see Winter, 1978; Daschbach *et al.* 1981). Other authors, however, specify, with more or less detail, the circumstances in which vocalisations are produced, and even when not labelled as distress calls, many can be clearly related to a distress context. Examples include different degrees of separation with the mother or the group (Bermejo & Omedes, 1999; Charles-Dominique, 1977; Chivers, 1975; Epple, 1968; Hohmann & Herzog, 1985; Macedonia, 1993; Marler, 1972; Moody & Menzel, 1976; Pola & Snowdon, 1975; Tenaza, 1976), uncomfortable physical stimulation or rough play (Charles-Dominique, 1977; Chivers, 1975; Epple, 1968; Macedonia, 1993), prevention from suckling (Bermejo & Omedes, 1999; Harcourt *et al.*, 1993; Macedonia, 1993; Marler, 1972), aggressive or agonistic interactions (Hohmann & Herzog, 1985; Macedonia, 1993; Palombit, 1992), incapability of continuing movement (Harcourt *et al.*, 1993; Macedonia, 1993; Palombit, 1992; Robinson, 1979), hunger (Epple, 1968; Moody & Menzel, 1976), improper alloparental care (Todt, 1988; Todt *et al.*, 1995), and removing the infant from its carrier’s back (Epple, 1968; Moody & Menzel, 1976; Winter *et al.*, 1966). Isolation from the mother, peers or social group seems to be nearly universal in eliciting distress calls.

#### 4.1.2 Howler monkey distress calls

Information on immature howler monkey calls is, not surprisingly, scarce and concentrated mostly on *Alouatta palliata*. Thus Carpenter (1934), in his very detailed account of mantled howler behaviour, describes a series of distress vocalisations emitted by young animals. He noted emission of *cries* by fallen infants and of little *chirping squeals* in a “situation provocative of play”. He described one instance of *cry* emission by an infant faced with a gap it could not cross. Altmann (1959), working in the same field site, expands the repertoire and describes a *whimper* that “seemed to be given by immature monkeys in frustrating situations” (e.g. prevention from suckling and prevention from

making a crossing). Both works predate the use of spectrograms to represent vocalisations. Baldwin and Baldwin (1976), still working with the same species, provide an extensive repertoire with several spectrograms. They divided the *whimper* in three sub-categories and mention a variety of situations in which they were emitted by immatures and also adults, including “mildly startled, surprised, threatened or pestered” juveniles and rough play. They also added a few more distress calls. Among those, there were *caws* uttered by infants when they were lost or if the mother refused contact. Older infants and juveniles produced *yelps* and *screeches* when “a large animal startled, lunged at or swatted at” them, and infants *squeaked* and sometimes *barked* when involved in rough play and trying to escape. Finally, Calegario-Marques and Bicca-Marques (1995) published a brief account of *A. caraya* vocalisations, restricted to a short verbal description of the types of call and the situations of use. They refer to: a stress call produced by infants of both sexes and juvenile and sub-adult females in aggressive situations, play and attempts of allomaternal care; a *snarl*<sup>1</sup> emitted by all age-sex classes in stress situations (with no further details), and play; and a *cry* uttered by infants and juveniles in stressful situations (referring to separation from the group as an example).

During my pilot study, I noticed that a group of calls emitted primarily by immatures (*screeches*, *cries*, and *screech-cries*, named collectively here as the *screech* complex) seemed to be related both structurally and functionally. All of them, along with the *moo* calls discussed in the previous chapter, appeared to be chiefly associated with various distressful situations. These included prevention from suckling, being removed from the carrier’s back, lagging behind while following a mother, facing a wide gap, receiving a mock bite, being prevented from interacting with a newborn, among others. In this chapter, I am going to focus on this particular group of calls. Although largely produced by immatures, I will also present the data on the adult usage, and highlight the possible similarities and differences. My aim here is to go a step beyond typical repertoire studies and substantiate the above impressions with quantitative data and also to propose hypotheses on the possible functions played by each of the types or the complex as a whole. This should provide a sound basis for the advancement of

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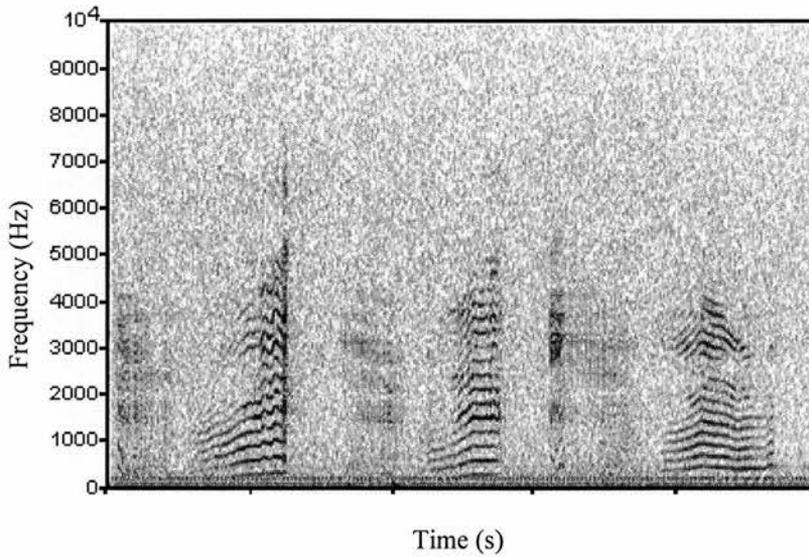
<sup>1</sup> The names of the call types were translated by me from the Portuguese names provided.

study of these call types, and allow their subsequent use to answer other research questions.

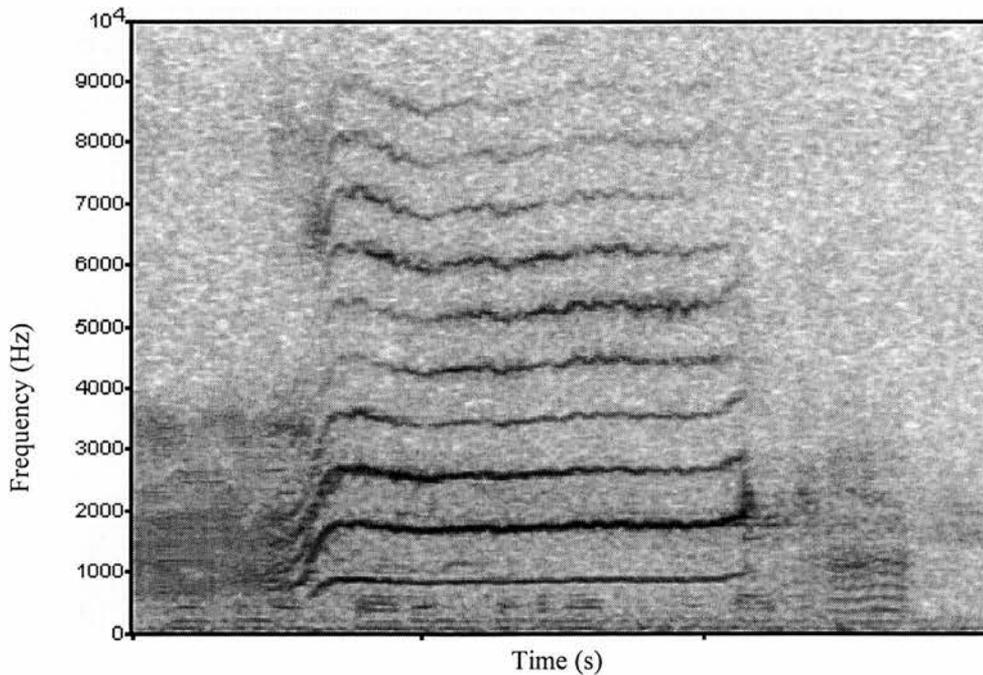
#### 4.1.3 Study calls

*Screeches* (see Figure 4.1) are quite variable calls whose diagnostic feature is a 2-unit structure. In their most typical form the calls consist of a noisy unit followed by a tonal one. The noisy unit is composed of a wide band of noise with a raspy characteristic (in some spectrograms this unit appears as if it was composed of a series of closely spaced clicks). Occasionally it is possible to see a rich harmonic structure subjacent to it. The unit may at times start with a tonal section, frequency modulated in a quavering way, which soon gives way to the noisy sound. In a variant, the noisy band is substituted by a tonal sound, highly frequency modulated in a quavering way (a *cry*, see below). The tonal unit generally presents a low fundamental, a rich harmonic structure, with as many as 10-15 overtones, and an upswing frequency modulation. However, it can present variation in terms of: harmonic content, presence or absence of frequency modulation, general shape of the frequency modulation (upswing and slightly convex are the most common forms), and the presence of quavering. Each cycle lasts approximately 1s. This call type is commonly emitted in bouts of closely spaced calls.

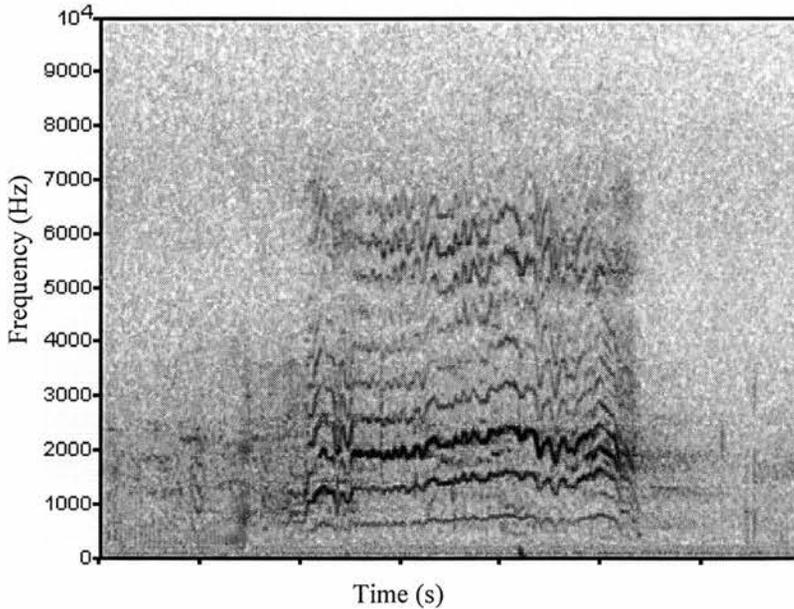
*Cries* are relatively long calls (between 1 and 2s), characteristically high pitched and tonal, with many overtones and energy normally concentrated on the second and third harmonic (see Figure 4.2 and Figure 4.3). The fundamental frequency, as judged from the spectrograms, is higher than the tonal units of *screeches*, which they resemble. Frequency modulation is typically quavered, although some nearly whistle like calls may occur. As with all types in the complex, there is considerable variability in this vocalisation, and it can merge in variable degrees with the others (compare Figure 4.2 and Figure 4.3). Rarely produced in isolation, it usually follows or is followed by *screeches*, *screech-cries* or *moos*.



**Figure 4.1** Sequence composed of 3 *screeches*. Note the variability in the shape of frequency modulation and in the presence of quavering of the tonal unit. Gaussian window. Time window: 0.03 s. Bandwidth = 43.3 Hz. Increments on the x-axis represent 0.5s intervals.

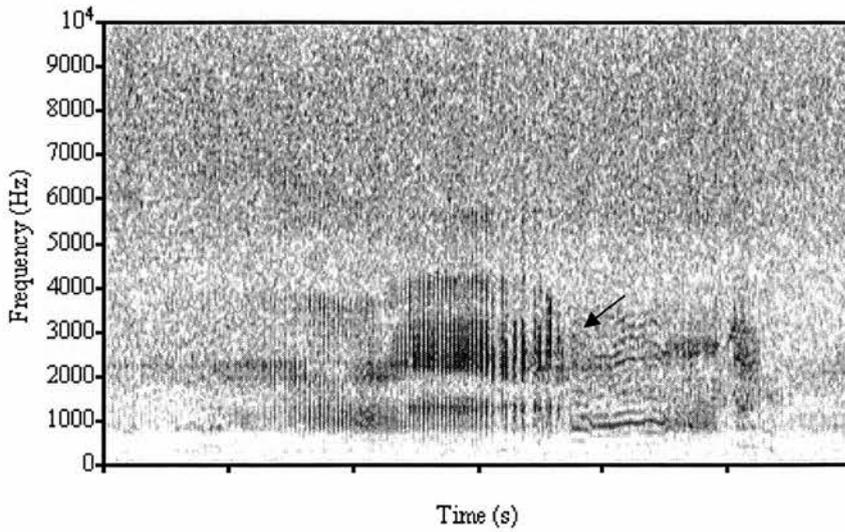


**Figure 4.2** *Cry* call preceded and followed by atonal components. Note the quavering frequency modulation, and the higher pitch with respect to the tonal units of a screech. Gaussian window. Time window: 0.04s. Bandwidth = 32.5 Hz. Increments on the x-axis represent 0.5s intervals.

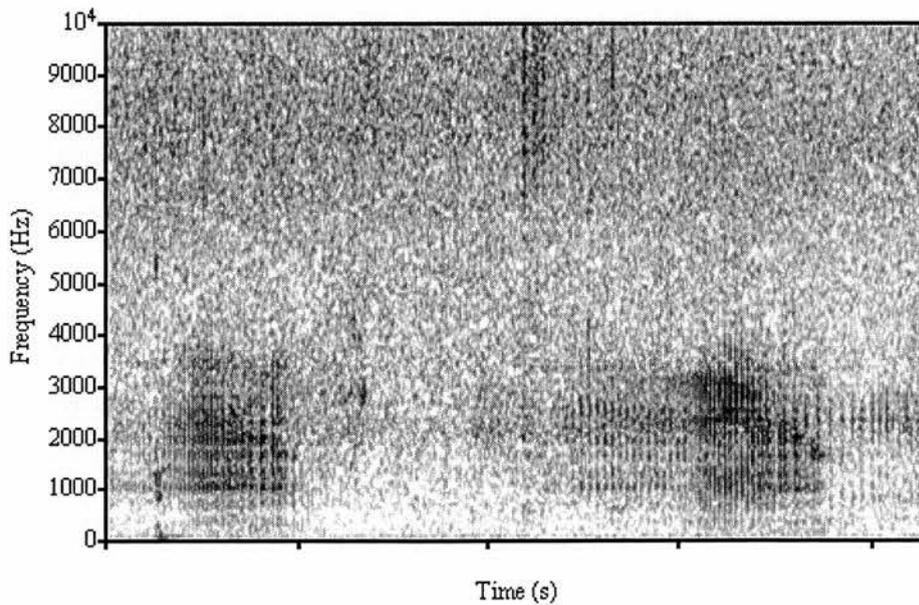


**Figure 4.3 Spectrogram of a *cry* call. Note the longer duration and the intense quavering. Energy still concentrates on the 2nd and 3rd harmonics. Gaussian window. Time window: 0.04s. Bandwidth = 32.5 Hz. Increments on the x-axis represent 0.5s intervals.**

Contrary to *cries*, the *screech-cries* are noisy, atonal sounds, covering a broad range of frequencies, mostly between 1 and 4 kHz, that bear a resemblance to the atonal unit of *screeches*. They have a chattering character, which becomes clear in spectrograms using short windows, as they are composed of a series of shortly spaced clicks. Sometimes it is possible to see two or 3 darker bands (formants?). This call is also highly variable, and towards the end of the study at least two variants could be perceived, the typical *screech-cries* and ones with connection to *moos*.



**Figure 4.4** Spectrogram of a *screech-cry*. Note the closely spaced bursts of sounds and the two bands of noise. At the arrow transition to another call type. Gaussian window. Time window: 0.02s. Bandwidth = 64.9 Hz. Increments on the x-axis represent 0.5s intervals.



**Figure 4.5** Spectrogram of two *screech-cries*. It is possible to see the individual clicks but individual bands are not clear. Gaussian window. Time window: 0.02s. Bandwidth = 64.9 Hz. Increments on the x-axis represent 0.5s intervals.

## 4.2 Methods

### 4.2.1 Predictions

Following the basic analytic procedures, I first looked to see whether each of the call types was associated with a given age-sex class and also to a given behavioural state. Following that, I attempted to verify if each of this set of related vocalisations is related to particular stressful situations. Under the hypothesis that the calls from the *screech* complex are linked to anxiety or distress levels, I made two predictions:

1. Infants and juveniles should call more *before* the termination of a stressful situation than after. This prediction can be tested in two ways. The first is to compare calling rates in equal time periods before and after the cessation of the stressful situation (as signalled by the occurrence of a critical event). The alternative is to compare the number of instances in which the animals called more before than after the termination with the number of cases in which the individuals called more after the cessation of the stress;
2. Conversely, infants and juveniles should call more after than before an event that signals the start of a stressful situation. A related prediction is that the time lag between a stressful event and the last preceding call is larger than the latency between the critical event and the first succeeding call.

To test the first prediction, I chose the event 'gap crossing'. The reason for the choice is that, for infants, gaps too wide to be easily crossed are likely to represent a stressful situation because of the separation from the mother or the group. During the whole course of the study, I noticed that infants presented a suite of behaviours when faced with a wide gap that indicated that these situations seemed indeed to be stressful. Since it was not always possible to discern exactly when an animal came across a gap (the stressful event), particularly a non-focal one, I analysed the cessation of the condition. The data included both *ad libitum* notes stating that a youngster had crossed a wide gap, by whichever means employed (e.g. using another as a bridge, riding the back of

another animal, jumping) or had either given up or taken a detour. I also used the regularly collected behavioural category ‘bridge’.

To test the second prediction, I studied two other events from the point of the start of the supposed stress, ‘conflicts’ and ‘invitation to play’. The first one includes the following events (all regularly collected): carrier removing the infant from its back or preventing access to it; mother preventing other infants from interacting with a newborn; and mock or real bites. All these events represent a conflict of interest between the immature and another animal, as the first were either prevented from continuing to perform an action, or they were prevented from obtaining access to something they apparently wanted. The justification for lumping the events was outlined before (see Chapter 3). Invitation to play was operationally defined during the study as any instance when an animal bites or pulls a part of another individual’s body in a non-aggressive context. At times, the invited animal prevents the attempts, and does not engage in play, or is slow to do so, and this is accompanied by facial displays and calling, presumably related to the discomfort or uneasiness of the situation. I considered the calling of both the actor and the recipient: non-receptive behaviour on the part of the recipient might generate frustration on the actor, and invitations of dominant or larger individuals might be accompanied by calling to prevent agonistic behaviour. Invitations to play also included interaction with newborn and very small infants, which took the form of attempts to touch or pull the newborn. In those cases, it was not uncommon for the mother to block the attempts or interrupt an interaction.

#### *4.2.2 Data analysis*

To compare call occurrence before and after the ‘gap crossings’ and ‘conflicts’, I first excluded those instances with equal numbers of calls before and after the event, including the cases with no calls at all. For the remaining occurrences, I computed the number of cases when the animal called more before the critical event than after (‘call before’) and the reverse (‘call after’). I considered both 5 and 1-minute periods bordering the event for these calculations. Another procedure was to construct graphs of likelihood of calling

in consecutive time bins of equal length both before and after the event, to check the profile of the calling behaviour surrounding the event of interest.

For the event ‘invitation to play’, I tested the second prediction using only time lags between calling and the behaviour, due to practical reasons. To do so, I calculated the time lag between the event and the last occurrence of a given call type *before* it, and also the latency between the invitation and the first emission of the call *after* it. I did these calculations both for the actor and the recipient of the invitation.

The problem of multiple occurrences of the target event close in time to each other was dealt with in similar ways as in chapter 3 for the events ‘gap crossing’ and ‘conflict’. For the analysis of latencies between a call and the event ‘invitation to play’ I did not need any special criterion. Through the way that the data are retrieved, a given call could never be counted twice in the same category (before or after an event). However, calls emitted between two instances of ‘invitation to play’ could be (and were) counted twice, in different categories, but only if there was just one call between the events. In these situations, the call was used to calculate the latency after the first event and the latency before the second. As with the other criteria, this is a conservative procedure.

All the analyses were performed on each call type separately.

#### 4.2.3 Statistical procedures

To verify if individuals had similar call rates, I used a goodness-of-fit chi-square test. To compare call rate between states, I applied a goodness of fit test on each individual that had a non-trivial sample size. The observed number of calls on each state was compared to the expected values had the animal called in proportion to the time it spent on the behavioural state. For *screech cries*, I could also test the rates using a one-way ANOVA. First, I tested each state for normality and homoscedasticity (call rates of each individual were the data points). I then proceeded with the test itself, with the states being the different treatments and the individuals comprising the data points. Post-hoc test employed was Tukey’s Honest Significant Difference (HSD).

To compare call occurrence before and after ‘gap crossings’ and ‘conflicts’, I tested the two figures: ‘call before’ and ‘call after’ (see above)

against a 1:1 hypothesis (equal number of cases classified as ‘call before’ and ‘call after’) with a binomial test.

I used Mann-Whitney tests to compare the latencies of ‘invitations to play’ with respect to the last and the first occurrence of a call type (before and after the invitation respectively).

Power analysis was conducted whenever possible due to the available options of the software utilised.

### 4.3 Results - Individual differences and association with behavioural states

When considering overall number of emissions of a given call type, there are reasons to believe that the figures underrate the real values. I certainly missed many calls emitted by non-focal animals, merely due to the focusing of attention on another individual. This is evident when comparing call rate during focal hours (when there are probably just a few missed calls) with the figures calculated over the whole study (see Tables, 1, 3 and 5), the second value being much smaller than the first, although they should be similar.

#### 4.3.1 Screeches

During the main study I registered 2751 *screeches*, giving an average rate of 2.04 calls per hour of observation. Apart from the general source of underestimation cited above, for this call type there is an additional one. During part of the study I registered a bout of *screeches* merely by noting its start and end: the actual number of calls in between is unknown for these cases, and yet they contributed only one data point to the pool.

#### **Individual differences**

As it is clear from Table 4.1 that this is an almost exclusive infant/juvenile call, I tested for individual differences among individuals from these classes only, using the focal rates since they constitute more reliable estimates of the individual rates. Comparing individuals 7, 8, 10-13 (all infants and juveniles) shows that they do differ in call emission:  $\chi^2 = 283.3$ ,  $p < 0.001$ ,  $df = 5$ ,  $n = 423$ , (power to detect a medium effect approaches 1). The smallest animals (10, 11, 12, and 13) produced at least 10 times as many calls as the older individuals (7, 8). Restricting the analysis to the animals for which I had data during the dependency period (10-13) shows that they still differ in call production:  $\chi^2 = 19.8$ ,  $p < 0.001$ ,  $df = 3$ ,  $n = 405$  (power to detect a medium effect approaches 1). However, excluding infant 13, which was present only

during a short period, and it was dependent for the whole time, shows that individuals 10-12 do not have different values of call emission ( $\chi^2 = 1.89$ ,  $p > 0.05$ ,  $df = 2$ ,  $n = 376$ , power to detect a medium effect approaches 1).

**Table 4.1 Frequency of *screeches* and call rate per individual considering both the whole data set and only the focal periods.**

| Individual        | n (total) <sup>a</sup> | Call rate <sup>b</sup> | n (focal hours) <sup>c</sup> | Call rate (focal hours) <sup>d</sup> |
|-------------------|------------------------|------------------------|------------------------------|--------------------------------------|
| 1 (Ad. ♂)         | 0                      | 0                      | 0                            | 0                                    |
| 2 (Ad. ♂)         | 0                      | 0                      | 0                            | 0                                    |
| 3 (Sub-ad. ♂)     | 0                      | 0                      | 0                            | 0                                    |
| 4 (Sub-ad. ♂)     | 3                      | 0.002                  | 1                            | 0.010                                |
| 5 (Ad. ♀)         | 1                      | 0.001                  | 0                            | 0                                    |
| 6 (Ad. ♀)         | 7                      | 0.005                  | 4                            | 0.037                                |
| 7 (Juv. ♀)        | 31                     | 0.023                  | 6                            | 0.065                                |
| 8 (Juv. ♀)        | 30                     | 0.022                  | 12                           | 0.125                                |
| 9 (Sub-ad./Ad. ♀) | 2                      | 0.001                  | 0                            | 0                                    |
| 10 (Inf./Juv. ♀)  | 531                    | 0.393                  | 126                          | 1.389                                |
| 11 (Inf./Juv. ♀)  | 726                    | 0.537                  | 158                          | 1.635                                |
| 12 (Inf./Juv. ♂)  | 324                    | 0.343                  | 92                           | 1.491                                |
| 13 (Inf. ♀)       | 107                    | 0.549                  | 29                           | 3.348                                |
| Unidentified      | 989                    | 0.732                  |                              |                                      |
| Total             | 2751                   | 2.036                  |                              |                                      |

<sup>a</sup> Number of calls that could be assigned to an individual considering the focal samples of all animals together.

<sup>b</sup> Total number of calls assigned to each individual divided by the total number of data collection hours (from all animals together). For individuals 12 and 13 I considered the sum of the data collection times of all animals only during the period that each individual was present.

<sup>c</sup> Number of *screeches* emitted by an individual considering its focal samples only.

<sup>d</sup> Call rate in this column was calculated dividing those calls emitted by a given animal during its focal data collection by the data collecting time of the individual concerned only, and excluding periods of no visibility.

### Differences in calling between behavioural states

Observing calling rate across different behavioural states (Table 4.2), only a few animals provide non-trivial rates of calling (the immatures 10, 11, 12 and 13). Therefore, I examine only these individuals statistically. Comparing the number of calls in each state with the value that would be expected if the calls

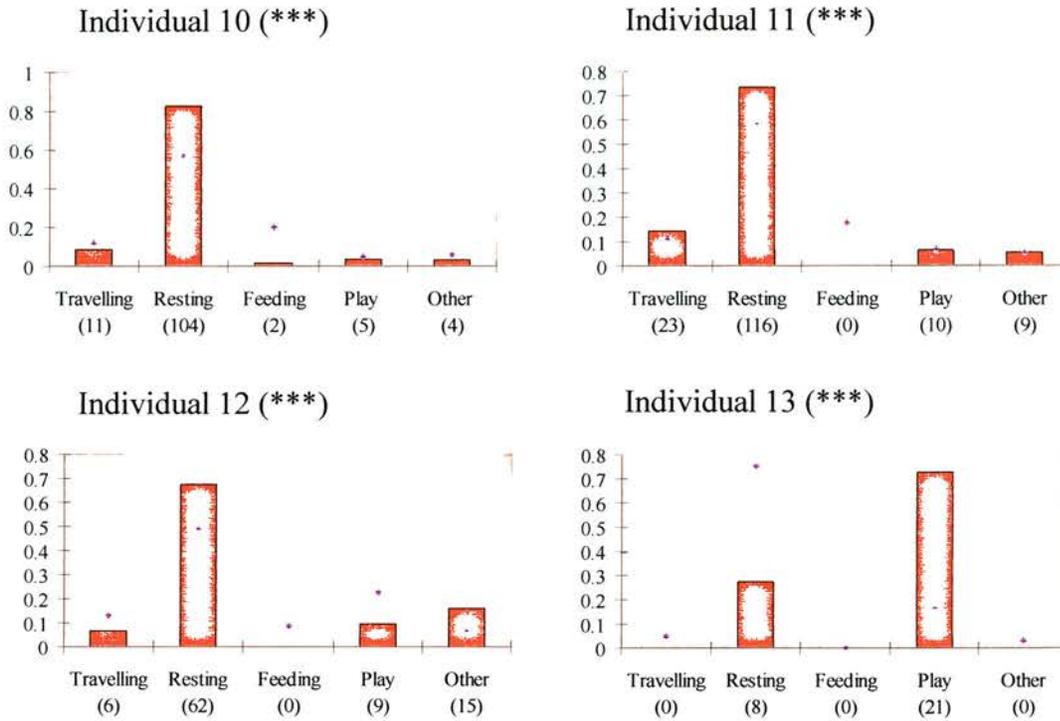
were produced according to the proportion of time spent on the state showed significant differences for all individuals analysed: Ind.10:  $\chi^2 = 38.6$ ,  $p \ll 0.001$ ,  $n = 126$ , power = 0.776; Ind. 11:  $\chi^2 = 35.7$ ,  $p \ll 0.001$ ,  $n = 158$ , power = 0.8722; Ind. 12:  $\chi^2 = 36.3$ ,  $p \ll 0.001$ ,  $n = 92$ , power = 0.6218; Individual 13:  $\chi^2 = 63.6$ ,  $p \ll 0.001$ ,  $n = 29$ , power = 0.2421 (df = 4 for all individuals except 13 for which df = 3, as feeding was not considered for this individual, power values calculated in order to detect a medium difference). Deviations from expected values follow similar patterns in the different individuals analysed (see Figure 4.6). Call emissions during resting are higher than expected, and the opposite is the case during feeding. Proportion of calls during travel and play generally follow the expected values. Infant 13 is unusual in that the proportion of call emissions during play is much higher than expected based on the time it spent on this behaviour. This infant was dependent the whole period it was present in the group (it disappeared after some time), and the data are thus restricted to very early infant development. Most of its play emissions were in the context of attempts by others to interact, by pulling or attempting to kidnap, behaviours performed regularly towards newborn and fully dependent infants. In this situation, infants invariably emit long series of calls from the *screech* complex.

**Table 4.2 Frequency of emission of screeches and call rates according to the state of the caller\***

| Individual        | Travelling | Resting    | Feeding  | Play       | Other     |
|-------------------|------------|------------|----------|------------|-----------|
| 1 (Ad. ♂)         | 0 (0)      | 0 (0)      | 0 (0)    | 0 (0)      | 0 (0)     |
| 2 (Ad. ♂)         | 0 (0)      | 0 (0)      | 0 (0)    | 0 (0)      | 0 (0)     |
| 3 (Sub-ad. ♂)     | 0 (0)      | 0 (0)      | 0 (0)    | 0 (0)      | 0 (0)     |
| 4 (Sub-ad. ♂)     | 0 (0)      | 1 (0.01)   | 0 (0)    | 0 (0)      | 0 (0)     |
| 5 (Ad. ♀)         | 0 (0)      | 0 (0)      | 0 (0)    | 0 (0)      | 0 (0)     |
| 6 (Ad. ♀)         | 0 (0)      | 4 (0.05)   | 0 (0)    | 0 (0)      | 0 (0)     |
| 7 (Juv. ♀)        | 0 (0)      | 3 (0.05)   | 0 (0)    | 3 (0.54)   | 0 (0)     |
| 8 (Juv. ♀)        | 0 (0)      | 8 (0.14)   | 2 (0.09) | 0 (0)      | 2 (0.50)  |
| 9 (Sub-ad./Ad. ♀) | 0 (0)      | 0 (0)      | 0 (0)    | 0 (0)      | 0 (0)     |
| 10 (Inf./Juv. ♀)  | 11 (1.03)  | 104 (2.00) | 2 (0.11) | 5 (1.18)   | 4 (0.74)  |
| 11 (Inf./Juv. ♀)  | 23 (2.11)  | 116 (2.06) | 0 (0)    | 10 (1.50)  | 9 (1.61)  |
| 12 (Inf./Juv. ♂)  | 6 (0.75)   | 62 (2.05)  | 0 (0)    | 9 (0.65)   | 15 (1.56) |
| 13 (Inf. ♀)       | 0 (0)      | 8 (1.23)   | 0 (0)    | 21 (14.29) | 0 (0)     |

\* Values outside the parentheses indicate the number of calls registered in a given behavioural state. Call rates (values in brackets) calculated dividing the number of calls emitted when on a given behavioural context (during focal periods) by the number of hours that the individual spent on it.

<sup>a</sup> Play includes attempts to interact with newborn infants and also invitations to play, besides the play behaviours *sensu strictu*. For ind. 12 and 13 includes attempts of interaction made by other animals when they were newborn.



**Figure 4.6 Comparison of the proportion of total number of *screeches* emitted on each behavioural state (solid bars, sample sizes for each state within brackets) with the proportion of time spent on each state (dots). Within brackets codes for the significance values of the chi-square test performed on the individual.**

#### 4.3.2 Cry calls

##### Individual differences

I registered 1368 emissions of this call type during the observational period, a much smaller value than for *screeches* (average rate of 1.01 calls/hour of study). Adult and sub-adult males, and also the individual 9, were very rare emitters (see Table 4.3), and were therefore excluded from further analysis. Note also that, differently from *screeches*, rates from the older juveniles (7 and 8) approximate more closely that of the younger individuals, and the adult females are not infrequent callers (with the exception of individual 9). Comparing the focal values of individuals with non-negligible number of calls (5- 8, and 10-13) shows a significant difference in call emission between them:  $\chi^2 = 130.5$ ,  $p \ll 0.001$ ,  $df = 7$ ,  $n = 320$  (power to detect a medium difference = 0.99). However, restricting the analysis to the individuals which had data during the dependent

period (10-13) demonstrates that they do not differ:  $\chi^2 = 2.58$ ,  $p > 0.5$ ,  $df = 3$ ,  $n = 217$  (power to detect a medium difference = 0.97). Note that the call rate of female 5 is much lower than that of female 6, which is similar to the older juveniles. Interestingly, female 5 seems to be the higher ranking one of the two. So, besides a clear age difference in call emission, there could also be other factors involved in call production.

**Table 4.3 Frequency of *cries* and call rate per individual considering both the whole data set and only the focal periods.<sup>a</sup>**

| Individual        | n (total) <sup>b</sup> | Call rate <sup>b</sup> | n (focal hours) <sup>c</sup> | Call rate (focal hours) <sup>d</sup> |
|-------------------|------------------------|------------------------|------------------------------|--------------------------------------|
| 1 (Ad. ♂)         | 1                      | 0.001                  | 0                            | 0.000                                |
| 2 (Ad. ♂)         | 0                      | 0.000                  | 0                            | 0.000                                |
| 3 (Sub-ad. ♂)     | 0                      | 0.000                  | 0                            | 0.000                                |
| 4 (Sub-ad. ♂)     | 6                      | 0.004                  | 1                            | 0.010                                |
| 5 (Ad. ♀)         | 52                     | 0.038                  | 9                            | 0.086                                |
| 6 (Ad. ♀)         | 107                    | 0.079                  | 24                           | 0.222                                |
| 7 (Juv. ♀)        | 65                     | 0.048                  | 25                           | 0.271                                |
| 8 (Juv. ♀)        | 140                    | 0.104                  | 45                           | 0.467                                |
| 9 (Sub-ad./Ad. ♀) | 6                      | 0.004                  | 3                            | 0.030                                |
| 10 (Inf./Juv. ♀)  | 163                    | 0.121                  | 71                           | 0.783                                |
| 11 (Inf./Juv. ♀)  | 220                    | 0.163                  | 77                           | 0.797                                |
| 12 (Inf./Juv. ♂)  | 170                    | 0.180                  | 59                           | 0.956                                |
| 13 (Inf. ♀)       | 67                     | 0.344                  | 10                           | 1.155                                |
| Unidentified      | 371                    | 0.275                  |                              |                                      |
| Total             | 1368                   | 1.013                  |                              |                                      |

<sup>a</sup> *Cries* registered for an individual considering the focal samples of all animals together.

<sup>b</sup> Total number of *cries* of each individual divided by the total number of data collection hours (from all animals together). For individuals 12 and 13 I considered the sum of the data collection times of all animals only during the period that each one was present.

<sup>c</sup> Number of *cries* emitted by an individual during focal periods.

<sup>d</sup> Number of *cries* emitted by an individual during focal periods divided by its data collecting time (excluding periods of no visibility).

### Differences in calling between behavioural states

Turning to the pattern of calling according to behavioural state (see Table 4.4), I proceeded to analyse only individuals 5-8 and 10-13 statistically, as the

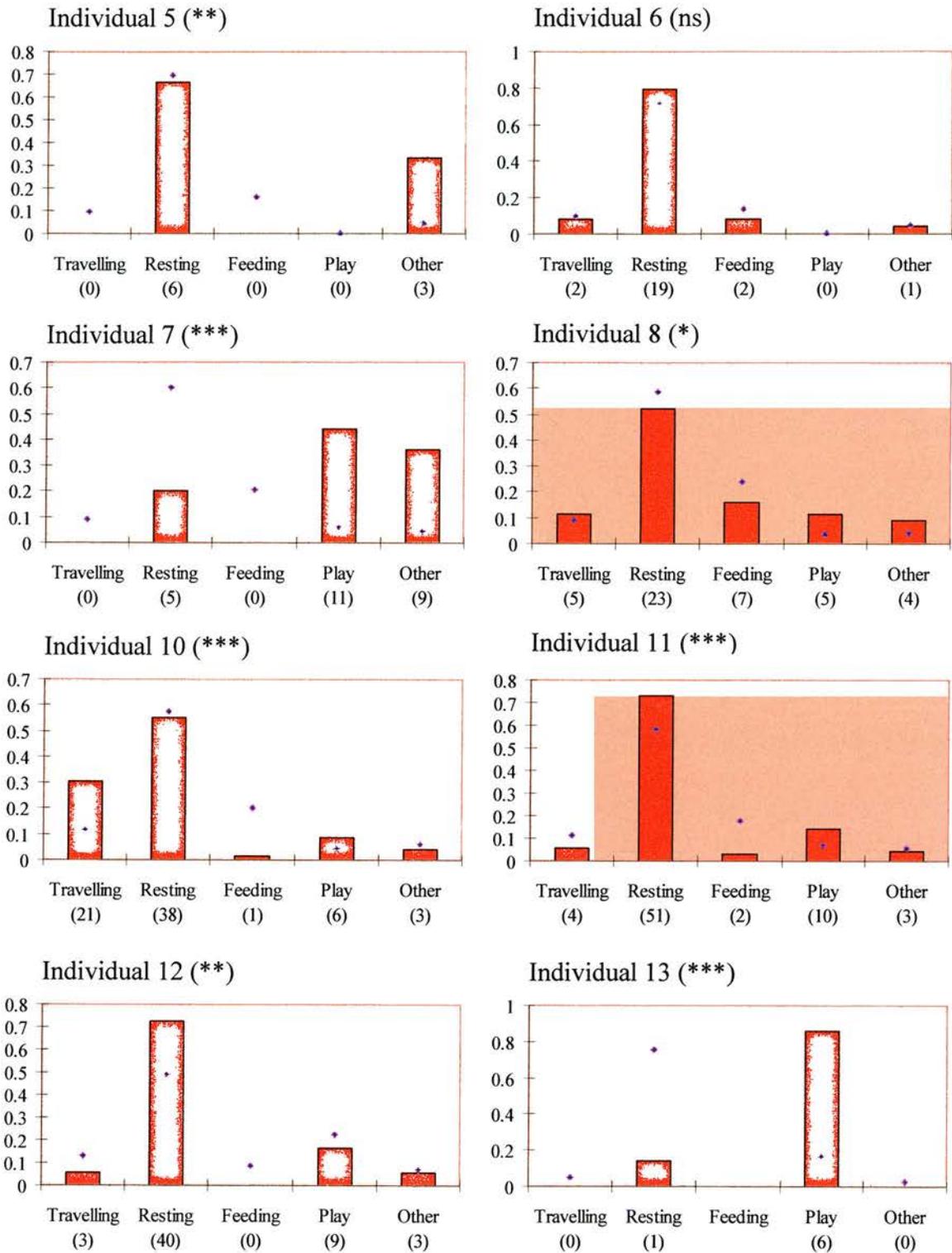
remaining ones either did not call at all or did so extremely rarely (when considering the analysed data, one should still bear in mind the smallness of the sample size of some individuals). Test results show that nearly all animals did not called in proportion to the time they spent performing a given behaviour: Ind. 5:  $\chi^2 = 18.2$ ,  $p < 0.01$ ,  $n = 9$ ; Ind. 6:  $\chi^2 = 0.74$ ,  $p > 0.05$ ,  $n = 46$ ; Ind. 7:  $\chi^2 = 131.1$ ,  $p \ll 0.001$ ,  $n = 25$ ; Ind. 8:  $\chi^2 = 10.4$ ,  $p < 0.05$ ,  $n = 44$ ; Ind. 10:  $\chi^2 = 35.2$ ,  $p \ll 0.001$ ,  $n = 69$ ; Ind.11:  $\chi^2 = 23.2$ ,  $p < 0.001$ ,  $n = 68$ ; Ind.12:  $\chi^2 = 14.7$ ,  $p < 0.01$ ,  $n = 55$ ; Ind.13  $\chi^2 = 23.5$ ,  $p < 0.001$ ,  $n = 7$  (df = 4 for all except ind. 13 for which df = 3). Power values to detect a medium difference are: Ind. 5: 0.094; Ind. 6: 0.3308; Ind. 7: 0.1892; Ind. 8: 0.317; Ind. 10: 0.4852; Ind.11: 0.4787; Ind.12: 0.3924; Ind.13: 0.0898. Looking at the difference between observed and expected proportions in different individuals (Figure 4.7) shows that there is a poor agreement between them with regard to the pattern of differences. Despite the obvious problems with sample sizes, a possible reason for the lack of a general agreement is that this call type could be linked to a class of behavioural events that do not depend much on the behavioural state. Thus, for example, a food attraction call is associated with feeding by definition, while calls related to agonistic behaviours can occur in a wide variety of behavioural states. However, a few trends are suggested by the graphs. Calling during feeding and, in general, travelling is lower than expected, while play figures are generally higher than expected (excluding the adult females, which almost never play). The extreme disparity between observed and expected values during play for the infant 13 are due to the inclusion of situations in which other animals attempted to interact with the newborn. These occasions were accompanied by prolonged bouts of calling.

**Table 4.4 Frequency of emission of *cries* and call rates according to the state of the caller\***

| Individual        | Travelling | Resting   | Feeding  | Play <sup>a</sup> | Other    |
|-------------------|------------|-----------|----------|-------------------|----------|
| 1 (Ad. ♂)         | 0 (0)      | 0 (0)     | 0 (0)    | 0 (0)             | 0 (0)    |
| 2 (Ad. ♂)         | 0 (0)      | 0 (0)     | 0 (0)    | 0 (0)             | 0 (0)    |
| 3 (Sub-ad. ♂)     | 0 (0)      | 0 (0)     | 0 (0)    | 0 (0)             | 0 (0)    |
| 4 (Sub-ad. ♂)     | 0 (0)      | 0 (0)     | 1 (0.05) | 0 (0)             | 0 (0)    |
| 5 (Ad. ♀)         | 0 (0)      | 6 (0.08)  | 0 (0)    | 0 (0)             | 3 (0.62) |
| 6 (Ad. ♀)         | 2 (0.19)   | 19 (0.24) | 2 (0.14) | 0 (0)             | 1 (0.19) |
| 7 (Juv. ♀)        | 0 (0)      | 5 (0.09)  | 0        | 11 (1.99)         | 9 (2.2)  |
| 8 (Juv. ♀)        | 5 (0.56)   | 23 (0.41) | 7 (0.30) | 5 (1.32)          | 4 (0.99) |
| 9 (Sub-ad./Ad. ♀) | 0 (0)      | 0 (0)     | 3 (0.16) | 0 (0)             | 0 (0)    |
| 10 (Inf./Juv. ♀)  | 21 (1.96)  | 38 (0.73) | 1 (0.05) | 6 (1.41)          | 3 (0.55) |
| 11 (Inf./Juv. ♀)  | 4 (0.37)   | 51 (0.90) | 2 (0.12) | 10 (1.50)         | 3 (0.54) |
| 12 (Inf./Juv. ♂)  | 3 (0.38)   | 40 (1.32) | 0 (0)    | 9 (0.65)          | 3 (0.31) |
| 13 (Inf. ♀)       | 0 (0)      | 1 (0.15)  | 0 (0)    | 6 (4.08)          | 0 (0)    |

\* Values outside the parentheses indicate the number of calls registered in a given behavioural state. Call rates (values in brackets) calculated dividing the number of *cries* emitted when on a given behavioural context (during focal periods) by the number of hours that the individual spent on it.

<sup>a</sup> Play includes attempts to interact with newborn infants and also invitations to play, besides the play behaviours *sensu strictu*. For ind. 12 and 13 includes attempts of interaction made by other animals when they were newborn.



**Figure 4.7 Comparison of the proportion of cries emitted on each behavioural state (solid bars, sample sizes for each state within brackets) with the proportion of time spent on each state (dots). Within brackets codes for the significance values of the chi-square test performed on the individual.**

### 4.3.3 Screech-cries

#### Individual differences

I recorded 2276 occurrences of *screech-cries* throughout the study, which gives an average of 1.7 calls registered per hour of observation. As has been the case with all calls analysed so far, individuals differ significantly in their rate of calling ( $\chi^2 = 402.13$ ,  $p \ll 0.001$ ,  $df = 8$ ,  $n = 686$ , power to detect a medium difference approaches 1; analysis conducted on individuals 5-13 only, see Table 4.5). This applies even for a comparison between the individuals 10 through 13, for which I had data during the dependent period in their infancy ( $\chi^2 = 75.72$ ,  $p \ll 0.001$ ,  $df = 3$ ,  $n = 418$ , power to detect a medium difference approaches 1). However, the ordering of animals with respect to their call rate and the relative magnitude between them is roughly similar to the one observed for the *cries*, except that individual 9 is a frequent emitter of *screech-cries* but not of *cries*, and the opposite happens with individual 8. Thus, the data shows significant individual differences, which seem to be partially due to age effects, on top of which individual effects apply.

**Table 4.5 Frequency of *screech-cries* and call rate per individual considering both the whole data set and only the focal periods.<sup>a</sup>**

| Individual        | n (total) <sup>b</sup> | Call rate | n (focal hours) <sup>c</sup> | Call rate (focal hours) |
|-------------------|------------------------|-----------|------------------------------|-------------------------|
| 1 (Ad. ♂)         | 0                      | 0.000     | 0                            | 0.000                   |
| 2 (Ad. ♂)         | 1                      | 0.001     | 0                            | 0.000                   |
| 3 (Sub-ad. ♂)     | 3                      | 0.002     | 2                            | 0.019                   |
| 4 (Sub-ad. ♂)     | 17                     | 0.013     | 7                            | 0.067                   |
| 5 (Ad. ♀)         | 70                     | 0.052     | 12                           | 0.115                   |
| 6 (Ad. ♀)         | 255                    | 0.189     | 86                           | 0.794                   |
| 7 (Juv. ♀)        | 174                    | 0.129     | 80                           | 0.867                   |
| 8 (Juv. ♀)        | 133                    | 0.098     | 31                           | 0.322                   |
| 9 (Sub-ad./Ad. ♀) | 139                    | 0.103     | 59                           | 0.596                   |
| 10 (Inf./Juv. ♀)  | 360                    | 0.266     | 136                          | 1.499                   |
| 11 (Inf./Juv. ♀)  | 323                    | 0.239     | 121                          | 1.252                   |
| 12 (Inf./Juv. ♂)  | 271                    | 0.287     | 117                          | 1.896                   |
| 13 (Inf. ♀)       | 177                    | 0.909     | 44                           | 5.080                   |
| Unidentified      | 353                    | 0.2615    |                              |                         |
| Total             | 2276                   | 1.685     |                              |                         |

<sup>a</sup> Calls registered for an individual considering the focal samples of all animals together.

<sup>b</sup> Total number of *screech-cries* of each individual divided by the total number of data collection hours (from all animals together). For individuals 12 and 13 I considered the sum of the data collection times of all animals only during the period that each one was present.

<sup>c</sup> Number of calls emitted by an individual during focal periods.

<sup>d</sup> Number of calls emitted by an individual during focal periods divided by its data collecting time (excluding periods of no visibility).

### Differences in calling between behavioural states

As a larger number of animals presented calling rates that were not negligible (see Table 4.6), it was possible to compare the states using a one-way ANOVA (with the individuals as the data points). Using the data from individuals 6 through 12 shows that call rates were normally distributed in all states, except for feeding: Shapiro-Wilk test statistics and significance values for travelling, resting, feeding, play, and others are respectively 0.899 ( $p > 0.05$ ,  $df = 7$ ), 0.910 ( $p > 0.05$ ,  $df = 7$ ), 0.606 ( $p < 0.001$ ,  $df = 7$ ), 0.840 ( $p > 0.05$ ,  $df = 7$ ), and 0.864 ( $p > 0.05$ ,  $df = 7$ ). The variances were homogeneous: Levene's test statistic = 1.25 ( $p > 0.05$ ). Comparing the states according to their rate of call

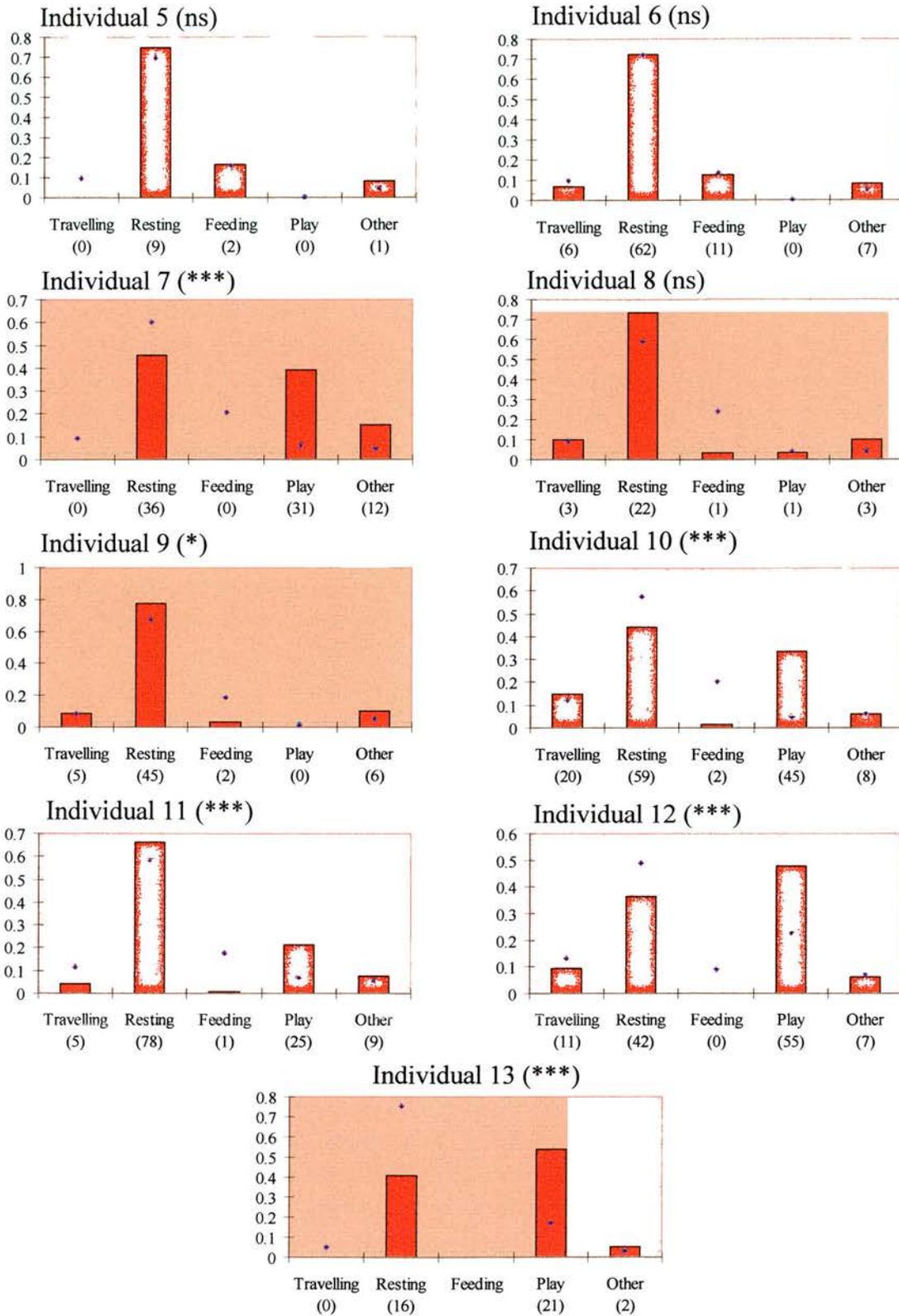
shows that they do differ (One-way ANOVA  $F_{4,30} = 4.997$ ,  $P < 0.01$ ). Post hoc tests reveal differences only between feeding and others and between play and others (Tukey's HSD  $p < 0.01$  and  $p < 0.05$  respectively). However, as expected due to the small number of data points in the main test, power is very low (0.1631 to detect a medium effect). So, in order to expand the analysis, I conducted a chi-square analysis on the frequent callers, in the manner done for the previous calls (see Figure 4.8). Results of the chi-square tests are as follows (df = 4 for all except ind. 13 for which df = 3): Ind. 5  $\chi^2 = 1.54$ ,  $p > 0.05$  (n = 12); Ind. 6  $\chi^2 = 2.61$ ,  $p > 0.05$  (n = 166); Ind. 7  $\chi^2 = 192.6$ ,  $p \ll 0.001$  (n = 79); Ind. 8  $\chi^2 = 8.84$ ,  $p > 0.05$  (n = 30); Ind. 9  $\chi^2 = 12.34$ ,  $p < 0.05$  (n = 58); Ind.10  $\chi^2 = 267.0$ ,  $p < 0.001$  (n = 134); Ind.11  $\chi^2 = 60.8$ ,  $p < 0.001$  (n = 118); Ind.12  $\chi^2 = 47.3$ ,  $p < 0.001$  (n = 115); Ind.13  $\chi^2 = 39.9$ ,  $p < 0.001$  (n = 39). Power values to detect a medium difference are: Ind. 5: 0.1104; Ind. 6: 0.8898; Ind. 7: 0.5474; Ind. 8: 0.2219; Ind. 9: 0.4127; Ind. 10: 0.8047; Ind.11: 0.7454; Ind.12: 0.7329; Ind.13: 0.3175. For the individuals with significant results, emissions during play are above expectancy (with the exception of the individual 9, which engaged in playing more rarely for most of the study). The pattern during feeding (values lower than expected) is in accordance with the previous calls (and also with *moos*). The category "other" has a proportion of calls as expected or higher, something also shared between the three call types. There is no consistent trend for travelling and resting.

**Table 4.6 Frequency of emission of *screech-cries* and call rates according to the state of the caller\***

| Individual        | Travelling | Resting   | Feeding   | Play <sup>a</sup> | Other     |
|-------------------|------------|-----------|-----------|-------------------|-----------|
| 1 (Ad. ♂)         | 0 (0)      | 0 (0)     | 0 (0)     | 0 (0)             | 0 (0)     |
| 2 (Ad. ♂)         | 0 (0)      | 0 (0)     | 0 (0)     | 0 (0)             | 0 (0)     |
| 3 (Sub-ad. ♂)     | 0 (0)      | 1 (0.02)  | 1 (0.06)  | 0 (0)             | 0 (0)     |
| 4 (Sub-ad. ♂)     | 0 (0)      | 3 (0.04)  | 4 (0.21)  | 0 (0)             | 0 (0)     |
| 5 (Ad. ♀)         | 0 (0)      | 9 (0.12)  | 2 (0.11)  | 0 (0)             | 1 (0.21)  |
| 6 (Ad. ♀)         | 6 (0.58)   | 62 (0.80) | 11 (0.75) | 0 (0)             | 7 (1.33)  |
| 7 (Juv. ♀)        | 0 (0)      | 36 (0.65) | 0 (0)     | 31 (5.60)         | 12 (2.96) |
| 8 (Juv. ♀)        | 3 (0.34)   | 22 (0.39) | 1 (0.04)  | 1 (0.26)          | 3 (0.74)  |
| 9 (Sub-ad./Ad. ♀) | 5 (0.62)   | 45 (0.68) | 2 (0.11)  | 0 (0)             | 6 (1.24)  |
| 10 (Inf./Juv. ♀)  | 20 (1.87)  | 59 (1.14) | 2 (0.11)  | 45 (10.58)        | 8 (1.48)  |
| 11 (Inf./Juv. ♀)  | 5 (0.46)   | 78 (1.38) | 1 (0.06)  | 25 (3.74)         | 9 (1.61)  |
| 12 (Inf./Juv. ♂)  | 11 (1.38)  | 42 (1.39) | 0 (0)     | 55 (3.95)         | 7 (0.73)  |
| 13 (Inf. ♀)       | 0 (0)      | 16 (2.45) | 0 (0)     | 21 (14.29)        | 2 (8.02)  |

\* Values outside the parentheses indicate the number of calls registered in a given behavioural state. Call rates (values in brackets) calculated dividing the number of *cries* emitted when on a given behavioural context (during focal periods) by the number of hours that the individual spent on it.

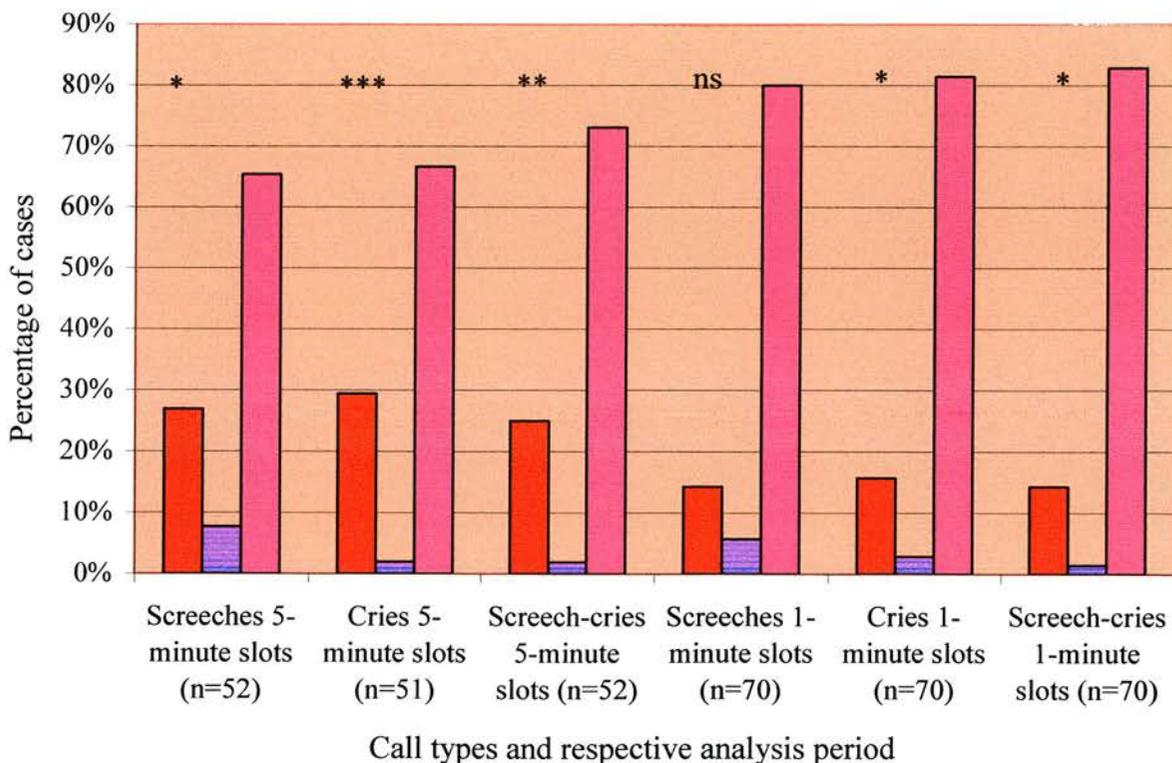
<sup>a</sup> Play includes attempts to interact with newborn infants and also invitations to play, besides the play behaviours *sensu strictu*. For ind. 12 and 13 includes attempts of interaction made by other animals when they were newborn.



**Figure 4.8 Comparison of the proportion of screech-cries emitted on each behavioural state (solid bars, sample sizes for each state within brackets) with the proportion of time spent on each state (dots). Within brackets codes for the significance values of the chi-square test performed on the individual.**

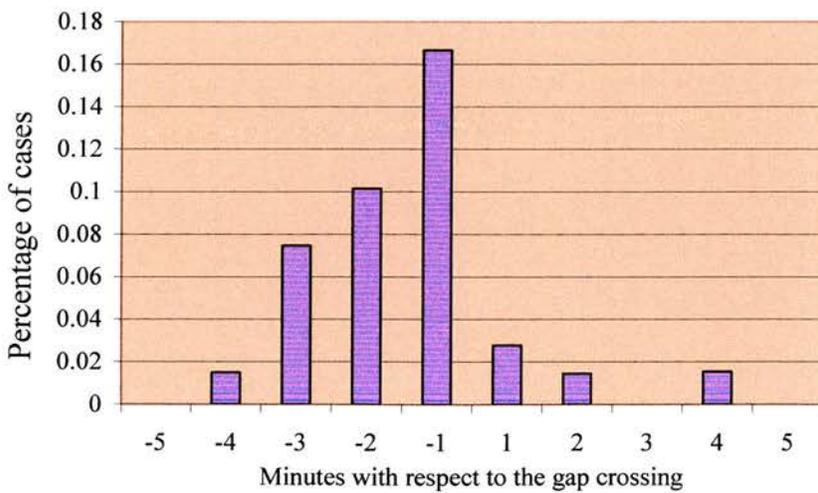
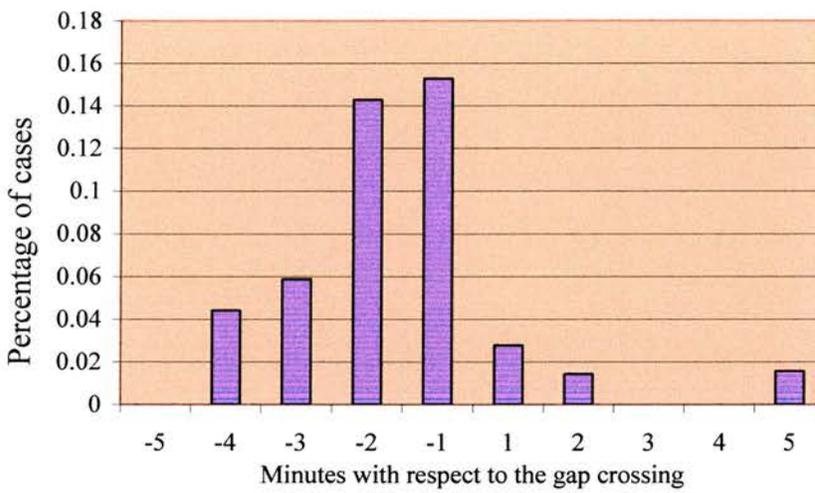
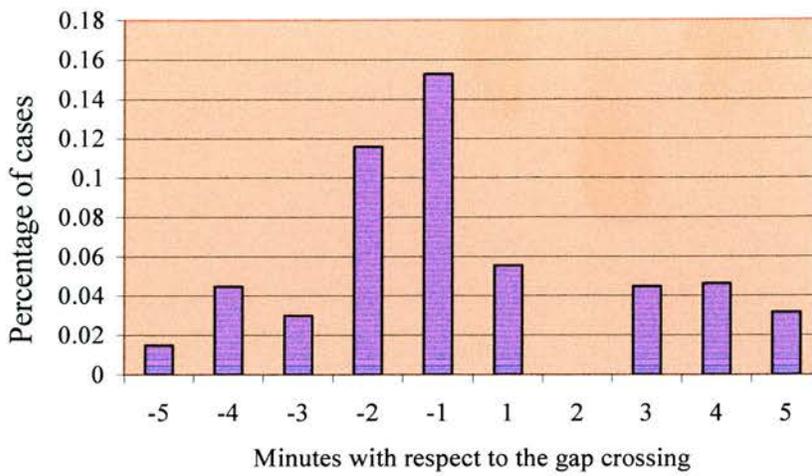
#### 4.4 Results - Relationship with stressful events

I first analysed call emission with respect to the gap crossings, a situation that elicited calling only in infants and juveniles. Recall that the prediction, under the anxiety/distress hypothesis for the function of a call, is that animals should call more before than after the event. Strikingly, the majority of cases were not accompanied by calling (see Figure 4.9). However, for those instances associated with vocalisations, there were a higher number of cases with more calls before the critical event than the opposite. When these two figures were compared against a 1:1 null hypothesis with a binomial test, the results were significant in nearly all instances (data for 5-min periods before/after, *screeches*  $n = 18$ ,  $P < 0.05$ ; *cries*  $n = 16$ ,  $P < 0.001$ ; *screech-cries*  $n = 14$ ,  $P < 0.01$ ; data for 1-min periods before/after, *screeches*  $n = 14$ ,  $P > 0.05$ ; *cries*  $n = 13$ ,  $P < 0.05$ ; *screech-cries*  $n = 11$ ,  $P < 0.05$ ).



**Figure 4.9** Percentage of cases (gap crossings and detours/desistances) with **■** more calls before than after the critical event; **■** more calls after than before; **■** no calls (always with respect to equivalent time periods of 5 or 1 minutes as specified). Significance level symbols are for the binomial tests comparing the first two categories only.

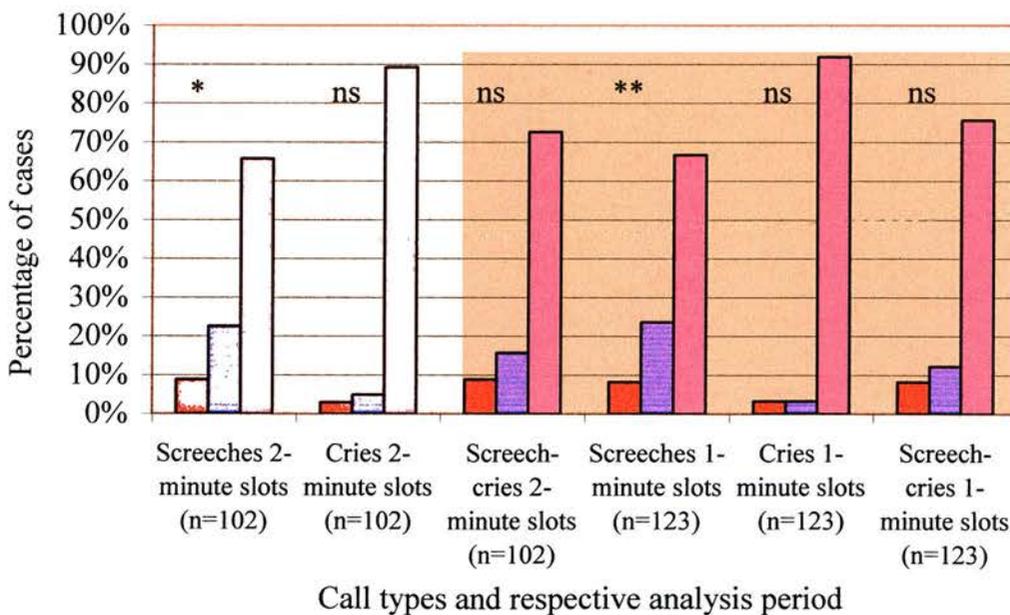
To further investigate the temporal relationship of these call types to gap crossing (and alternative tactics as detours or desistances), I compared their emission, in successive one-minute bins, for the five minute periods preceding and following the critical event. For each of the vocalisations considered there is an abrupt decline in call occurrence after the event, further substantiating the conclusion that there is a connection between the calling behaviour and the overcoming of the distressful situation (Figure 4.10).



**Figure 4.10** Percentage of cases with at least one call in a given time period. Percentages were calculated separately for the 10 consecutive 1-minute slots, symmetrically distributed before and after the crossing of the gap. Top graph – *screeches*; middle graph – *cries*; bottom graph – *screech-cries*. Figures on the x-axis represent the *i*th period with respect to the gap-crossing event. Sample sizes varied for each slot from 63 to 72.

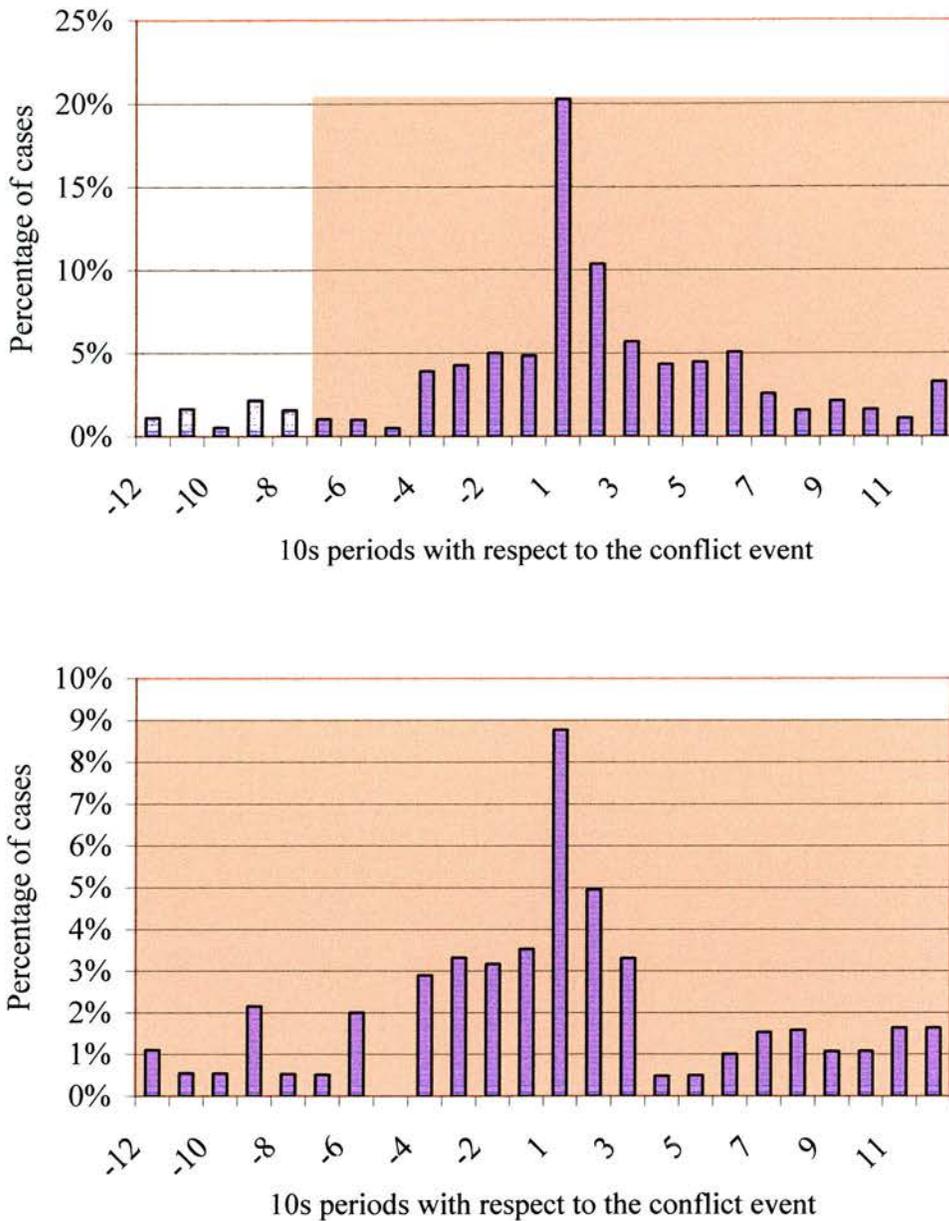
I now turn to the analysis of events that indicate the start of a stressful situation. Recall that the prediction is that calling should be more frequent *after* the event than before. The first event to be analysed was ‘conflict’. Since in the case of gap crossing most of the calling was concentrated on the 2 minutes adjacent to the target event, I restricted the analysis of percentage of cases with more calls before or after to 1 and 2-minute periods (instead of 1 and 5-minute periods). When considering successive time periods with respect to the target event, I reduced the length of the time bins to 10 seconds, which should give a more fine-grained picture of the succession of events just after the start of the stress.

There were a high number of cases with no calls (see Figure 4.11). For those instances accompanied by calls, cases with more *screeches* after the conflict occurred more often than the opposite, considering either 2-minute or 1-minute analysis periods (binomial tests respectively  $n = 32, p < 0.05, n = 39, p < 0.01$ ). However, for *cries* and *screech-cries*, all analyses were non-significant (binomial tests considering 2-minute periods: *cries*,  $n = 8, p = 0.73$ ; *screech-cries*,  $n = 25, p = 0.23$ ; considering 1-minute periods: *cries*,  $n = 8, p = 1$ ; *screech-cries*,  $n = 25, p = 0.42$ ).



**Figure 4.11 Percentage of cases with: ■ more calls before than after the conflict; ■ more calls after than before; ■ no calls (always with respect to equivalent time periods of 2 or 1 minutes as specified). Significance level symbols are for the binomial tests comparing the first two categories only.**

Over time, the pattern of emission is dissimilar for the call types (Figure 4.12). Concerning the *screeches*, there is a roughly four-fold increase in the percentage of cases with calls in the 10s immediately following the conflict, in comparison with the same time period before the event. The time period 10-20s after the event still possesses a large value, but after that calling seems to return to the levels before the event. The general profile of the graph for the *screech-cries* is similar, but the increase after the conflict is not as dramatic. As *cries* presented very few cases accompanied with calls, the graph for this call type was omitted. Note that for *screech-cries* the four bins preceding the conflict show a higher number of cases with calling in comparison with preceding periods. Although there might be an effect of multiple occurrences of conflicts on data files (thus calls occurring after some conflicts are also counted as occurring before the succeeding events), it is worth considering this as a genuine result. Anecdotal observations indicate a very predictable occurrence of this call type when an animal was approached by a larger or dominant individual, possibly indicating a submissive function for this call. In that case, calling before an actual conflict might be expected, as an immature could have learned from previous interactions that a manual prevention/mock bite is likely in a given situation.

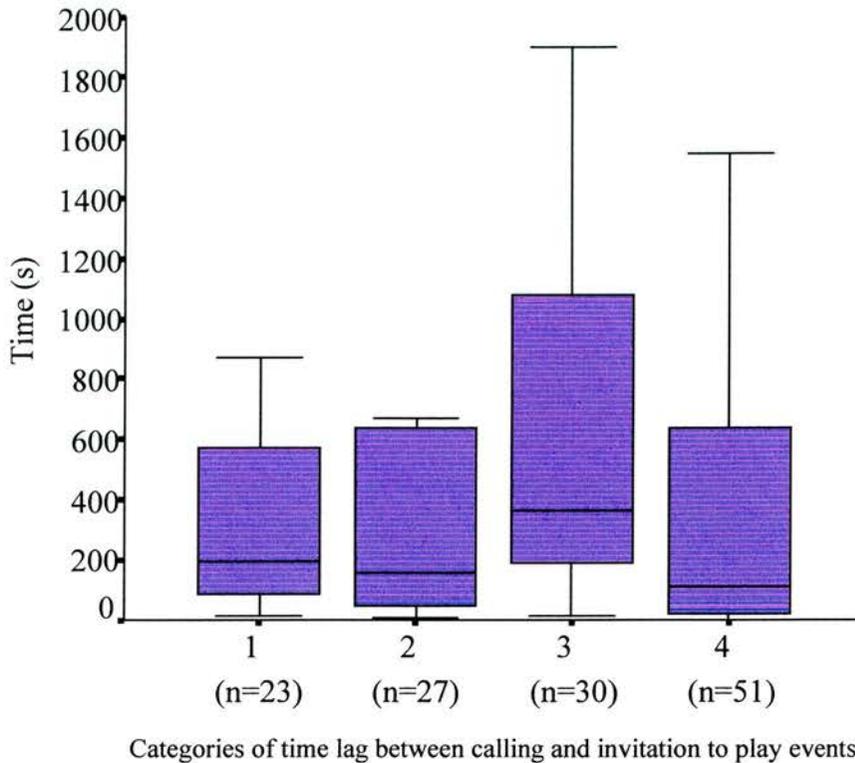


**Figure 4.12** Percentage of cases with at least one call in a given time bin. 24 consecutive 10-seconds slots symmetrically distributed before and after the conflict were considered. Top graph – *screeches*; bottom graph – *screech-cries*. Figures on the x-axis represent the  $i$ th period with respect to the conflict. Sample sizes varied for each slot from 180 to 228.

I next analyse the event “invitation to play”, here considered as the point where an individual starts inciting another to play, by pulling, holding (with hands or mouth) or biting some part of the body of the other animal. As an individual is not always keen on engaging in playing, and the provoking individual can be insistent or a larger/dominant animal, invitation can be

conceived as being occasionally mildly stressful. If a given call type is associated with distress, then the prediction is that, for the receiver of the invitation, the time before *next* call emission should be smaller than the time since *last* call emission invitation. However, if an animal is inviting a dominant one, it might also feel mildly distressed, or it may assure friendly intentions/submission. Then, one can also predict that, for the actor, the latency to call after an invitation should be smaller than the time lag between the last call emission and the invitation

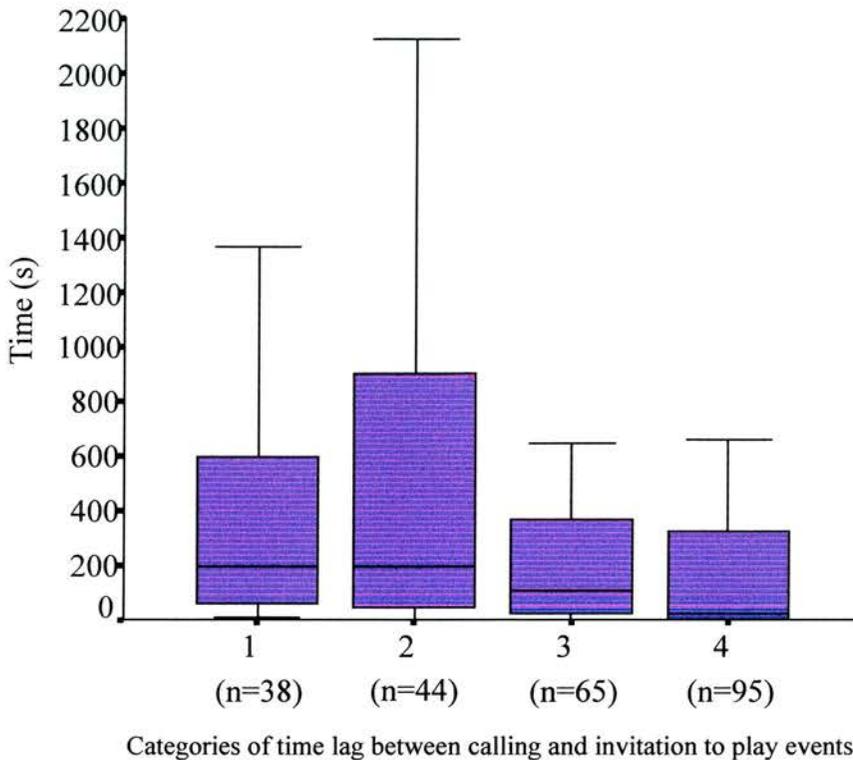
*Screeches*, despite being the commonest of the calls from the screech complex, had the smallest number of invitations accompanied by a call (preceding and/or following the event). Also note that there is a large spread of variation in the data (note the height of the boxplots in Figure 4.13). Emissions of calls long after an event are unlikely to bear any relation with it. Thus, the large variance combined with the smaller number of retrieved data points suggests that this call type is the least associated with invitations to play. None of the time variables were normally distributed (Shapiro-Wilk test, time since *last* call – actor  $W = 0.750$ ,  $p < 0.001$ ,  $df = 23$ ; time before *next* call – actor -  $W = 0.719$ ,  $p < 0.001$ ,  $df = 27$ ; time since *last* call – receiver  $W = 0.880$ ,  $p < 0.01$ ,  $df = 30$ ; time before *next* call – receiver  $W = 0.756$ ,  $p < 0.001$ ,  $df = 51$ ). Therefore, I resorted to non-parametric tests to compare the time variables. As very few events had calls both before *and* after the invitation (which asks for a paired analysis), it was justified to use Mann-Whitney test, instead of Wilcoxon sign ranks test. Thus, for the cases that did present calling, time before *next* call was significantly shorter than time since *last* call, but only for the recipient of the invitation (Mann-Whitney tests, actor –  $U_{23,27} = 307.5$ ,  $p > 0.05$ ; receiver –  $U_{30,51} = 536.5$ ,  $p < 0.05$ ). Contrasting actor and recipient on each of the variables shows that the time since *last* call was significantly shorter for the actor ( $U_{23,30} = 230.5$ ,  $p < 0.05$ ), but there was no difference for time before *next* call ( $U_{27,51} = 612.5$ ,  $p > 0.05$ ).



**Figure 4.13** Boxplot of the time variables (in seconds) between calling (*screeches*) and invitation-to-play events. (1) time since *last* call –actor; (2) time before *next* call – actor; (3) time since *last* call –receiver; (4) time before *next* call – receiver.

Turning to the *cries*, there were a slightly larger number of cases of invitation to play accompanied by calling (compare sample sizes on Figures 4.13 and 4.14). Considering that this call type is the less common of the complex, this fact is relevant. Time variables were also not normally distributed (Shapiro-Wilk test, time since *last* call –actor  $W = 0.744$ ,  $p < 0.001$ ,  $df = 38$ ; time before *next* call – actor -  $W = 0.800$ ,  $p < 0.001$ ,  $df = 44$ ; time since *last* call –receiver  $W = 0.660$ ,  $p < 0.01$ ,  $df = 65$ ; time before *next* call – receiver  $W = 0.608$ ,  $p < 0.001$ ,  $df = 95$ ). Contrasting the time variables for each category of participant shows that time before *next* call was significantly shorter than time since *last* call for the recipient of the invitation (Mann-Whitney test  $U_{65,95} = 2324.5$ ,  $p < 0.01$ ), but not so for the inviter himself (Mann-Whitney test  $U_{38,44} = 785$ ,  $p > 0.05$ ). Comparing actors and receivers with respect to each time lag showed, differently from the *screeches*, that receivers had significantly shorter times before *next* call than actors (Mann-Whitney test  $U_{44,95} = 1214$ ,  $p < 0.001$ ), with no difference with

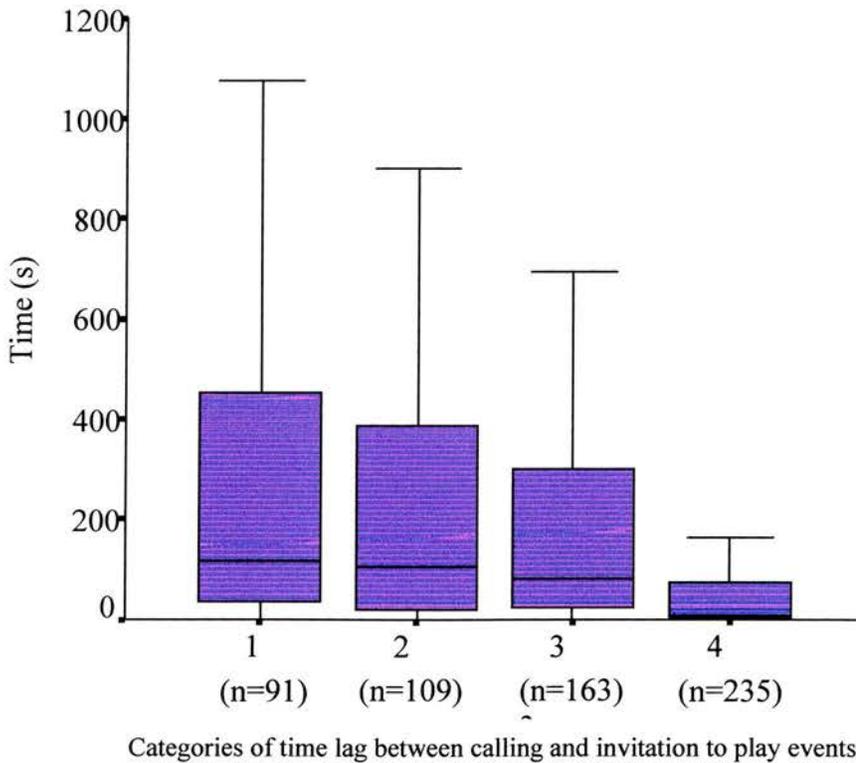
respect to time since *last* call (Mann-Whitney test  $U_{38,65} = 979$ ,  $p > 0.05$ ). So, those results point to a more clear relation between production of *cries* and being invited to play.



**Figure 4.14** Boxplot of the time variables (in seconds) between calling (*cries*) and invitation-to-play events. (1) time since last call –actor; (2) time before next call – actor; (3) time since last call –receiver; (4) time before next call – receiver.

Regarding the *screech-cries*, they were by and large the most common call type in these situations, judging from the number of retrieved cases. Again, none of the time variables were normally distributed (Shapiro-Wilk tests, time since *last* call –actor  $W = 0.716$ ,  $p < 0.001$ ,  $df = 91$ ; time before *next* call – actor -  $W = 0.627$ ,  $p < 0.001$ ,  $df = 109$ ; time since *last* call –receiver  $W = 0.633$ ,  $p < 0.01$ ,  $df = 163$ ; time before *next* call – receiver  $W = 0.440$ ,  $p < 0.001$ ,  $df = 235$ , see Figure 4.15). The receivers of invitations to play had a significantly shorter time before *next* call than time since *last* call (Mann-Whitney test  $U_{163,235} = 10028$ ,  $p < 0.001$ ), but the same did not occur with the individuals that were inviting (Mann-Whitney test  $U_{91,109} = 4690.5$ ,  $p > 0.05$ ). Comparing the two categories of participant with respect to each time variable shows receivers with

significantly shorter times before *next* call than actors (Mann-Whitney test  $U_{109,235} = 6761$ ,  $p < 0.001$ ), but the same did not happen with times since *last* call (Mann-Whitney test  $U_{91,163} = 6785$ ,  $p > 0.05$ ). A further indication of an association between invitation to play and the emission of *screech-cries* by the invitees comes from variance data. A homoscedasticity test shows that variances are not homogeneous between the four categories (Levenne's test  $F_{3,594} = 5.4$ ,  $p < 0.01$ ). Looking at the graph, it is very clear that the first three categories are roughly similar with respect to their patterns, but time lags between an invitation and a subsequent call by the recipient are much less varied. Coupled with the fact that they are also significantly shorter, this indicates that a higher number of the registered calls actually refer to the invitation, since calls emitted long after an event probably do not relate to it.



**Figure 4.15** Boxplot of the time variables (in seconds) between calling (cries) and invitation-to-play events. (1) time since last call –actor; (2) time before next call – actor; (3) time since last call –receiver; (4) time before next call – receiver. Above category labels is the sample size of the category.

Comparing each time variable across call types produces further revealing results. With regard to actors, there was no difference between the

three call types with respect to times since *last* call (Kruskal-Wallis test  $H = 1.605$ ,  $df = 2$ ,  $p = 0.448$ , power = 0.79 for a medium effect to be detected<sup>2</sup>), but the test for times before *next* call closely approached significance (Kruskal-Wallis test  $H = 5.875$ ,  $df = 2$ ,  $p = 0.053$ , power = 0.85 for a medium effect to be detected). I thus conducted post-hoc tests between pairs of call types using an experiment-wise error rate of 0.0167. All comparisons failed to reject the null hypothesis (Mann-Whitney tests: *screeches* x *cries* –  $U_{27,44} = 562.5$ ,  $p = 0.709$ ; *screeches* x *screech-cries* –  $U_{27,109} = 1205$ ,  $p = 0.146$ ; *cries* x *screech-cries* –  $U_{44,109} = 1845.5$ ,  $p = 0.026$ ). However, significance was again approached when comparing *cries* with *screech-cries*, the first presenting larger values than the second. Thus, there might be a tendency for actors to resort first to *screech-cries* after an invitation. Conducting the same analysis for the recipients showed highly significant results both for times since *last* call (Kruskal-Wallis test  $H = 16.762$ ,  $df = 2$ ,  $p < 0.001$ , power = 0.96 for a medium effect to be detected) and times before *next* call (Kruskal-Wallis test  $H = 32.095$ ,  $df = 2$ ,  $p < 0.001$ , power = 0.99 for a medium effect to be detected). Using the same experiment-wise approach ( $\alpha = 0.0167$ ) shows that, for the times since *last* call, *screeches* present significantly longer values than both other call types, which do not differ between themselves (Mann-Whitney tests: *screeches* x *cries* –  $U_{30,65} = 524$ ,  $p < 0.001$ ; *screeches* x *screech-cries* –  $U_{30,163} = 1323$ ,  $p < 0.001$ ; *cries* x *screech-cries* –  $U_{65,163} = 5292.5$ ,  $p = 0.991$ ). This result points once again to the lack of association between *screeches* and provocation to play, and also that the other two call types might be emitted before the invitation, without any preference. The results for times before *next* call shows differences between all call types, although between *cries* and *screech-cries* it only approached significance (Mann-Whitney tests: *screeches* x *cries* –  $U_{51,95} = 1668.5$ ,  $p < 0.01$ ; *screeches* x *screech-cries* –  $U_{51,235} = 2984$ ,  $p < 0.001$ ; *cries* x *screech-cries* –  $U_{95,235} = 9370$ ,  $p = 0.022$ ). *Screeches* present the longer values, *screech-cries* the shorter ones, with *cries* resting in between.

<sup>2</sup> The power calculation is done for an ANOVA of equivalent sample size. Non-parametric equivalents of parametric tests generally have slightly less power.

## 4.5 Discussion

Here, I am going first to summarise the findings so far for each of the call types, then speculate on their possible functions. After, I will propose an observational design that could be used to collect detailed data to test some of the ideas advanced.

### 4.5.1 Screech calls

The most common of this call complex, the *screeches*, were given nearly as frequently as *moo* calls. Also, they were emitted almost exclusively by immatures, with infants producing them much more frequently than juveniles. Adults were very sporadic emitters. Calling frequency is low during feeding (something shared by all three types), and higher than expected during resting. This last fact does not help much in understanding its function since, as emphasised before, resting encompassed a variety of behavioural states, and there is a multiplicity of events that can be associated with it.

Younger animals called significantly more often before crossing a gap than after it, and call occurrence dropped dramatically after the crossing. On the other hand, when immatures had a conflict of interest, they *screeched* significantly more often *after* the event than before, although the number of cases accompanied by any call was low. This also points to this call being a general outcome of distress, perhaps caused by the frustration generated by the conflict. The sharp increase in the percentage of cases with call on the first ten seconds after the event is a strong indication of the close association between conflict and screeching.

Few cases of invitation to play were available to analyse the time lags between calling and the event, but these showed that time before the first call after the invitation was significantly shorter than time since *last* call for the recipient of the invitation. Performing the same analysis with the animal that was inviting the other produced no significant difference. Comparing the actor and the recipient showed no difference with respect to the period between the invitation and the next call, but actors had smaller periods between an invitation and a preceding call than recipients. This might have been caused by multiple

occurrences of invitations, shortening an otherwise longer interval between an event and a preceding call.

From all this evidence, it seems that the screech is associated with stressful contexts, but less so with the lower intensity ones. The lack of a clear association with behavioural states (apart from a low frequency during feeding), is an indication of a wide range of situations in which it is emitted (corroborated by anecdotal observations), which is consistent with a rather general function. The low number of cases of invitation to play followed by *screeches* is revealing, as presumably this situation presents a very low level of stress; similarly, anecdotal observations showed that approach by larger or dominant individuals (presumably a situation with low stress level) did not induce this call. I also noticed that *screeches* were often produced during attempts to interact with newborn monkeys in the first weeks of life. It was a very common occurrence for a youngster to approach a female with a newborn and harass her during its attempts to interact with the baby. The usual response of the female was to try to avoid the youngster, by turning her back or attempting to leave them, and on occasions she would manually prevent or mock bite them. All those forms of prevention would lead to intensive *screeching* by the harassing infant, and this sequence of interactions could go on for several minutes in a row (the infants were very persistent in their attempts)<sup>3</sup>. So, it seems that frustration is a major component in eliciting this call.

It is interesting to note that the description of the most common call registered by Calegato-Marques and Bicca-Marques (1995) in their study of *A. caraya* (labelled as “stress cry” by them) seems to indicate that it referred to screeches. They describe it as a “call of high amplitude, composed by two syllables ..., emitted with an open mouth and exhibiting the teeth, especially the lower ones” (my translation). They mention the following situations of use: aggressive behaviour (emitted by subordinates being aggressed by dominants), play, and attempts of allomaternal care of newborn animals. Although we do not have access to the criteria used by the authors to define play and aggression, these observations seem to partially agree with the data presented here.

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<sup>3</sup> Interestingly, the animals usually called in a particular way, with the infant touching the body of the female with its mouth, usually at the beard or the face.

Concerning data from other species, comparison is quite difficult. In Baldwin & Baldwin (1976), the spectrograms are of poor quality, and there is no mention of the parameters used to build them, limiting a visual comparison. They point to several calls produced by infants of *A. palliata* in contexts similar to the ones in which howlers emitted screeches in this study. However, some of those situations are very common in eliciting calls in primates (see Introduction), and without proper spectrograms it is not possible to verify if the contextual similarity is matched by structural relatedness as well. In previous studies of *A. palliata* (Altmann, 1959; Baldwin & Baldwin, 1973; Carpenter, 1934) the information is scarce and a useful comparison is not possible. In a study of social relations of *A. seniculus* (Neville, 1972), there is reference to a vocalisation emitted by immatures described as a “rusty door opening” or “squeaky-door screech”. Neville’s depiction would suit very well the sound here classified as screech. The kind of situations in which the animals produced this call in his study also presents various similarities (refusal of access to a recent infant, dispute over food, approach to a mother with a recent infant, agonistic contexts, playing youngsters towards unwilling older animals). Therefore, it is possible that, at least in one other species of the genus, there is a call structurally and functionally similar to the *screeches*. Thus, it would be worth confirming this resemblance with a more detailed study, as well as expanding the comparison to the other species of the genus.

#### 4.5.2 Cries

Of all calls of the complex, animals uttered cries least frequently, and a less clear discrepancy between smaller infants and older animals was noted. However, there still seems to be a trend of decreased calling with increasing age. Interestingly, female 6 and her offspring consistently presented higher call rates than their similar aged counterpart on the cluster of female 5 and her offspring (5 x 6; 7 x 8, 10 x 11, and 12 x 13). Female 6 seemed to be subordinate to female 5 and this extended to her offspring. As by definition subordinate individuals receive more aggression, are more frequently the losers in conflicts, or have a broader range of situations leading to stress and anxiety, the observed differences fit in with a function of cries related to stressful situations.

Most animals did not call in proportion to the time spent performing a given behaviour. The clearest results were a low proportion of cries during feeding and a higher than expected proportion during play. There was no clear relationship with resting or travelling. Infants and juveniles gave significantly more cries before crossing a gap than after. Surprisingly, few cries were emitted by infants and juveniles in conflicts (as defined here), and instances with more calls *after* the conflict were as likely as the opposite. Regarding invitations to play, a higher number of cases were accompanied by cries than by screeches, which is interesting given the relative rarity of cries. Analysis of time lags showed that the production of cries was mainly associated with the recipients of a provocation and with the time period following it.

Thus, it seems clear that *cries* bear a relation to stressful situations. Based on *ad libitum* observations, I tentatively propose that this call type is indicative of a high or enduring stress and thus uttered in a more restricted range of situations, or after a continued stress. This would account for the rarity of emissions. The anecdotal observations that support this view are: cries were given during the few agonistic events observed; in gap crossing situations or attempts to interact with newborns, *cries* would be normally produced after a long *screeching* sequence; some of these sequences had *screeches* in a *crescendo* of intensity and pitch and then a *cry* was uttered. At the moment, I assume that cries emitted in different situations are the same call type, although confirmation has to await detailed structural studies. A fact that goes against the idea of high or enduring stress is the observed relation with invitation to play events rather than with conflicts of interest, which might be expected to present a higher level of stress than the former.

It has been argued that sudden changes in crying parameters can increase the chance of a care-giving response (Todt, 1988; Todt et al., 1995), and I suggest that a change in call type (from *screeches* to *cries*) might produce the same effect. Alternatively, screeches and cries could be referential calls, associated with distinct events presenting the same level of stress. However, these two hypotheses are not mutually exclusive, since the very reason why animals produce different calls in distinct situations could be different stress/anxiety levels associated with them. Clearly more work is necessary to advance this matter further.

Calegario-Marques and Bicca-Marques (1995) have a call type labelled cry, described as a “continuous vocalisation less sonorous than an intense whimper” (my translation), produced by infants and juveniles in stress situations (separation from the group is cited as an example). From this limited description it is not possible to assess if it refers to the call here labelled as cry. Neville (1972) mentions one occurrence of a bout of cries in a gap situation, which were described as light, plaintive, and bird-like.

#### 4.5.3 Screech-cries

This call is heard as commonly as the *screeches*, but not in bouts. Adult females are consistent callers, and one of the sub-adult males (individual 4) produced a couple of *screech-cries*. However, as with the other call types in the complex, calling decreased with increasing age. For the individuals with significant association between calling and behavioural states, emissions during play were above expectancy, a trend also present for *cries* but not as clear, and definitely not the case for the *screeches*. The pattern of fewer emissions than expected during feeding is in accordance with the previous calls, and also with *moos*. There was no consistent trend for travelling and resting. A significantly higher number of cases occurred with more calls before than after crossing a gap but only a minority of gap crossing was accompanied by calling, perhaps surprising given the frequency of the call. The likelihood of calling dropped pronouncedly after the event. There was no difference in calling behaviour before and after conflict events, but the likelihood of a conflict event possessing a call immediately after was circa three times higher than just before it. *Screech-cries* were emitted shortly after invitations to play, by the recipient, significantly so when compared to the time between the last call and the invitation.

As with the other members of this complex, *screech-cries* are related to stressful events, and of the three calls, it was the one given most often after invitations and uttered significantly closer in time to the event than the other two. Besides invitations to play, I also observed this call type to be emitted in other situations of mild distress. For instance, there was a nearly invariable association of this call with the approach of a larger or dominant individual. Although this situation can represent a potential threat to the subordinate, it is perhaps a less

serious one. Similarly, it was the main call type emitted by females when in oestrus and harassed by males other than the alpha, or when any male inspected their genitalia outside oestrus periods. Potentially, this call type may be composed of a series of distinct types, grouped here merely due to their noisy character. Towards the end of the study, I noticed that at least two variants may exist, one similar to the noisy part of a screech and another that seemed to have a relation with a *moo*. It is a matter for future studies to verify if there is an association between sub-types and specific situations.

As usual, reference in the literature that allows proper comparison is severely limited. Calegari-Marques and Bicca-Marques (1995) describe a “vocalisation of smaller amplitude than the stress cry [mentioned above], similar to a dog snarl...” (my translation). Adults, sub-adults and infant and juvenile females during stress situations and play emitted this call in their study. From these very general comments it seems that they lumped the screech-cries as considered here and *snarls* emitted during play (and also some ambiguous, approach-avoidance, situations). The two call types seem indeed to have a structural relation, and a continuum between them may exist.

#### 4.5.4 Relation with moos

Throughout the chapter, it probably became evident to the reader that most of the behavioural events which were analysed were the same ones used in the study of infant and juvenile *moo* calls. This is not surprising, since the hypothesis was the same, and so were the predictions. In fact, all four call types could have been analysed under the heading of distress calls. The division was adopted merely because it was interesting to see a single call type performing apparently different functions.

However, it is also interesting to attempt to see the four call types of immature animals under an unified perspective. As it was the case with the calls of the screech complex (explored above), the association of *moos* with stressful context also presented its particularities. The most clear-cut result in this respect is the higher number of gap crossings that were associated with *moos* in comparison with the call types of the *screech* complex. This reinforces the notion, made explicit on the previous chapter, that *moos* might possess an

association with maintaining contact between individuals during the whole ontogenetic trajectory of the call.

But it is also relevant that all four call types were emitted, no matter how infrequently, in almost all the circumstances analysed. Looking at the data files, it is possible to see that, in most cases, more than one call type was associated with a particular occurrence of the events studied (gap crossings, conflicts, etc.). Furthermore, some transitions between types seemed to be produced, most noticeably between *screech-cries* and other types. These leave many questions unanswered, such as:

- Are the call types real or forming a graded series?
- Is there a temporal structure in bouts of emission containing different call types?
- If so, what source of information is encoded in the structure? Is the syntax phonological or lexical?

In the study design proposed below, I suggest various data collection procedures and analysis techniques that could be used to answer those important questions.

#### *4.5.5 General discussion*

When considering the possible function(s) of a call emitted in distress situations, one can differentiate at least two levels of explanation.

Proximately, a call may be a direct reflection of the emotional status of the animal. Evidence for all calls of the screech complex seems to point to at least some degree of call specificity with respect to the level of presumed stress of a context. However, I can not rule out the possibility of some contextual specificity of these calls, which would then have the potential for referential labelling for the listeners. What can be asserted is that the calls considered here do have an explicit association with distressing events, although each in a somewhat different way. Also, those possibilities are not exclusive, that is, a call might have a referent but also be triggered typically by a specific emotion associated with that particular referent.

But, when considering the responses of other animals to a call, it is more appropriate to refer to its ultimate (social) function, without necessarily implying intentionality either for the sender or the recipient (Cheney & Seyfarth, 1999; Seyfarth & Cheney, 2003). And here, there seems to be at least three possible alternatives for a call produced in conflict or stressful situations:

- Call for help/ elicit care-giving response: the outcome is the approach of another animal and the cessation of the stress/conflict through a behaviour of the approaching animal; or the production of a care-giving response
- Announcement of disagreement or discomfort during an interaction, which can lead to retaliation: here one expects either a change/cessation in behaviour on the part of actor and a concomitant termination of calling, or escalation. Signalling a mild threat presents many similarities and can be included in this category;
- Signalling submissive status to prevent an agonistic interaction or terminate one in course.

It is interesting to note that in the first and the last case, although there may be an initial coupling of calling with emotional state, there is also an inherent potential for disengagement. Under the call for help/care-giving alternative, the responses from other animals, which lead to an overcoming of the stressful situation, can generate an association with reward. This, in turn, can lead to manipulative attempts on the part of the infant, leading to a decrease in the emotional threshold for calling. In this case, from the outside the vocalisation can still be regarded as a call for help, but the mechanism for call production has changed. Distinguishing between these alternatives therefore is not easy. With respect to the submissive signals, an animal who is not feeling threatened in any way, might use the call when performing a behaviour that is likely to generate aggression (begging for food, access to a newborn). As the probability of aggression might be judged from past experiences, it is also very difficult to tease apart the emotional and the manipulative component of a submissive call. Finally, the first and second functions can be combined into one. In this case, an animal is both announcing its disagreement/discomfort, but this generates either

a care-giving response on the part of the harassing individual, or the approach of another, either intervening in the interaction or providing care.

Concerning the calls studied here, screeches apparently function as both calls for help/care-giving and signals of submissive status. The evidence for the first case comes mainly from gap situations, as there were many cases of approaches of another animals towards calling ones. To make a more firm case three additional sources of evidence would be necessary. First is the frequency of gaps of a given width that generate calling. Second is the frequency of gap situations accompanied by calling that led to help from another individual. Finally, one would need to know the frequency of gap situations that were **not** accompanied by calling but that led to help from another individual anyway. For all of those, tracking the ontogenetic changes would provide further valuable information. There is also limited evidence for this function from riding and breast-feeding instances. On occasions, an animal would allow a calling infant to ride (sometimes even approaching it) and calling would terminate. Screeching also preceded some breast-feeding episodes, and intense calling followed cases when the mother interrupted a bout of suckling or prevented access to the nipple. Comparison of calling behaviour before and after the event was not possible since the animal could not call when suckling. Evidence for a submissive function comes mainly from the emission after conflicts of interest (especially between infants and their mothers). However, these might equally be viewed as attempts to generate a care-giving response, given some of the situations in which conflict occurred. The very conspicuous emission of bouts of screeches when trying to get access to a newborn infant also supports the idea of a submissive function, or a kind of “preventive manipulation”. A further source of evidence towards a function of triggering a care-giving response is the fact that the call is nearly exclusively given by infants. As adults do not, by definition, require care, calls related to this function should drop out of the repertoire. A similar argument applies the possible function of calling for help. The main source of evidence here comes from gap crossing: I never observed adults to help each other in gap situations (unless an adult was approaching branches for an infant and another took advantage). Thus, if assistance is not provided, calls aimed at requiring it should also disappear. In contrast, this should not occur with

calls signalling submission or disagreement, because situations whereby they are necessary do not disappear with adulthood, just their nature changes.

The cry call, on the other hand, seems more clearly a submissive signal, but also functioning to call for help. The best evidence for submission was emission accompanying the most intense aggressive interactions, with physical contact (and not included in the category of conflicts analysed here). As there were very few such aggressions, it is not possible to evaluate if the calls served to call for help from other animals. Interference was noted on a couple of occasions, but the direction of help was not clear. Chases were not accompanied by cries. The fact that this call type is not associated with the minor conflicts considered here may also have implications. The two classes of conflict presumably pose different threat levels. Since submission is undoubtedly an issue in serious aggressive interactions, this then leads to the question whether the calls more commonly produced in the situations considered here are in fact submissive ones or can be viewed more as manipulative attempts to generate care-giving responses. Also intriguing is the association with invitations to play, presumably very mild agonistic situations when the addressee is not willing to engage in play. The strongest evidence that the cry functions as a call for help comes again from the gap cases. Here, I propose the hypothesis that cries are indicators of more intense distress, and thus more likely to generate help than the other ones (Todt, 1988; Todt et al., 1995). Then I make the following predictions to be tested in the future. First, the longer the animal stays in a gap situation, the more likely it is to produce a cry. Second, the chance of another animal providing help is higher when an immature cries compared with the cases when it only produces other call types.

Finally, the screech-cries seem to function in all three roles, although especially in announcement of disagreement and in submission. Evidence for the announcement of disagreement comes mainly from the compelling association with invitations to play. If the call indeed announces disagreement, I would predict a stronger association between calling and invitation instances not followed by play than with cases that did lead to play. Also, in cases not followed by play, I would expect to see an increase in the chance and intensity of escalation (manual prevention, mock bites, and attacks, in that order) with time. Two kinds of *ad libitum* observations are of further relevance for understanding

this call. First, females call when sexually harassed by males that are not the alpha (or even by the alpha, when they are not on oestrus). This observation seems to reinforce the notion of a disagreement function, and then the prediction of an increase in the chance and intensity of escalation with time would also apply. Second, animals commonly give this call when a dominant individual approaches them. Here it is conceivably a submissive role, or at least an ambiguous one between submission and mild threat. However, it is not clear why a howler would need to signal its submission or threat to an approaching one. After all, I never observed an agonistic behaviour from animals approaching others at normal pace (as opposed to chases), and displacements were rare occurrences. Additionally, animals did not produce screech-cries more often in situations whereby displacing would be more of a concern (e.g. during feeding). Evidence for the call for help/elicite care-giving function comes again from the analysis of gap crossing events. I already mentioned above the possibility of further sub-division of this call type. Also of interest would be to study the relation between screech-cries (or its new divisions) and facial displays. This call type was commonly associated with a display characterised by the exhibition of the teeth produced by retraction of mouth corners, with variable degrees of mouth opening.

As a final observation, it is interesting to note that all the call types considered here (and also infant *moos*) were given much less than expected during feeding. The likely reason is that very few potential conflict or stressful situations were observed in this context. Displacement was rare, and feeding distances were sometimes very small without any signs of interference. Occasional displacements from feeding spots or food stealing were accompanied by crying or screech-crying in adults or screeching by infants, and approaches by dominant or larger individuals towards non-infants were followed by screech-cries as usual. Infants occasionally screeched when apparently begging for access to some particular food items (e.g. the large fruits of *Sterculea apetala*), behaviour reminiscent of attempts to interact with a newborn. Behaviour at tree holes for access to water was completely different: interference, displacement and calling were all very common.

#### 4.6 Proposed future study

A first aspect that merits attention in a more detailed study is to verify the differences in the temporal pattern of emission that seemed to exist between the call types. The best way to accomplish this is through inspection of continuous recording sequences, which prevents errors that might occur when noting down data in the field, and is also much more precise. Captive settings (bearing in mind the usual shortcomings) are ideally suited for these recordings, as the observer can more easily identify the start of a particular interaction and the recording distances are usually small. Also, by having continuous recording sequences, it will be possible to evaluate the transition probabilities between call types, and to conduct more refined time analysis to inspect the possibility of a syntactic structure. Moreover, one could look for phasic and tonic changes in structural parameters of a given call type along a continuous sequence of emissions, which could then be matched to the probability of responses by other animals. This would allow testing the hypothesis that sudden changes in one or a couple of parameters serve to trigger care-giving responses (Todt, 1988; Todt et al., 1995). Given that all call types were related to almost all the specific situations analysed (although with varying strengths), this suggests that they might be functionally more related to each other than assumed here, and therefore this approach might be fruitful in elucidating this possibility. On the other hand, one should not overlook a finer study of structure to inspect for the possibility of functional specificity or even referentiality.

With respect to observational design for field studies, a few improvements would seem useful. First, one should concentrate attention on infants for longer periods of time. This allows an increase in the number of interactions recorded, which then permits a finer division of the analysis categories considered here. For example, one could then compare the results of the analysis of prevention of access to the nipple, with the ones on removing the infant from its carrier's back, instead of lumping them all under a single label (conflict of interest). In the first case, it is possible to go even further, and compare passive prevention (mother turning its back) with a more active one, and in this case manual prevention against mock bites. Here the analyses of

sequences of behaviour (and transition probabilities) could be highly informative. For example, by comparing those instances when the infant was successful in attaining the desired outcome (access to the nipple, riding, etc.) with those unsuccessful ones, one can shed more light in the message being conveyed by each call type. By having a larger sample size, it is also possible to track the ontogenetic trajectory of the usage of the call types and the changes in mother-infant interactions. For example, one can compare the amount of calling necessary for obtaining help to cross a large gap, or for being allowed to ride in different phases of the development. Another consequence would be the possibility of controlling for general behavioural states in some comparisons (e.g. comparing call relation to approaches, manual prevention, etc. only within feeding or resting). One will also be allowed to contrast call behaviour in a specific context between states (e.g. time lag of calls with respect to approaches in feeding against resting, travelling, etc.).

With respect to gap crossing, it is essential to register all cases when an animal faces a gap, which would allow a finer test of the predictions considered here. Moreover, a classification of different types of gap in size and orientation categories would be necessary, and also useful for making further predictions. For size one could have spaces that can be crossed: with a normal stride, with a large step, only by bridging, and finally spaces that can only be overcome by jumping (maybe considering one, two, and so on body lengths to give a measure of difficulty of the jump). Obviously, for those categories one should consider not the very tips of the branches, but the last stable substrates on each side, which necessarily involves a degree of subjectivity. For orientation, horizontal, diagonal and vertical gaps could suffice. With this kind of data one could test, for example, the prediction that animals would be expected to call more, the more difficult it is to cross a gap.

Another useful improvement is to have an independent measure of stress or anxiety, by using finer measures of scratching behaviour. Thus, for example, instead of merely scratching and touching as used in this study, one could register the actual number of bodily contacts, the rate (number of contacts by time), the region of the body that was contacted, etc. One more development could be the register of all occurrences of rare events that might throw some light

on the function of these calls, specifically aggressive behaviours (chases, fights, and physical attacks) and activities around tree water holes.

An aspect of the study of calls of this complex that should merit special attention actually refers more to analysis improvements. By having high quality recordings with simultaneously collected detailed behavioural and circumstantial data, sound analysis can provide information to many interesting aspects of the complex. An obvious starting point is to conduct a number of different measures on a large sample of calls, provisionally classified by ear into one of the three types. Then, one should subject the measures to a discriminant analysis to see if the calls can be easily differentiated on the basis of the measurements or if they are graded (for an example see Robinson, 1984; for an example see Todt et al., 1995). The same technique could be used to investigate individual differences, which are normally very important in calls from immature animals (for applications see Norcross et al., 1999; Oda, 2002; Randall, 1995; Smith et al., 1982; Teixidor & Byrne, 1999). One could also search for the existence of sub-types, and if these are consistently associated with particular contexts or referents.

Finally, the potential to use this call type in playback experiments should not be neglected. Here, one could mainly use the calls to answer questions not directly related to their functions, e.g., to tackle issues of individual recognition; group recognition, etc. The classical paradigms of using latency to look at the speaker or duration of the stare would be very appropriate. Additionally, one could design other experimental set-ups in captivity, aimed at advancing further the comprehension of the function of the calls. For example, situations likely to cause distress could be artificially created, by isolating a youngster, or positioning it in a place where it cannot leave by its own means, thus simulating a gap situation. Presenting video footage of different individuals (dominants and subordinates) in threat postures could serve to test for the submission role of a given call. Here one is limited only by the creativity of the researcher.

In sum, future studies and analysis should focus on: the verification of possible temporal structure on emissions of the different types (which can have implications for the study of syntax or to test hypothesis about the mechanisms of crying); on a much finer-grained division of behavioural categories for data collection; on discriminant analysis to check if the calls are graded or discrete, if

they are individually distinctive and if there are meaningful sub-types; playback experiments under natural and controlled settings.

## CHAPTER 5: LOUD CALLS

*“It is probable, however, that the noise serves to intimidate their enemies”* Bates (1892) quoted in Carpenter (1934).

*“howling is a kind of music which the animals produce and enjoy”* Renger (1830) quoted in Carpenter (1934).

### Abstract

In howler monkeys, both the specialised anatomy of the vocal apparatus and the time and energy invested in loud call production (contrasting with their energy-saving lifestyle) suggest that long-range vocalisations may play an important role in their lives. In this chapter I present data to investigate the function(s) of the roar of black howler monkeys, and their spacing pattern and system. Natural calling behaviour was mainly spontaneous and influenced by abiotic variables (sunrise time, temperature and occurrence of extreme weather events). However, inter-group encounters were very effective in eliciting calls at all times of the day. Calling occurred throughout the home range and frequency of calling related to the intensity of use of a given area, but only due to the lack of calling from poorly used areas. The group called less than expected in border areas, and more in the centre of the range. During playback experiments, simulating the presence of a stranger group, the monkeys' reaction varied according to the position of the speaker - inside (I) or in overlap (O) areas. Contrasting I with O trials, the alpha male: roared more frequently than expected in I (but not in O), and significantly earlier than O; tended to call at or after the speaker site in I and from neutral locations in O; started moving earlier and approached the speaker faster in I; tended to move towards the speaker in I and neutrally in O; and ground travel (a rare behaviour) and patrolling were observed mostly in I. The roars of black howlers seem to be related to inter-group spacing, as in other howler species. We suggest that roars provide a mechanism for advertisement of occupancy, and an aggressive display during encounters to reinforce occupancy, and provide a way of settling disputes without chases and fights. Roars do *not* seem to function in a system of mutual avoidance, as in other howler species, nor do they operate in conventional and regular reinforcement of border locations.

## 5.1 Introduction

### 5.1.1 Loud calls

Within the large array of vocalisation types found across primate species, high amplitude calls always generated an amount of interest proportional to their volume. Research has been conducted in most genera in which this kind of vocalisation is found and a range of different functions has been proposed (reviewed in Table 5.1, where I classified the proposed functions according to the nature of the main recipient(s) of the emissions into inter-specific, intra-group or inter-group, as the nature of the problems and scope vary accordingly). Species of the genus *Alouatta* produce very strong and characteristic loud calls. A modified and specialised anatomy of the vocal apparatus is associated with these vocalisations, whose most noteworthy component is the greatly enlarged hyoidean bone (Schön, 1971; Schön Ybarra, 1988). It was even suggested that this anatomical commitment might affect other aspects of howlers' lives, such as positional behaviour (Schön-Ybarra, 1984).

The expression 'loud call' may seem at first a highly subjective and anthropocentrically oriented one. However, one can operationally define a loud call as any vocalisation which has the potential to regularly reach listeners outside the home range of the producer. In fact, this definition can be applied to most of the cases of primate loud calls reviewed in Table 5.1. Furthermore, despite the apparent diversity of suggested functions, many of them come down to the ultimate function of control of access to resources, in particular of space but also of mating partners. The key point is that both these functions refer usually to outsiders. Accordingly, in most studies in which a vocalisation has been explicitly labelled as a 'loud' or 'long-distance' call, one of these two functions was suggested. Another main hypothesis in the literature is that loud calls possess a role related to predator avoidance (Byrne, 1981, 1982; Gautier & Gautier, 1977; Wich & Sterck, 2003; Zuberbühler, 2001 a, b; Zuberbühler et al., 1997). However, three different specific functions can be performed by vocalisations related to predator avoidance. The first is to announce the presence of a predator (presumably to group members) the classical alarm calls (Hohmann

& Herzog, 1985; Range & Fischer, 2004; Seyfarth et al., 1980 a, b; Wich & Sterck, 2003; Zuberbühler et al., 1997)

. In this case, it is not necessary for the call to be loud, unless the individuals are usually separated by large distances. Therefore, alarm vocalisations that do not fit the criterion proposed above should not be classified as loud calls, to avoid confusion in the literature. The second possible function of a vocalisation linked to predator avoidance is the deterrence of stealth predators, by announcing to them that they have been spotted (Zuberbühler, 1999 b, 2000 a, 2001 b; Zuberbühler et al., 1997). As the announcement is made to close predators, it is also not definite that all calls possessing this function could be labelled as loud calls. The third possibility is for a given vocalisation to serve as an honest indicator of group size, and thus of its capacity to defend itself against attacks (Byrne, 1981, 1982). As this function does not require the close presence of listeners, calls with this function do not present any objection in advance to their classification with other loud calls.

**Table 5.1 Review of work conducted with high-amplitude vocalisations, indicating the (suggested or inferred) category of recipients (1 – inter-specific; 2 – intra-group; 3 – inter-group) and their proposed function and/or context of emission\*.**

| Species                                | Loud call | Recipient    | Suggested function or context of emission  |
|--|-----------|--------------|--|
| <i>Avahi laniger</i> <sup>a</sup>      | Whistle   | 2 (?), 3 (?) | Describes intra-specific functions for loud calls in general.  |
| <i>Cheirogaleus major</i> <sup>a</sup> | Whistle   | 2 (?), 3 (?) | See <i>A. laniger</i> .  |
| <i>C. medius</i> <sup>a</sup>          | Whistle   | 2 (?), 3 (?) | See <i>A. laniger</i> .  |
| <i>Galago alleni</i> <sup>a</sup>      | Croak     | 2 (?), 3 (?) | See <i>A. laniger</i> .  |
| <i>G. crassicaudatus</i> <sup>a</sup>  | Cry       | 2 (?), 3 (?) | See <i>A. laniger</i> .  |
| <i>G. demidoff</i> <sup>a</sup>        | Chatter   | 2 (?), 3 (?) | See <i>A. laniger</i> .  |
| <i>G. garnettii</i> <sup>a</sup>       | Cry       | 2 (?), 3 (?) | See <i>A. laniger</i> .  |
| <i>G. matschiei</i> <sup>a</sup>       | Woo       | 2 (?), 3 (?) | See <i>A. laniger</i> .  |
| <i>G. moholi</i> <sup>a</sup>          | Bark      | 2 (?), 3 (?) | See <i>A. laniger</i> .  |
| <i>G. senegalensis</i> <sup>a</sup>    | Woo       | 2 (?), 3 (?) | See <i>A. laniger</i> .  |
| <i>G. zanzibaricus</i> <sup>a</sup>    | Chatter   | 2 (?), 3 (?) | See <i>A. laniger</i> .  |
| <i>Indri indri</i> <sup>b</sup>        | Song      | 2,3          | Advertise occupation of a region to near-distant groups and the present location to neighbouring groups; for nomadic animals, the songs from a period of time may indicate the density of an area; reaggregation of the group; maybe alert/alarm; provide information on group composition; reproductive function; maybe aid in group formation; plays a role in inter-group encounters. |
| <i>Lemur catta</i> <sup>c</sup>        | Howls     | 2,3          | Possibly a loud call. Proposed to function in male advertisement and advertisement of group presence and location.   |
| <i>Loris tardigradus</i> <sup>a</sup>  | Whistle   | 2 (?), 3 (?) | See <i>A. laniger</i> .  |
| <i>Microcebus murinus</i> <sup>a</sup> | Trill     | 2 (?), 3 (?) | See <i>A. laniger</i> .  |

|  |   |              |   |
|--|---|--------------|---|
| <i>Mirza coquereli</i> <sup>a</sup>        | Trill                                     | 2 (?), 3 (?) | See <i>A. laniger</i> .   |
| <i>Nycticebus cougang</i> <sup>a</sup>     | Whistle                                   | 2 (?), 3 (?) | See <i>A. laniger</i> .   |
| <i>N. pygmaeus</i> <sup>a</sup>            | Whistle                                   | 2 (?), 3 (?) | See <i>A. laniger</i> .   |
| <i>Perodicticus potto</i> <sup>a</sup>     | Whistle                                   | 2 (?), 3 (?) | See <i>A. laniger</i> .   |
| <i>Ateles geoffroyi</i> <sup>d</sup>       | Whinnies                                  | 2            | Given in many different contexts; Travel whinnies might be contact calls  |
| <i>Callicebus moloch</i> <sup>e</sup>      | Resonating notes, song phrases            | 2, 3         | “during vigorous and prolonged disputes”, may “help to maintain territories”, signalling occupation; also during inter-group encounters |
|  | Duets; call sequences                     |              | Spacing between groups (defining and reinforcing a boundary)  |
| <i>Callithrix jacchus</i> <sup>f</sup>     | Phee                                      | 2,3          | Territorial; produced after separation  |
| <i>Leontopithecus rosalia</i> <sup>g</sup> | Long calls                                | 2            | During vigilant behaviour; “may be functional in maintaining and developing the pair bond”  |
| <i>Saguinus fuscicollis</i> <sup>h</sup>   | Loud long calls                           | 2, 3(?)      | Possible hostile connotations; also emitted in exchange between different cages   |
| <i>S. mystax</i> <sup>i</sup>              | Long calls                                |              | Produced when individuals were separated.   |
| <i>S. oedipus</i> <sup>j</sup>             | Normal long calls; Combination long calls | 2, 3         | Territorial (emitted in antiphonal exchanges )<br>Possibly a “lost” call  |
| <i>Cercocebus albigena</i> <sup>k</sup>    | Whoopgobble                               | 2,3          | Maintain inter-group distance/inter-group avoidance; increase group cohesion and maybe direct group movements                           |
| <i>Cercopithecus diana</i> <sup>l</sup>    | Long-distance calls                       | 1,2          | Advertise to predators that they have been detected; “semantic signals that denote different types of predators”                        |
| <i>C. campbelli</i> <sup>m</sup>           | Loud male calls                           | 2            | Predator alarm calls – referential.   |
| <i>Macaca fascicularis</i> <sup>n</sup>    | Krahooh                                   |              | Not established.  |

|  |                         |       |   |
|--|-------------------------|-------|---|
| <i>M. silenus</i> <sup>o</sup>               | Loud calls              | 1,2   | Maybe cohesion and rallying; maybe regulating interspecific group spacing (with <i>P. johnii</i> )  |
| <i>Papio</i>                                 | Bark                    | 2     | “may ultimately function to avoid separation from others”   |
| <i>cynocephalus</i> <sup>p</sup>             | Wahoo                   |       | Indicator of dominance  |
| <i>P. papio</i> <sup>q</sup>                 | Type 1 and 2 Loud calls | 1,2,3 | Nocturnal volleys were suggested to provide predators with honest information on the number of adult males on a group.  |
|  | Barks                   |       | Avoidance of separation, keeping contact between sub-groups, reaggregation  |
|  | Sharp/Shrill Bark       |       | Alarm   |
|  | Various calls           |       | Agonism   |
| <i>Colobus guerezda</i> <sup>r</sup>         | Roar                    | 1,3   | Maintain intergroup distance. Intimidation of predators   |
| <i>Presbytis johnii</i> <sup>o</sup>         | Loud calls              | 1     | Maybe regulating interspecific group spacing (with <i>Macaca silenus</i> )  |
| <i>P. thomasi</i> <sup>s</sup>               | Loud calls              | 3     | Indicate strength and reduce the risk of chases and fights in the context of deterring rivals and preventing infanticide.                                       |
| <i>Hylobates klossii</i> <sup>t</sup>        | Songs                   | 1     | Also emitted in the presence of predators with audience effect.   |
|  |                         | 3     | Maintain exclusive use of sleeping trees and mate attraction (male songs); announce presence on the territory and the location of the boundaries (female songs) |
| <i>H. lar</i> <sup>u</sup>                   | Loud calls              | 3     | Female calls: exclusion of outside females; Male calls: courting and/or aggressive towards outside females.   |
| <i>H. muelleri</i> <sup>v</sup>              | Song duets              | 3     | Mediate intergroup spacing  |
| <i>Symphalangus syndactylus</i> <sup>w</sup> | Various calls           | 3     | Maintenance of inter-group spacing  |
| <i>Pongo pygmaeus</i> <sup>x</sup>           | Long call               | 3     | Spacing between males   |
| <i>Pan paniscus</i> <sup>y</sup>             | High-hoot               | 2     | Communication between parties; assemble of individuals; maybe stimulation of call by distant animals  |
| <i>P. troglodytes</i> <sup>z</sup>           | Pant-hoot               | 2     | “maintain contact with and to recruit allies and associates”  |
|  |                         | 2     | Pant-hoots given at arrival at food trees signal status. Maybe attraction of oestrous females.  |
|  |                         | 3     | “Advertise presence and numerical strength”   |

\* I included in this table calls explicitly labelled as loud or long-distance calls, vocalisations which were described as very intense, and also the long calls of callitrichids traditionally grouped with loud calls and showing a similar range of functions. Howler monkeys were explicitly left out of the table as the researches are described in more detail in the text. On a few articles/species it is quite difficult to extract more precise information than the one mentioned. In *Callicebus moloch*, for example, a plethora of vocalisations is described as being loud, or many different types are described and said to be part of loud phrases or sequences (Moynihan, 1966; Robinson, 1979a). I restricted the mention here to the most obvious and clear cases. In other articles it is not altogether clear what is the function defended by the author, or functional considerations were actually not the scope of the study. This review is far from exhaustive.

<sup>a</sup>Zimmermann (1995); <sup>b</sup>Pollock (1986); <sup>c</sup>Macedonia (1993); <sup>d</sup>Teixidor and Byrne (1999); <sup>e</sup>Moynihan (1966), Robinson (1979b; 1981); <sup>f</sup>Norcross & Newman (1997); <sup>g</sup>McLanahan and Green (1977); <sup>h</sup>Moody and Menzel (1976); <sup>i</sup>Snowdon (1985); <sup>j</sup>Cleveland & Snowdon (1982); <sup>k</sup>Chalmers (1968), Waser (1975; 1976; 1977; 1978); <sup>l</sup>Zuberbühler et al. (1997); <sup>m</sup>Palombit (1992a); <sup>n</sup>Herzog and Hohmann (1984), Hohmann & Herzog (1985); <sup>p</sup>Cheney et al. (1996), Kitchen et al. (2003); <sup>q</sup>Byrne (1981); <sup>r</sup>Marler (1969; 1972); <sup>s</sup>Steenbeek (1999), Wich et al. (2002 a, b), Wich and Sterck (2003); <sup>t</sup>Tenaza (1976); <sup>u</sup>Raemakers and Raemakers (1985); <sup>v</sup>Mitani (1985 a, b); <sup>w</sup>Chivers (1975); <sup>x</sup>Mitani (1985c); <sup>y</sup>Hohmann and Fruth (1994); <sup>z</sup>Mitani & Nishida (1993), Clark and Wrangham (1994), Wilson (2003)

The two main groups of functions (control of access to resources and predation avoidance), mentioned above for primate loud calls, are not a speciality of the order; quite the opposite, the findings echo what has been found in a wide variety of vertebrate taxa. In fact, these are among the functions most commonly ascribed to acoustic signals, regardless of their intensity and the social structure characteristic of the taxonomic group. For example, a territorial or space defence role has been suggested for wolf howling (Harrington & Mech, 1978 a, b; 1983), foot-drumming in kangaroo rats (Randall, 1995), roe deer barking (Reby et al., 1999), advertisement calls of green frogs (Bee et al., 1999) and countless examples for bird songs (see Catchpole & Slater, 1995). Proposals of a function related to access to females are also very common (red deer: Clutton-Brock & Albon, 1979; McComb, 1991; elephants: Poole, 1999). Functions related to predator avoidance have also been made (Reby et al., 1999).

### 5.1.2 Howler monkeys' loud calls

Howler monkeys are slightly unusual among primates since both males and females produce loud calls, and these are emitted usually at the same time during group sessions. This pattern is normally found in monogamous species that jointly defend a border, such as the titi monkeys and the hylobatids, but is rare otherwise (*Colobus polykomos* females sometimes emit loud calls, Zuberbühler, pers. com.). Accordingly, most authors that have worked with howler monkeys do not differentiate the participants in a given chorus, and they are merely treated as loud call sessions. However, when conducting a functional study, one should remain sensitive to potential sex differences in usage and function of loud calls. After all, males and females have different ecological needs, and usually differ in the strategy used to solve their problems. Because of these differences, the sexes also differ in their interests, which has a large impact on functional analysis. For example, if in a given species males migrate and females stay in the natal group, the first would be more concerned with take-over attempts, while the later would be more interested in securing an area in a long-term basis. I will deal in more detail with the issue of potential functional differences in the discussion section.

Almost all the functional proposals for loud calls of the different species of howler monkeys revolve around the usual ultimate functions of regulation of use of space and access to reproductive partners, although many differences arise at other explanatory levels. Note that, at first glance, the diversity of functions found in Table 5.1 could seem to argue against this notion of two main groups of functions (besides predator avoidance functions). However, the variety derives from the different levels of explanation considered. For example, one can have explanations about mechanisms to achieve an ultimate function (e.g. regulation of use of space by definition and reinforcement of boundaries or mutual avoidance) or proximate functions (for example announcing location or resource holding potential).

Regulation of use of space is the most common suggestion for howler monkeys' loud calls (Altmann, 1959; Baldwin & Baldwin, 1976; Bernstein, 1964; Carpenter, 1934; Chiarello, 1995; Chivers, 1969; Collias & Southwick, 1952; Crockett & Eisenberg, 1987; Drubbel & Gautier, 1993; Horwich & Gebhard, 1983; Kitchen, 2004; Southwick, 1962; Whitehead, 1987, 1989), although the suggestions vary considerably in finer detail.

One group of studies (Altmann 1959; Bernstein, 1964; Collias & Southwick, 1952; Drubbel & Gautier 1993; Horwich & Gebhard 1983) seems to advocate a territorial function in a more classical way; that is, the defence of a given area, which usually implies its exclusive use with little or no overlap. However, the proposals are in general either vague or based on outdated concepts, and/or the study was short term. Altmann (1959) stated that *A. palliata* groups defend territorial boundaries through vocal battles, although his suggestion seems to include elements of mutual avoidance.

Another set of studies (Carpenter 1934, Southwick 1962, Chivers 1969, Baldwin & Baldwin 1976) conducted with *A. palliata* proposes that this species' loud calls lead to mutual avoidance between groups. This system generates a pattern of spatially or temporally overlapping home ranges with some exclusive areas. Chivers (1969) adds the observation that, if the groups were very close, approach and vocal battle would follow instead of avoidance, with one or both groups eventually retreating. Whitehead (1987), working with the same species, advanced a slightly different proposal, in that the loud calls promote inter-group avoidance via reciprocation of movements. Later he complemented the model

demonstrating that this species also shows a site-dependent response to intruders, defending favoured rich patches (Whitehead 1989a).

Turning to regulation of access to mating partners, Sekulic suggests that the daytime roars of male *A. seniculus* are used in assessment of opponents for access to females (Sekulic, 1982 b; Sekulic & Chivers, 1986). Additionally, in the only work that I am aware of that deals specifically with female calls, she hypothesises that the roars of female *A. seniculus* serve to deny access of extra-troop females, or even of troop females, to the troop male (Sekulic, 1982 a, 1983 b). She also proposes that female roars could work to prevent access to limited resources by joining individuals, to guarantee space in the troop for their own offspring and could also provide a reinforcement of the pair bond. She even described female-only sessions, apparently directed at other females.

Chiarello (1995) also advocates assessment of opponents as the function of *A. fusca* loud calls, but does not make explicit the source of conflict, whether space or access to females. Also, Kitchen (2004), working with *A. pigra*, shows that the animals provide and use information on the numeric odds between groups (number of defending to intruding males) through the loud calls. However, apart from a general statement of resource defence, the author does not mention which resource is at stake.

Concerning alternative proposals, Sekulic (1982 b) found some evidence for use of loud calls in patch defence of valuable resources (fig trees) by *A. seniculus*. Although this behaviour certainly influences the spacing pattern, the data are somewhat limited and this possibility is not developed further. Whitehead (1989) proposes several additional functions for *A. palliata* loud calls, namely, attraction of reproductive partners (during group formation), coordination of group cohesion, broadcasting of information on resource localisation, and initiation and direction of movement. (Steinmetz, 2000) reported that *A. fusca* emitted roars when separated, but does not mention if this helped the reunion. The use of roars as aggressive displays was registered in some occasions (Calegario-Marques & Bicca-Marques, 1995; Chiarello, 1995; Sekulic, 1982 c, 1983 b). The emission of loud calls in threatening/alarm situations has also been reported (Altmann 1959, Baldwin & Baldwin 1976, Calegario-Marques & Bicca-Marques 1995, Sekulic 1982 c). In this respect, Carpenter (1934) describes quite vividly that after an attempt of predation of an

infant mantled howler by a felid (possibly ocelot), “*They [howlers] were roaring as I have rarely heard howlers roar*”. Local inhabitants of the Pantanal region of Brazil also anecdotally reported to me such very intensive calling in the presence of felids.

Thus, there is a general lack of consensus with respect to the functions of howler monkey loud calls, even within single species. Across species there is further variability. A potentially confounding factor in this variability is that there seems to be at least two main kinds of loud calls, generally labelled roars/howls and barks, in most of the species: *Alouatta caraya* (Calegario-Marques & Bicca-Marques, 1995; Thorington et al., 1984); *A. fusca* (Chiarello, 1995; Oliveira, 1997); *A. palliata* (Whitehead, 1987, 1989 b, 1995); *A. seniculus* (Drubbel & Gautier, 1993; Schön Ybarra, 1986). The studies on *A. palliata* dealt with both calls, but the pattern of loud calls in this species seems to be quite distinct from all others (Whitehead, 1995). Work on the other species generally focused on roars. Also, the research concentrates on two species, *A. palliata* and *A. seniculus*, with the others lagging behind.

During the pilot study and the initial phases of the main data collection, the observations pointed towards a function of *A. caraya* roars related to regulation of inter-group spacing. The preliminary impressions were that the spacing pattern (definition of spacing pattern and system follows Waser, 1977) seemed to be one of exclusive use of an area, maybe with a thin overlap region at the borders. In this chapter I provide observational data on loud call emissions by the study group as this can substantiate the first initial hints on their function, and also serve as a basis against which playback results and future studies can be compared. Next, I describe the behaviour of the study group during natural inter-group encounters. I then describe the results of a playback experiment carried out with the aim of understanding the regulation of use of space of the study group.

### 5.1.3 Alternative proposals

In the discussion section, alternative proposals in the literature concerning functions of loud calls (not only for howlers) will be evaluated in the light of my data and on available information on the genus and the species. However, many of the proposals are somewhat secondary, and can be discarded at an early phase.

Other suggestions cannot be evaluated with the kind of data that I collected. In the paragraphs that follow, I consider some of these alternative hypotheses. In doing so, I might on occasions touch on data not formally presented yet. The purpose here is to discard some ideas at an early stage (or show that they might work under some conditions or as alternative functions), and concentrate the focus both on the preliminary working hypothesis and on the main alternatives later on. I now turn to the alternative proposals.

### **Female calls**

Sekulic (1982 a; 1983 b) also proposes several functions for female roars. (1) Roars directed at solitary females (sessions initiated by females or exclusively female sessions) are seen as ritualised aggressions to prevent them from joining the troop, for three reasons: “limited food resources....; protection of space within the troop for resident female offspring; ... prevention of access to mates” (Sekulic, 1983 b, p. 302). (2) Calls towards troop females serve to deny access to dominant males. (3) Howling alongside the males would reinforce the pair-bond and make them protect infants against infanticide. (4) Finally, females might call to incite male competition and select the one most likely to remain dominant. The hypotheses proposed for *A. seniculus* female calls (apparently directed at females do not seem to apply to *A. caraya*. Females never roared alone nor did they initiate any calling session during the study. Also, the dominant female (number 5) constantly chased and displayed towards the sub-adult female (number 9) for a long time, but never used loud calls in her aggressive behaviours. The dominant female did seem to suppress calling from female 6 by embracing her during some group sessions, although the calling itself did not seem directed at the subordinate. Also, on the single occasion when I observed an isolated female inside the home range of the group, none of the group females emitted roars nor chased the invader, who retreated quietly. Concerning the pair-bond reinforcement hypothesis, it is not possible to evaluate it with the data at hand. Group take-overs have been associated with infanticide and infant disappearance in this species (Rumiz, 1990). So, it remains a possibility to be tested. In connection with this hypothesis, I observed that female calling during roar sessions seemed to provide an incentive for louder or longer

calling. For example, when a session was waning, female (or sub-adult male) calling would generate a rebirth of the session by the alpha male, which can be seen as a form of support to the dominant. It is not clear if this would reinforce in some way the pair-bond or not, and if it would make any difference under the risk of infanticide.

### **Intra-group cohesion**

Besides playing a role in inter-group spacing, Whitehead (1989 b) suggests that mantled howlers' roars perform four additional functions, all taken from Waser's (1977) original list of seven possible functions of loud calls. Observing a reduction of inter-individual distances after some playback trials, he advocates that the loud calls aid in the co-ordination of intra-group cohesion. However, the reduction was a *response* to a playback from an unfamiliar group. He doesn't present any evidence that the animals showed the same behaviour to the vocalisations of their own group. Therefore, the distance reduction could have been a reaction to a possible threat. Moreover, suggesting this function for a loud call makes sense only in species that typically have large inter-individual distances. Howler monkeys are notoriously gregarious, which makes the use of an extremely loud call for this end unnecessary, and possibly disadvantageous, by announcing the location of animals to neighbours and potential predators. It is also not parsimonious to advance this function for a vocalisation that is long and continuous. On the other hand, reduction of group spread may still occur as a side effect of loud calls, as they obviously provide a focal point that could help animals to keep track of the group. In fact, there are suggestions that incipient roars (see next topic for a description of *A. caraya* call types) might be used that way.

### **Information on the localisation of feeding resources**

He then considers the function of broadcasting information on resource localisation (Whitehead, 1989 b). The evidence was a clumped use of space and an association between calling and activity fields, which could provide information to neighbours about the location of edible resources. However, stated

in this way, broadcasting is not a function per se, but an unintentional and undesired result. The original proposal was the transmission of information to other *group* members (Waser, 1977), a function that is only worth considering in species whose individuals forage widely spaced.

### **Attraction of reproductive partners**

Whitehead (1989 b) presents some anecdotal evidence supporting a role in the attraction of reproductive partners. However, only emigrating males attempting to form a new group could use loud calls this way. As I did not observe a group formation situation with certainty, it is not possible to comment on this function for *A. caraya*. I noticed an isolated male inside the home range on a couple of occasions, and this individual never vocalised (though it could have been the male of a pair involved in an expulsion episode, see below).

### **Co-ordination of group movements**

Finally, he suggests a role for loud calls in the initiation and subsequent direction of group movements, based on a relationship between calling patterns and subsequent movements (Whitehead, 1989 b). For the same reasons presented for the reduction of individual distances, it is not necessary and may even be prejudicial for a gregarious species to use a loud call for co-ordination of group travel. There was no indication whatsoever that roars of the study group were associated to initiation of travel, and even less so to directing of group travels. In fact, many sessions occurred *after* a travelling bout.

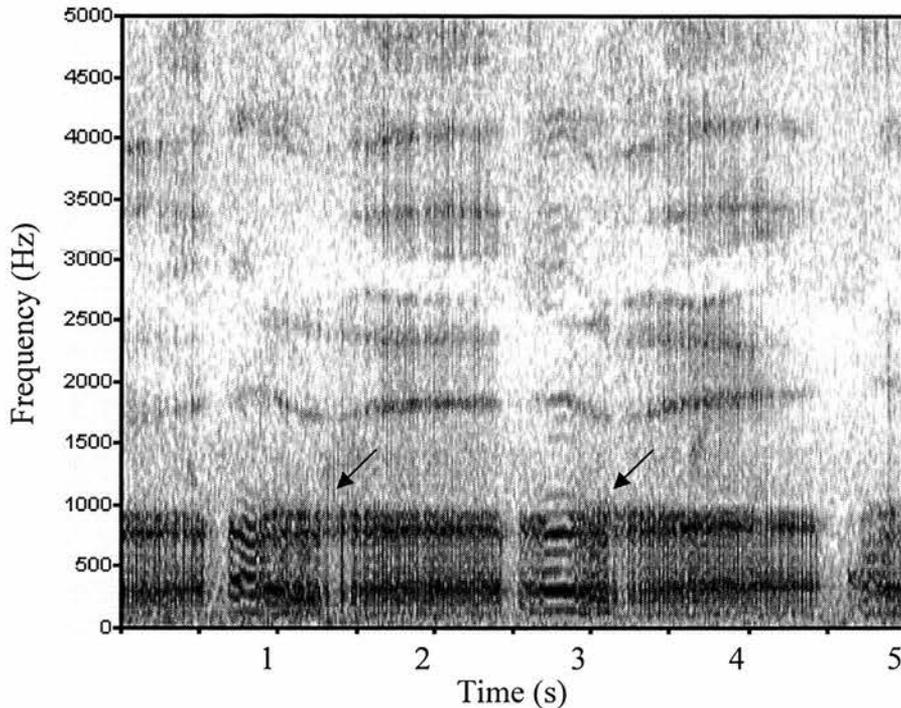
### **Agonistic contexts**

Animals may emit loud calls in intra-group agonistic contexts, associated with displays, chases, attacks or submissive behaviours, either by the contestants themselves or by third parties (e.g. Byrne 1981, Kitchen et al., 2003). Functions in this context can be varied. At least in one species, loud call emissions have been shown to be an indicator of dominance (*Papio cynocephalus ursinus*, Kitchen et al., 2003). Howler monkeys occasionally use roars in agonistic

contexts (Calegario-Marques & Bicca-Marques 1995, Chiarello 1995, Sekulic 1982 c, 1983 a), but I never registered loud calls in agonistic contexts during my study.

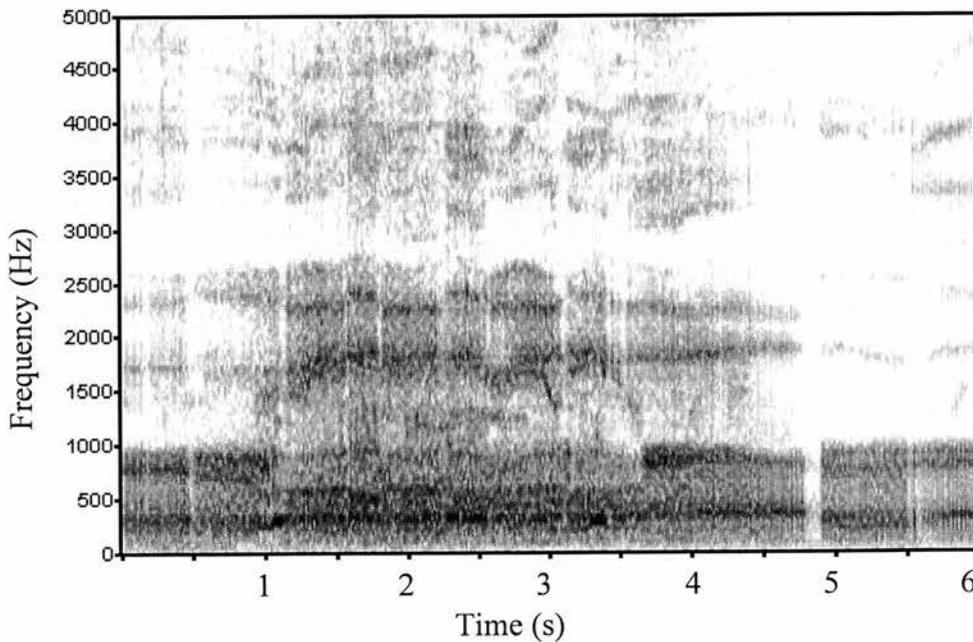
#### 5.1.4 *Alouatta caraya* call types

Black howler monkeys (*A. caraya*) produce at least two main kinds of loud calls, here labelled roars and barks to follow the nomenclature. Both males and females produce these two call types. Roars (Figure 5.1) consist of apparently continuous sounds with a cyclic nature corresponding to alternating inhalation and exhalation phases (judging from abdominal movements), here denominated units. The call presents a mixed tonal/atonal quality with two main emphasised frequency bands, the first from 200-450Hz and the upper one from 600/700 up to circa 1000 Hz. These bands probably correspond to formant frequencies. On one of the phases (the one consistently presenting the shorter duration), it is possible to see sometimes an underlying tonal structure with several harmonics. Weak upper bands presenting frequency modulation can also be seen. The modulation takes the form of a downsweep on the shorter units and of an upsweep on the longer units, which might contribute to the sawing quality of the sound.



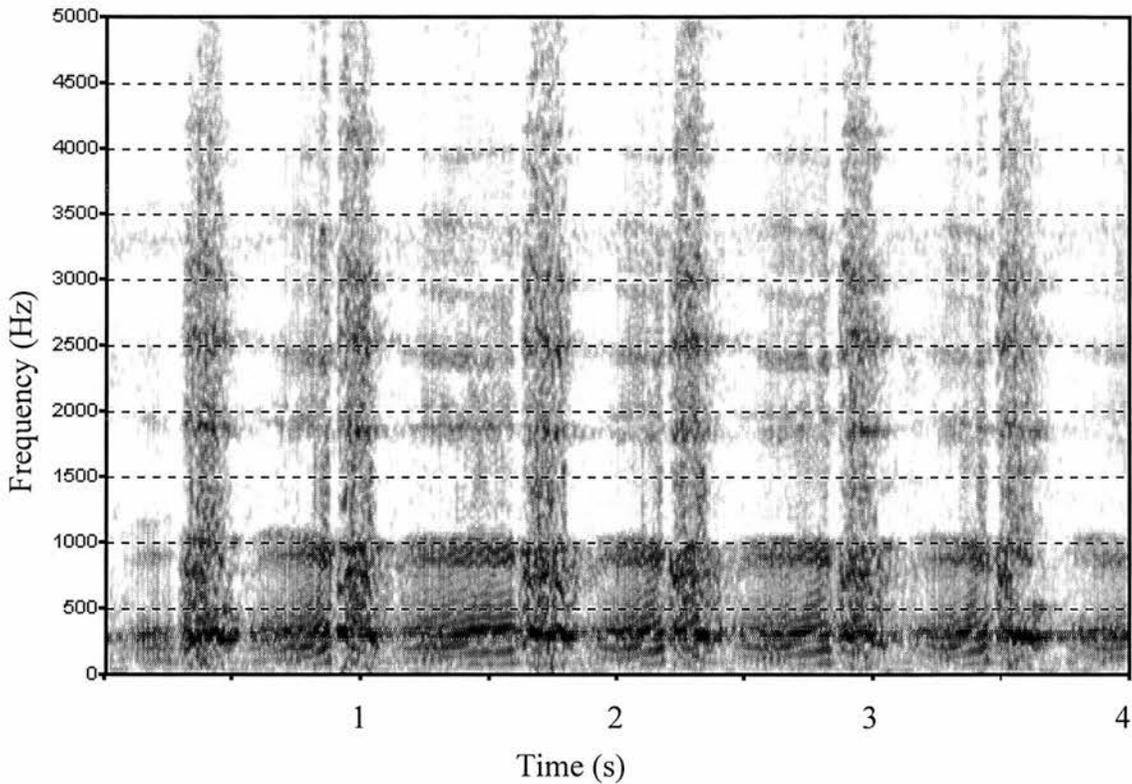
**Figure 5.1** Spectrogram of two complete inhalation/exhalation cycles of a roar. Time step: 0.03s. Gaussian window. Note the fading between the phases (arrows) and the frequency modulation of the band located between 1500 and 2000 Hz.

Periodically, within a roar emission, there are a group of inhalation/exhalation cycles that are louder than the adjacent ones and produced at a much faster rate. These, as a group, may be denominated climax, following descriptions of roars in other species (Schön Ybarra 1986, Drubbel & Gautier 1993, see Figure 5.2). Sometimes the climax is preceded by a crescendo of the normal syllables. For the climaxes, there are also two energy bands, and their general location is similar. Opposite to the “normal” units, however, the first band was broader than the second one (sometimes they were fused), giving the spectrogram the appearance of having been turned upside down. Also, energy at upper side bands was much clearer, but this could have been a result of the generally higher intensity. Frequency modulation was also clear on the upper bands, but not on the first two. Due to the usual joint participation of several individuals in the climaxes, the spectrograms very often look much less clear.

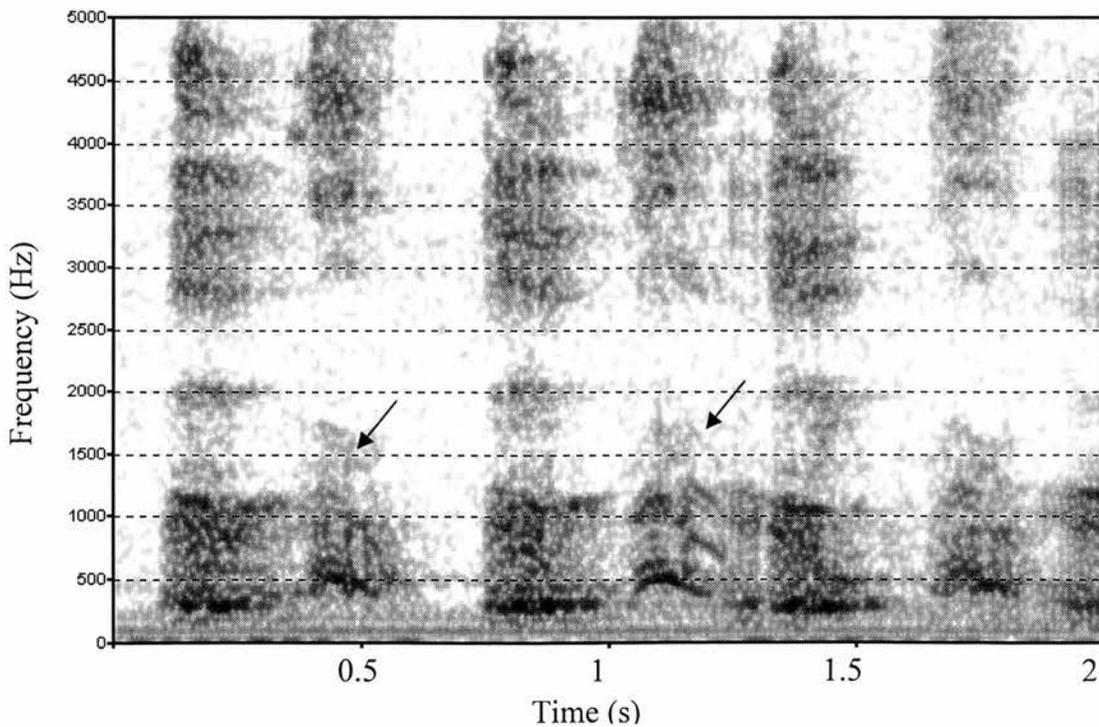


**Figure 5.2 Spectrogram of a climax section of a roar. Time step: 0.03s. Gaussian window.**

The barks are a highly variable vocalisation, characterised mainly by short plosive emissions in staccato fashion, lacking the nearly continuous quality of roars (Figure 5.3). Vocal emissions can occur only during expiration or include inspiration as well, when the animal is more excited. In this case, however, pauses between units are clearly perceived by the human ear, which does not happen with roars. If the alpha male is barking, he emits, from time to time, a roar climax-like vocalisation. Energy is distributed in a column of noise with some emphasised frequency bands of similar location with respect to the roars. The shorter unit (inferred to be the expiration sounds) is more noisy and intense. Female barks are higher pitched and more frequency modulated (Figure 5.4).



**Figure 5.3** Spectrogram of bark units. Time step: 0.03s. Gaussian window. The shorter unit composed of a more clear column of noise is the one that remains when only one unit is present. Therefore, it was inferred that it must be the expiration phase.



**Figure 5.4** Spectrogram of bark units showing female emissions (arrows). Time step: 0.03s. Gaussian window.

There is another loud call type considered on this study, the incipient roars, which can also be considered a sub-type of roar. They are emissions of just one or a few roar climaxes, sometimes accompanied by a few cycles of normal roaring. Duration is always very brief.

The main focus of this chapter will be on roar sessions. Both males and females participate on the bouts, although for the latter it is facultative. As at least one female participated in the majority of sessions, I am going to consider here roar sessions, without discriminating the participation of females. I will address the relevance of this joint participation, and possible reasons for the variability in the Discussion. Barks are usually emitted by a smaller number of individuals and, like the roars, females can or cannot participate. When I refer to barks, I also intend to mean bark sessions, irrespective of participants.

## 5.2 Methods

### 5.2.1 Data collection

To obtain a profile of the frequency of emissions of loud calls during the day, I registered the occurrence and type (roar or bark sessions) of loud call emissions by groups in the vicinity of the study group at every ten minutes (instantaneous sampling, Altmann 1974). There are a few potential problems of restricting the range of callers to my hearing radius. Detectability can vary according to time of the day (Waser & Waser, 1977), meteorological conditions (wind and rain noise), the place I was in the home range of the group, and with other sources of noise (birds, insects, etc.). Despite these problems, such data should constitute a reliable measure of the general temporal pattern of emissions along the day for at least of a handful of immediate neighbours, to which the data on the study group could be compared.

Concerning the study group, I noted all occurrences of loud call sessions, registering the following parameters: loud call type (roar, bark, or incipient roar), start and end time, participating individuals, tree number, particularly conspicuous meteorological events, and the occurrence of inter-group or inter-specific encounters. Two sessions of calling were considered distinct if more than one minute of silence separated them. I also made additional *ad libitum* observations, such as the extent of participation of individuals and their behaviour (and of others) during the session. I marked and numbered all trees on which the animals loud called. When transcribing the data, the quadrat number of the calling was also identified.

With respect to inter-group encounters, I did not collect data in a systematic way on the position of the neighbour groups. However, I defined an encounter operationally as every time that there was visual contact between the groups (real or presumed due to the positions of the animals), or cases when the presence of another group nearby could be easily inferred by sounds other than the loud calls. I also used a category of potential cases of inter-group encounter, when a neighbour group was found to be less than 100m from the study group (horizontal visibility within the canopy is presumably much better than my view diagonally from the forest floor). Given the likely importance of at least one of

the loud call types in regulating the spacing between groups, I gave special attention to close inter-group encounters, noting any conspicuous behaviour such as chases, displays, and movements of the groups with respect to each other.

### 5.2.2 Data management

To estimate the profile of emissions along the day, some adjustments were necessary. First, during the main study (10/2001-02/2003) the points for instantaneous data collection were based on clock time and were fixed along the days (always in 10 minute units with respect to the hour). However, the best way to portray and analyse the daily profile of emissions is with respect to sunrise time, as this varies along the year. Therefore, I converted the whole data set, by assigning each data point to the nearest 10-minute point *with respect to the time of sunrise*; inaccuracy in doing so is 5 minutes at most. As there was no systematic bias in the correction and the vocalisation sessions spanned several minutes in the vast majority of cases, it is unlikely that this procedure introduced any serious errors. In the extra field season (July/August 2003), I collected the instantaneous sampling already with respect to sunrise time, which was calculated for all years with the on-line facility provided in the U.S. Naval observatory website.

Second, as the pattern of emission seemed to vary with the seasons, and my field effort also varied along the year, I had to compensate for this potential confound. Thus, for each analysis point (10-minute marks with respect to sunrise), instead of calculating the percentage of days of the whole data set that contained a loud call, I computed monthly percentages, and averaged them to get the “year value”. As the number of data-collecting days for a given month varied from 8 to 28, the point percentages calculated for the months with a small number of days could be non-representative of the profile of that month. To try to minimise potential errors, for months that had data in two separate years, I averaged the two values, before using the month in the calculation of the yearly figure.

With regard to the profile of calling along the day for the study group, the registration of all occurrences of loud calls along with precise information on duration and timing allowed the calculation of additional summary measures,

besides the probability of calling on each 10 minute point. The supplementary parameters include the probability of calling *during* each 10 minute period with respect to sunrise (equivalent to a one-zero sampling technique), the rate of calling (min. of calling/min. of data collection) in each of these periods (or larger ones), and also the distribution of starting times of the sessions. The probability of calling *during* periods of time has the advantage that it avoids missing sessions smaller than 10 minutes altogether, which may occur with instantaneous data sampling.

### 5.2.3 Playback experiment

#### **Experimental design**

The focus of the experiment was on aspects that could help to understand the regulation of use of space in the species, and the possible role of the loud calls in the system. Therefore, I decided to contrast the behavioural response of the group to the simulated presence of another group at a fixed distance from the study animals, under three different conditions, namely, inside the home range (invasion condition), at the border (border or overlap condition) and outside the home range (outside condition). Border areas were defined as regions of the home range in which I saw both the study and a neighbour group to use. Areas defined as inside and outside the home range were used exclusively by the study and the neighbour group respectively. These definitions suffer from the shortcoming that I only had chance observations of the neighbour groups, as I did not follow them systematically. Thus, it might well be the case that neighbours effected deeper incursions on the home range of the study group.

In order to have a reasonable idea of the ranging area of the group, I delayed the start of the experimental series until August 2002, ten months after the beginning of the main field season. Notwithstanding, on the very day of two of the outside trials at the early stages of the series, the group expanded its home range in the direction of the speaker. Although this expansion could be a direct result of the trials, the group passed to use those areas on a regular basis, and further expansions (unconnected to trials) were observed later on. There are also alternative explanations for this. The group might have been using the area, and

it never happened that I was present on the days on which they did. The amount of time spent in the field, particularly at the first stages of the study casts doubt on this alternative hypothesis. Alternatively, the use of these areas might represent a seasonal feature, since I had never observed the group during August and September, but this is also unlikely, since the group continued to use the areas until the end of the study and during the extra season as well, during months on which I had collected data before. Finally, the expansion might have been going on or was something that would occur anyway, independently of the playbacks. The fact that other areas were later incorporated in non-experimental days lends some support to this idea. Whichever the reason, the fact is that these areas turned out to be overlap areas. Accordingly, these trials had to be re-classified as border ones.

Based on the intensity of use of the quadrat in which I placed the speaker, each trial was post-hoc classified in a number of different ways. I made an 'internal' classification, dividing the trials in categories of equal sizes, based on the ascending order of intensity of use of the quadrats *in which the playbacks were carried out only*. I also made 'external' classifications, according to the position of the experimental quadrat in a classification scheme involving *all* quadrats of the home range. I made two 'external' classifications, one based in the ascending array of frequency of use and another based on the cumulative percentage of use. On all cases I made separate 2 and 3 categories schema and classifications both using data over the whole year and during the month on which each trial was done. I employed external categorisation only for the data along the whole year (there is no simple way to make up similar lists using data from different months).

### **Preparation of test tapes**

To avoid possible confounding factors, and potentially increase the strength of the response, I decided not to use calls from groups in the vicinity of the study group as the source of the playback tapes, but instead calls from distant groups. The minimum distance of the recorded groups was estimated to be 1 km. Thus, even if there was the possibility of an auditory contact in some cases, it is likely that the calls arrived to the study group in a severely degraded manner, if

so. I made the recordings with the equipment mentioned in the general methods section. Distances to the microphone ranged from 15 to 50m. At the field station, I then selected parts of the recordings with 30s<sup>1</sup> of duration that had good quality in order to be used in the playback trials. For the extra field season, calls were digitised with CoolEdit 2000 at 44100 Hz and 16 bits, amplified with the software at the maximum level without clipping, sliced into exact 30s sections, and then re-recorded onto a tape. As the main purpose was to study the reaction to the presence of another group at selected locations, and not to a particular type of loud call, I used both roars and barks from stranger groups. To avoid one of the possible sources of pseudo-replication (Kroodsma, 1986; McGregor et al., 1992), I attempted to use different parts of recorded tapes every time. On 9 occasions I used a segment already played, but 3 to 8 months after the first broadcasting. No segment was used more than two times. I never conducted trials on consecutive days. Additionally, if the condition was “inside” (a highly non-natural situation), at least two non-experimental days separated the playbacks.

### **Playback procedures**

I did not conduct trials at dawn or early in the morning. As this was a period of the day when the animals were very likely to call spontaneously, it would be virtually impossible to distinguish between a loud call response to the playback from a regular session. All trials but one took place at least 3 hours after dawn (total range: 1:28-9:45, inter-quartile range: 5:20-7:17).

On an experimental day, I set off for the field and started collecting standard behavioural data. I then waited for a resting session to occur, preferably the long general resting ones after the morning activity bout. I would then look for a playback location according to the desired design. This had to be located between 90 and 110m from the alpha male (estimated distance based on the quadrat system - on one occasion the distance was 125m, but transmission conditions were good). I never repeated the same combination of speaker and

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<sup>1</sup> On the vast majority of cases playback duration was 30-35 s. Due to unforeseen reasons, one of the experiments presented a duration of 120 s and another one of 30s but spread over a period of 1 minute. I decided to keep the experiments as both were still under the normal duration of a session, and the response to the playback was not evidently unusual.

reception locations. If the group started moving, and the distance to the speaker changed to values outside the limits above, a trial at that particular location was abandoned. If the group emitted a loud call before the start of the playback, I waited at least one hour to broadcast the experimental tape. Also, if the design was an overlap or outside one, and a neighbour group called from the same side of the home range of the chosen location, the trial was aborted.

After selecting an appropriate tree, my field assistant hoisted the speaker (Technomad Vernal 15) into a tree branch using the technique described in Zuberbühler (2000a). With the help of a slingshot, a lead, to which a nylon string was attached, was shot over the chosen location, and the string would then hang over both sides of the branch. Then, a rope was attached to the string and pulled over the branch. Finally, the speaker was attached to the rope and hoisted. The speaker was always pointing towards the study group (no more than an estimated 30 degrees divergence) and usually located 3 to 10m from the ground (on two occasions I played from ground level). The speaker was connected to a tape recorder (Marantz PMD 430 or a Professional Walkman Sony WM-D6<sup>2</sup>) through a commercial amplifier (Jensen XA2100 or Stetsom CD2720). Playback volume was selected beforehand to be the loudest possible while avoiding distortion. Loudness in the field was judged to be less intense than a naturally occurring call (although Whitehead, 1987 argues that intensity is probably not so relevant when judging distances, so this might not even be a problem). I then left the field assistant in charge of operating the playback apparatus at a previously selected time, which, however, would function as a lower limit. Instructions were given to delay the broadcasting, if necessary to maximise transmission (moderate winds were a frequent condition in the area).

I then returned to the group and continued collecting regular behavioural data with the design described in the general methods chapter; the behavioural categories already included most of the potentially interesting ones. The only difference was to register the direction taken by the alpha male on its travelling sessions after the broadcasting. During and after trials, I also abandoned the pseudo-random list and focused attention exclusively on the alpha male. The

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<sup>2</sup> Due to frequent equipment problems and the limiting field conditions, on a few experiments I had to resort to other tape recorders: Sony-TCM 5000EV (1 trial) and commercial tape players (4 occasions).

playback time was chosen so as to allow at least 20 minutes of baseline data collection before it (range 7-127 min.; inter-quartile range: 30-52 min.). After the broadcasting, I conducted at least another 20 minutes of continuous data collection on the alpha male (range 10-180 min.; inter-quartile range: 30-85 min.). On two occasions, data collection time before the playback was smaller than 20 minutes (7 and 15). In both cases however, the general context was of a long group resting session. In three separate instances continuous data collection after the playback was smaller than 20 minutes (14, 0 and 10), due to unforeseen problems, failure of Psion data logger and losing track of the alpha male respectively. In all cases, the crucial information was intact however (time of start and direction of movements and loud calls). Comments (e.g. quality of the sound as heard by me, meteorological conditions) and descriptions of unusual behaviours were spoken onto the dictaphone or typed into the running Observer event recorder on the Psion handheld. After the first few trials, I passed to collect data on the alpha not only for the period immediately after the playback but for the remainder of the day as well (following the 50/10 min. scheme of data collection and pause). For the extra field season, I used a detailed check-sheet to collect directly the variables that were of interest, as selected in the preliminary analysis of the previous data (see Data analysis topic below).

As further criteria, if the quality of the sound was obviously poor (which happened three times, due to equipment problems), I discarded the results. Failure of the experimental apparatus, windy conditions and group moving or calling before the playback accounted for circa 15 trials being abandoned.

On three occasions, I experimented with the design, and played back twice to the animals on the same day, each broadcasting being separated by less than an hour from each other, and with no vocal or travel reaction from the group in between. I do not include the results of those trials in the analysis, but use them as a supporting source of evidence. For factual information on the trials (date, time of the playback, condition, analysis variables, etc.) please refer to Appendix B.

## Analysis variables

For each experimental trial, I computed the following variables:

- Occurrence of loud calls (yes/no), type (roar/bark/incipient roar) and latency to call after the playback;
- Time lag between a previous loud call and the playback;
- Null probability of calling before and after a trial based on normative data;
- Placement of the loud calls occurring after the playback according to the following categories: at the site (within a 20m radius of the speaker), before (the group moved towards the site before calling, but did not get within 20m of it), overshoot (the group travelled to the site and then continued in the same direction, calling more than 20m after passing the speaker), to the back (the group moved away from the playback location before calling), neutral (all other places). For the 'before', 'overshoot' and 'to the back' categories, I considered an area  $30^\circ$  to each side of the line that passes through the reception and playback locations, on each case in the appropriate direction (see Figure 5.5);

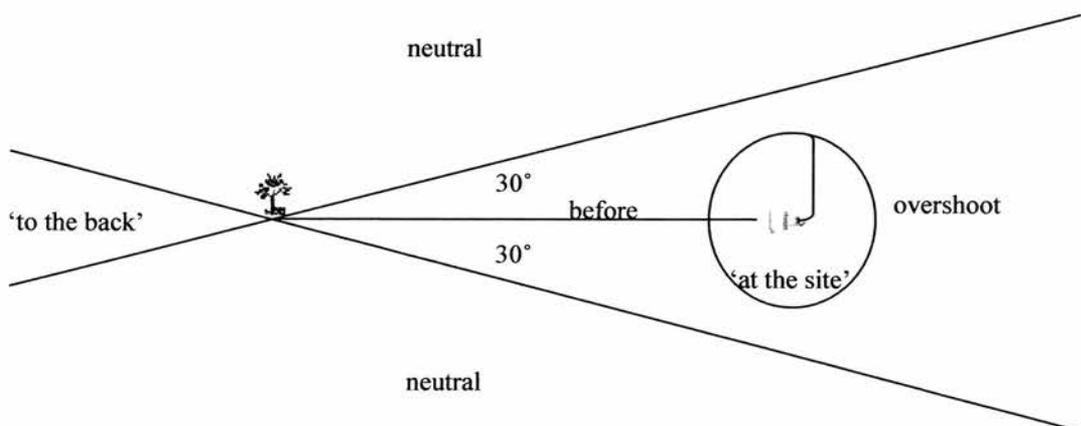


Figure 5.5 Diagram showing the categories of the variable "placement of the loud calls"

- Latency of the alpha male to start travelling. I considered only the first travel movement which took the animal more than 50m from the

starting point. A movement was considered to end when the animal spent more than 15 minutes in a state other than travelling;

- Time lag between the end of the last travelling bout by the alpha male before the trial, and the playback itself;
- Alpha male movement direction: approach (30° to each side of the vector connecting the reception point to the playback location), retreat (30° to each side of the vector 180° to the one above), neutral (all other movements, including lack of it).
- Displacement: position attained by the alpha male after it finished moving. I used the same five categories as for the loud call placement.
- Approach: latency to get within 20m of the speaker location;
- Patrolling behaviour: occurrence (yes/no) of any pattern of movement by the alpha male on which it separated from the group and travelled alone or followed by the second largest male, returning to the group later, thus effecting a closed trajectory;
- Occurrence (yes/no) of travel on the ground after a trial.

For comparing responses to the intensity of use of the quadrat in which a given playback was conducted, I excluded outside trials, because by definition this condition implied playback in areas where the animals never went or quadrats partially and very infrequently used. Associated with the lack of response in the few cases on which an outside trial was conducted, this could seriously bias the results by reinforcing an association between lack of response and low frequency of use, but confounded by the location.

#### *5.2.4 Statistical procedures and analysis criteria*

### **Observational data**

Some external factors (extreme weather events and inter-group encounters) seemed to elicit calling. To verify the association between these events and both the production of loud calls and the type of loud calls being emitted, I used a chi-square test of association (exact tests were preferred

whenever computational power allowed). To examine the influence of both sunrise time and temperature on the start of roaring behaviour, I made a multiple regression analysis of the timing of the first calling session on a given day on the sunrise time and minimum temperature of a given day. I used data referring to the time of the first call registered from the groups in the vicinity of the study area and only from the days when I had started collecting data before sunrise. If the first data point had a missing value, the day was not considered, and if the first data point had a bark only, I considered the first point with a roar. I also excluded those days with a call on the very first data point. The reason is that this situation meant that there probably were groups already calling when I arrived at the field site, and thus the start of the session was unknown. By using only those days when the first data point had no calls registered, I could be surer of the first session of a day. For the regression, I chose the forward method of entering variables, so I could see the one which contributed most to explaining the variance, and the additional effect, if any, of the remaining variable. As minimum temperature and sunrise times are both seasonally variable, I checked the variables for collinearity. The effect of temperature could be not so much in the timing of a loud call, but on its occurrence. Therefore, I also conducted a logistic regression of the occurrence (yes/no) of loud calls in the vicinity of the study group (on a given morning) on the minimum temperature of the day. To compare the duration of roar sessions under different conditions of weather or occurrence of inter-group encounters, I first tested the data for normality with Shapiro-Wilks test and for homoscedasticity with Levenne's test. Then, I proceeded with an independent samples t-test, transforming the data if necessary to restore assumptions.

To verify the relation between intensity of use with the percentage of calling sessions on different areas of the home range, I effected a Spearman's rank correlation. To test if the study group called more than expected from specific regions, I divided their range in 3 areas (west border, centre, and east border), and through a chi-square test, I compared the observed number of calls on each region to the expected value had the group called equally from the regions based on the time they spent on each one.

## Experimental data

With respect to the location conditions, I could compare only invasion and overlap trials, since I was able to conduct too few outside trials. To contrast the conditions with respect to continuous variables, I first tested them for normality with Shapiro-Wilks test and for homoscedasticity with Levenne's test. In case the variable in question was not normal, I attempted a transformation. For normal and homoscedastic data, I used t-tests to compare the location conditions. For normal and heteroscedastic data, I employed unequal variances t-tests. Data representing percentages or proportions were arc-sine transformed. Tests of association between categorical variables and experimental condition were conducted with chi-square test but using exact statistics. Similar tests were used when comparing two variables within a given condition (e.g. latency to move after the broadcast with the time lag between the last movement and the playback).

To test the relation between intensity of use of the quadrats on which I performed the playbacks with other continuous variables, I used Pearson's correlation for normal data and Spearman's rank correlation for non-normal data.

To compare invasion and overlap trials with respect to the proportion of trials on which a loud call was produced against the expected proportion given the time of the day they were conducted, I needed a null probability of calling. As each trial was conducted at a different time of the day, it was not possible to calculate a null probability of call emission applicable to all cases. So, I took a conservative approach. Recall that, by having detailed data on the study group, I had the probability of calling during each 10-minute period with respect to sunrise. Then, I calculated the probability of not observing a call in each 10-minute period, which is 1 minus the probability of having a call. Then, for each trial, I multiplied all the probabilities (of not observing a call) of the periods I was with the group on that particular day *after* playback time. This provided the null probability of recording *no* calls *after* the trial. Then, the probabilities of observing at least one call after the trials are the complements of these values. Next, I used the largest of these probabilities (of observing at least one call after the trials) in binomial tests to calculate (for each condition) the probability of getting the observed number of trials followed by loud calls by chance alone. The

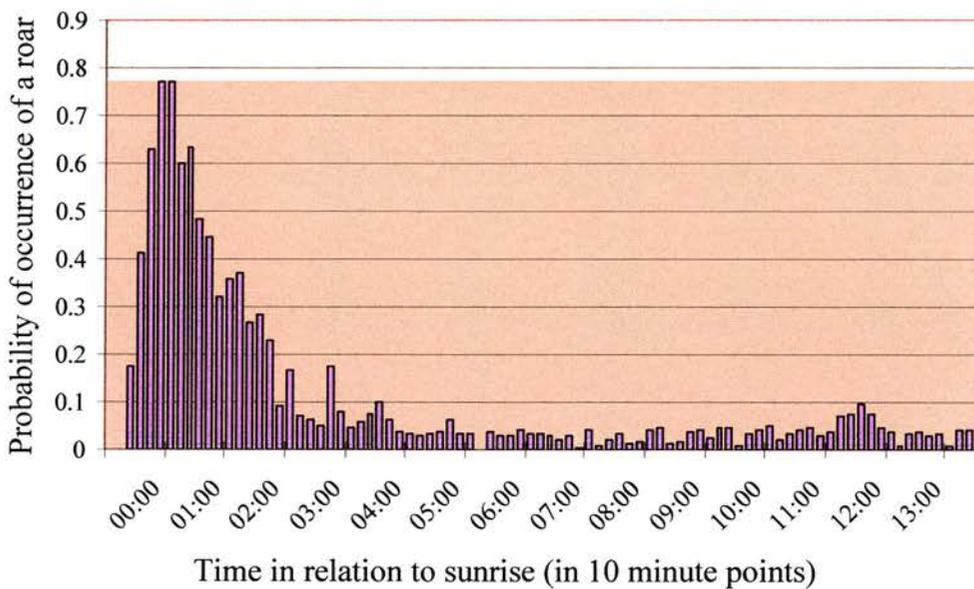
use of the largest figure after the trial is conservative because, given the range of observed values, it is more difficult to reject the null hypothesis.

### 5.3 Results – Observational data

When analysing the observational data, I first consider the rhythm of emission of roar and bark sessions throughout the day, as well as the variation of the pattern during the year. I also compare the rhythm profile of my group with the one of the groups in the vicinity. This analysis is a first approach in investigating the influence of some external variables (sunrise, season) on loud call production, but can also provide hints at the degree of spontaneity in emission (as opposed to the influence of abiotic and biotic factors). To further investigate the effect of environmental variables on calling, I analyse the effects of time of sunrise and minimum temperature of the day on the timing and occurrence of loud call sessions heard at the vicinity of the study group. This analysis also bears on the question of spontaneity of roar production, and the study of the influence of temperature can provide hints on the energetic costs of call emission. I then proceed to analyse the influence of extreme weather events and inter-group encounters (observed to apparently trigger loud calls) on the occurrence of sessions, on the type of loud call produced and on parameters of the production. The intention here is to confirm on a more solid basis previous anecdotal observations of the influence of these factors, and to comprehend the details of that influence. All the analyses mentioned so far were aimed at understanding some of the proximal mechanisms behind call production, because different hypotheses of the role of loud calls in an inter-group spacing system are related to different proximal mechanisms of production. I finish the section on behavioural observations by comparing the spatial distribution of roaring on the home range with the intensity of use of different areas. The purpose is to verify: (1) if calling frequency is influenced by the amount of time spent on a given area; (2) if calling is concentrated at particular locations (e.g. borders). The objective of this last analysis is to provide additional evidence pro or against hypotheses about the inter-group spacing system of the animals, since different systems are linked to distinct spatial patterns of calling.

### 5.3.1 Rhythm of call emission

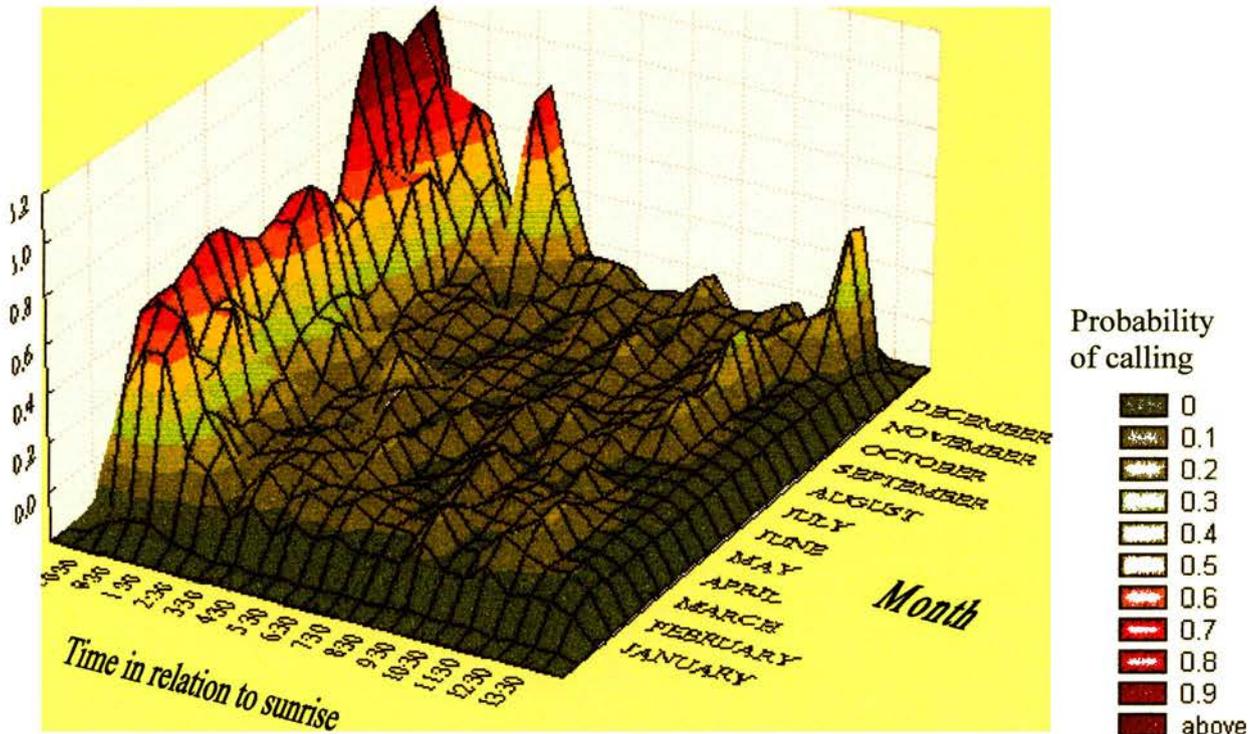
Concerning the distribution of calls during the day, there is a clear concentration of roars around dawn, with some of the analysis points reaching nearly 80 % (Figure 5.6). Calling was indeed a nearly daily occurrence for the early morning period. Only 8.3% (12 days) of the sampled days did not have any roar at all until 1:40 after sunrise. Interestingly, 8 of those were in August, one in June and 3 in May, all months in which weather systems can bring cold fronts to the site. On the other hand, 14 days (9.7%) contained roars in all ten-minute points from the start of the day until 1:00 after sunrise.



**Figure 5.6 Probability of a roar being heard at the vicinity of the study group along the day in 10-minute points with respect to sunrise (instantaneous time sampling). Tick marks refer to the bar immediately to the right. Each bar is an average of monthly probabilities. Total sample sizes varied for each bar from 1 (only the very extreme categories) to 188 days of data (majority of the points with more than 100 days of data).**

However, this daily pattern was not invariable along the year. Figure 5.7 shows marked seasonal differences. Particularly, during the peak of the dry season (June to August), there is a decrease in the probability of roar occurrence on the morning peak, and the peak seems also to extend less into the morning. Concerning other periods of the day, the patterns are less clear, and also less reliable (smaller probabilities of calling might suffer a stronger influence of

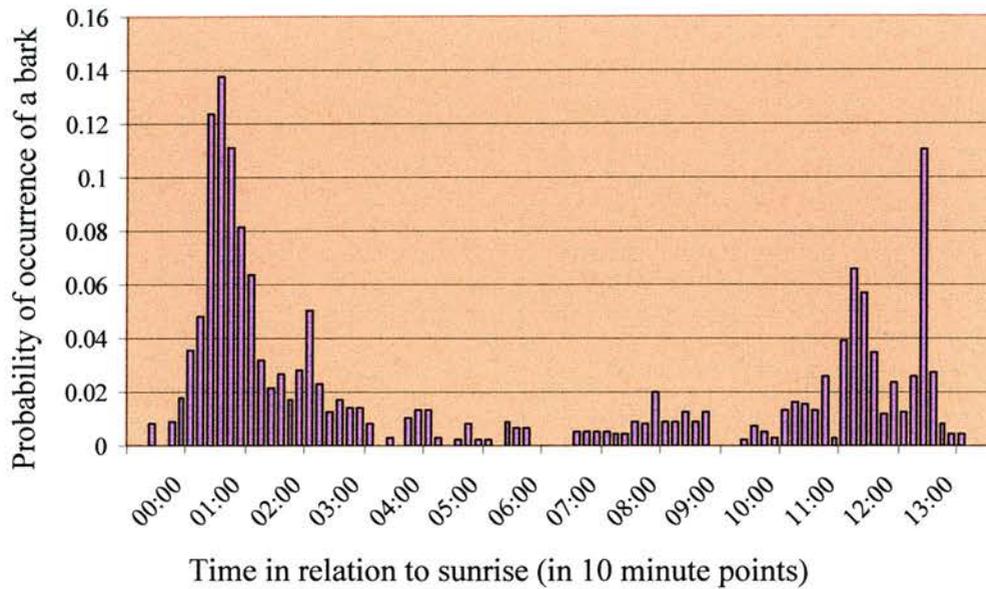
sampling problems). Despite these problems, there seems to appear a late afternoon peak in November and December, and also the last one witness high rates of calling throughout the morning.



**Figure 5.7** Probability of a roar being heard at the vicinity of the study group along the day (with respect to sunrise) according to the month. Please note that to build up this graph the STATISTICA software applies a smoothing function which distorts slightly the real values. Therefore, the graph should not be viewed as a completely accurate depiction of the pattern, but as illustrative of general trends.

Barks are a much less frequent call type than roars. Their daily distribution also has a morning peak, but a clear late afternoon one as well (Figure 5.8). Emissions of barks are usually much longer than roar sessions (see below); thus each emission is responsible for more data points than a roar session. Also, it was very rare to hear different groups barking at the same time, quite the opposite to what was observed with roars. Therefore, in terms of number of sessions, barks were even rarer than the graph might suggest.

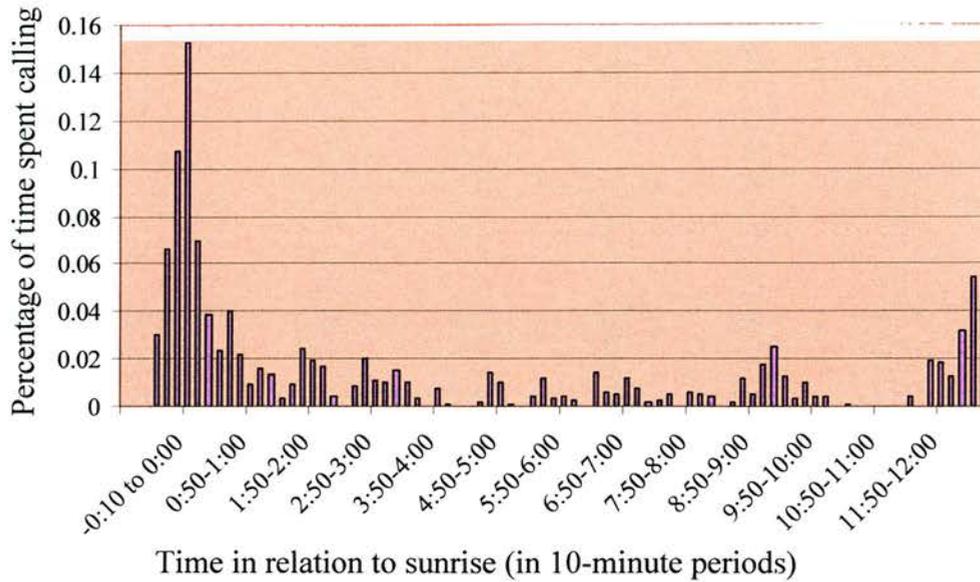
Contrasting with the roars, there were 111 days (76.5%) with no barks until 1:40. No days had barks in all periods from start of data collection until one hour after sunrise.



**Figure 5.8** Probability of a bark being heard at the vicinity of the study group along the day in 10-minute points with respect to sunrise (instantaneous time sampling). Tick marks refer to the bar immediately to the right. Each bar is an average of monthly probabilities. Total sample sizes varied for each bar from 1 (only the very extreme categories) to 188 days of data (majority of the points with more than 100 days of data).

Recall that the graphs above were built using the data collected every ten minutes concerning calls emitted by groups in the surrounding area that I could hear. Having characterised the general patterns for the vicinity of the study site, it is interesting now to contrast this information with the more detailed data from the study group. The basic profile of the group is fairly similar to the one on all groups (compare Figure 5.9 with Figure 5.6 above). However, the morning peak seems more concentrated around dawn, and the probabilities are obviously much smaller (since I am dealing with only one group, and not the set of groups nearby). The late afternoon peak might be slightly misleading, as it is based on a small sample size, and some of the days had calls originated by inter-group encounters. The study group had at least one roar session on the period between





**Figure 5.10** Rate of roaring emission by the study group along the day in 10-minute periods with respect to sunrise. Tick marks refer to the bar immediately to the right. Each bar is an average of monthly probabilities. Total sample sizes varied for each bar from 2 (only the very extreme categories) to 2047 minutes of data collection (majority of the points with more than 1000 minutes of data).

### 5.3.2 Effect of sunrise time and temperature

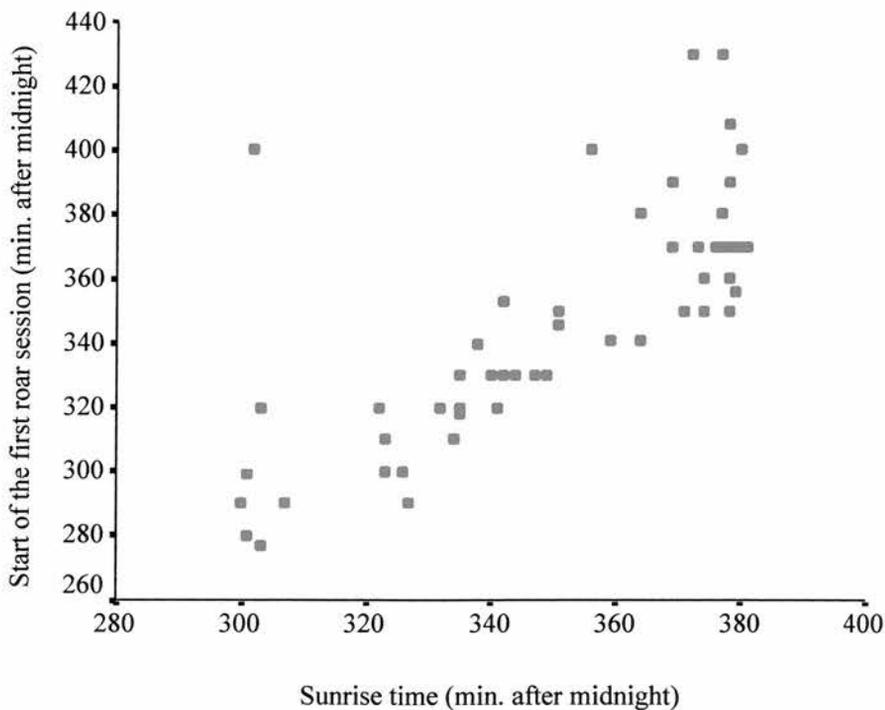
During all three field seasons, additional to the obvious relation between sunrise and the start of the dawn chorus, there seemed to be an influence of temperature. Anecdotal observations indicated that on cold days, particularly when a cold front swept the area, the morning session was either late or absent altogether. The number of groups calling in the vicinity also seemed to be smaller. Conducting a multiple regression analysis indicated a significant effect of sunrise time on the timing of the first session, but minimum temperature failed to contribute significantly to explaining the variation. The first variable to be entered in the model was sunrise time, which explained a great deal of the variance in the start of the first session registered on the day in the vicinity of the study group ( $R^2_{\text{adj.}} = 0.705$ ,  $F_{1, 55} = 134.8$ ,  $p < 0.001$ , see Figure 5.11 analysis conducted excluding the outlier on the upper left corner of the graph). Adding minimum temperature of the day did not improve the model significantly ( $R^2_{\text{change}} = 0.007$ ,  $F_{\text{change } 1, 54} = 1.406$ ,  $p_{\text{change}} = 0.241$ ), but it remained significant

overall ( $R^2_{\text{adj.}} = 0.707$ ,  $F_{2, 54} = 68.6$ ,  $p < 0.001$ ). Collinearity could be a problem in the analysis with the two variables, as minimum temperature and sunrise time are both clearly associated with season. However, this was not relevant on the data set used (Tolerance = 0.55, VIF = 1.8). A more serious issue could be due to the violation of the assumptions of the test, as the residuals were not normally distributed: Shapiro-Wilk test  $W = 0.87$ ,  $df = 57$ ,  $p < 0.001$ . However, ANOVA is known to be robust to violations, and the results were not qualitatively different when I repeated the analysis excluding the more deviant values one by one until the normality assumption was met.

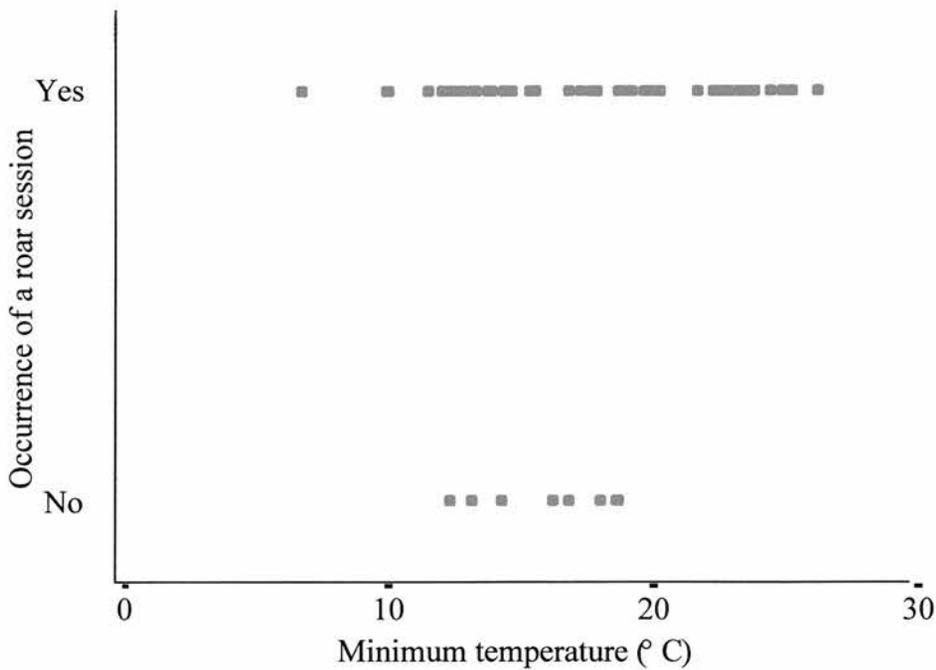
The effect of temperature, however, could be not so much on the timing of the calling sessions, but on their occurrence. Conducting a logistic regression of the occurrence of a morning calling session on the minimum temperature of the day shows a non-significant trend (Wald statistic = 2.59,  $df = 1$ ,  $p = 0.108$ ,  $n = 67$ , see Figure 5.12). Looking at the graph, it seems that the influence might be a complex one: on colder days the monkeys could loud call or not, but I nearly always registered a call in hotter days. I registered only one day that had a high minimum temperature and no calls.

In considering the results of the multiple regression, recall that I was very conservative with respect to inclusion of data. Not only was the day excluded if the first data point of the day had a missing value, but also if the very first data point had a loud call recorded (for the remaining criteria refer to the Methods section of this chapter). The reason for this exclusion was as follows. Having data on the very first observation point probably meant that some group in the vicinity was already calling when I arrived at the field site, and thus the start of the dawn session was unknown. Inclusion of these data points might artificially inflate the amount of variation in the timing of calling that is explained by sunrise time, since my own behaviour (time that I arrived at the field and thus started collecting data) was also influenced by sunrise. However, the same does not occur with temperature. As on the original data set, I considered only the days in which I had arrived before sunrise, I exclude possible temperature influences on my arrival at the site. Thus, by including the days with a call in the very first data point, I just introduce a lower limit on the data. However, I am able to see if there is any improvement of the regression model (due to a larger sample size) after inclusion of the minimum temperature as an independent

variable. As expected, sunrise still explained a lot of the variance on the timing of the calling in this expanded data set ( $R^2_{\text{adj.}} = 0.773$ ,  $F_{1,123} = 418$ ,  $p < 0.001$ ). However, the inclusion of the minimum temperature added a nearly significant change in explaining the variation, albeit small ( $R^2_{\text{change}} = 0.006$ ,  $F_{\text{change } 1, 122} = 3.46$ ,  $p_{\text{change}} = 0.065$ ), and the model remained significant overall ( $R^2_{\text{adj.}} = 0.779$ ,  $F_{2, 122} = 214.9$ ,  $p < 0.001$ ). Collinearity was not a problem (Tolerance = 0.63, VIF = 1.6). Conducting the logistic regression of the occurrence of a roar on the minimum temperature now produced a significant result (Wald statistic = 3.89,  $df = 1$ ,  $p = 0.049$ ,  $n = 135$ ). Thus, there are grounds to suggest that, apart from sunrise, there are complex weather influences on the temperature. On cold days the animals have a smaller chance of calling, and when they do they seem to call later.



**Figure 5.11** Scatterplot of the time of the first roar session of the day against the sunrise time (restricted data set). Both variables computed as minutes after midnight. For criteria see Methods section. Note the outlier at the upper left corner, which was excluded from the regression analysis.



**Figure 5.12** Scatterplot of the occurrence of a roar session in the morning, according to the minimum temperature of the day. Each dot represent one morning.

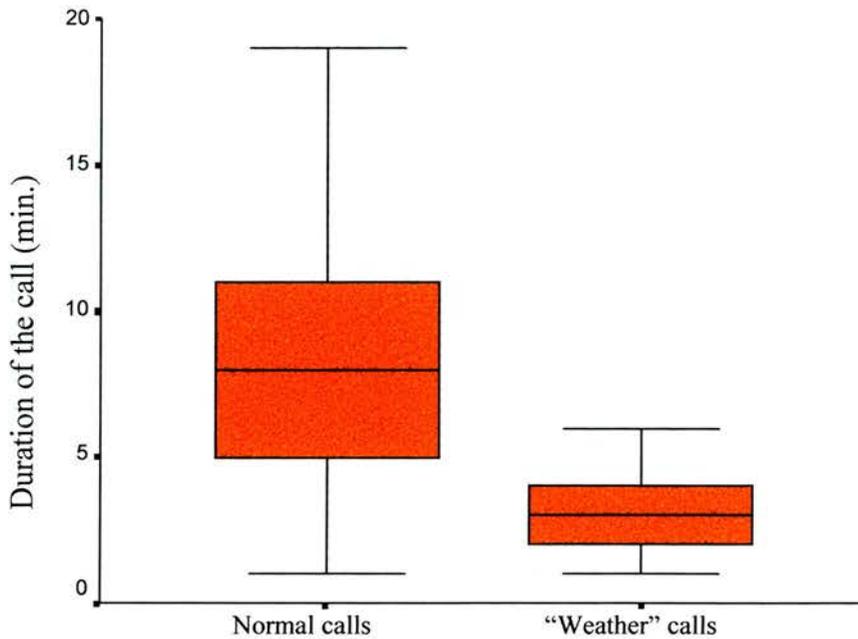
### 5.3.3 Triggering factors

Two factors were observed to apparently trigger loud calls: extreme weather events (onset of heavy rains, sudden gusts of wind, and increase in intensity of rain) and inter-group encounters. Although the majority of calls were not produced at the onset (or strengthening) of rain/wind (Table 5.2), there is an association between call type and these weather situations (Pearson chi-square:  $\chi^2 = 21.08$ ,  $df = 1$ ,  $p < 0.001$  – exact significance, power approaches 1 for a large effect to be detected, test conducted excluding barks due to small expected values). The emission of incipient roars at the specified meteorological conditions occurred almost three times more often than expected.

**Table 5.2 Occurrence of each kind of loud call under special meteorological circumstances.**

|                   |                | Call at the onset or strengthening of rain<br>or wind |     |       |
|-------------------|----------------|---|-----|-------|
|                   |                | Yes   | No  | Total |
| Type of loud call | Roar           | 19  | 200 | 219   |
|                   | Bark           | 0   | 8   | 8     |
|                   | Incipient roar | 14  | 26  | 40    |
|                   | Total          | 33  | 234 | 267   |

I then went on to compare the duration of roar sessions (excluding incipient ones, which by definition are very short) in both situations. As the duration data did not meet the assumptions of normality and homoscedasticity, I first square-root transformed the data, which restored both assumptions (Shapiro Wilk test for normality: sessions emitted in rain/wind conditions,  $W = 0.917$ ,  $df = 17$ ,  $p = 0.131$ ; remaining sessions,  $W = 0.989$ ,  $df = 193$ ,  $p = 0.16$ ; Levene's test of homogeneity of variance:  $F_{1,208} = 3.297$ ,  $p = 0.071$ ). Analysis of the transformed data shows that roars emitted at the onset or strengthening of rain or wind were significantly shorter than their counterparts emitted at other times (independent samples t-test  $t = -5.7$ ,  $df = 208$ ,  $p < 0.001$  see Figure 5.13, power to detect a large effect = 0.9341). Thus it seems that there is a clear difference between loud calls emitted in these special weather conditions and the remainder of the calls, as they were either incipient roars or shorter roar sessions.



**Figure 5.13** Box plots of duration of roar sessions under different meteorological circumstances. “Weather” calls refer to calls occurring at the start or strengthening of rain or strong winds.

Turning to the second factor that seemed to elicit calls (encounters with neighbouring groups), there was a clear relation between inter-group encounters and production of calls. In 265 non-experimental days of work, I registered at least one call in 122 days (46%). I witnessed 33 cases of inter-group encounters, 26 of those accompanied by loud calls ( $p < 0.001$  - binomial test using the percentage of days with calls as the expected proportion). Bear in mind as well that of the seven cases of inter-group encounter and no calls, I might have missed previous interactions in two cases, and three of the interactions were not close ones. However, as I don't have information on the location and movements of the adjacent groups with respect to the study one, it is not possible to discern if the detection of a neighbour group elicited the calling, or if loud calling in selected places actually draw the groups together, producing the encounter. *Ad libitum* observations support both ideas, although the first case seemed to be more frequent.

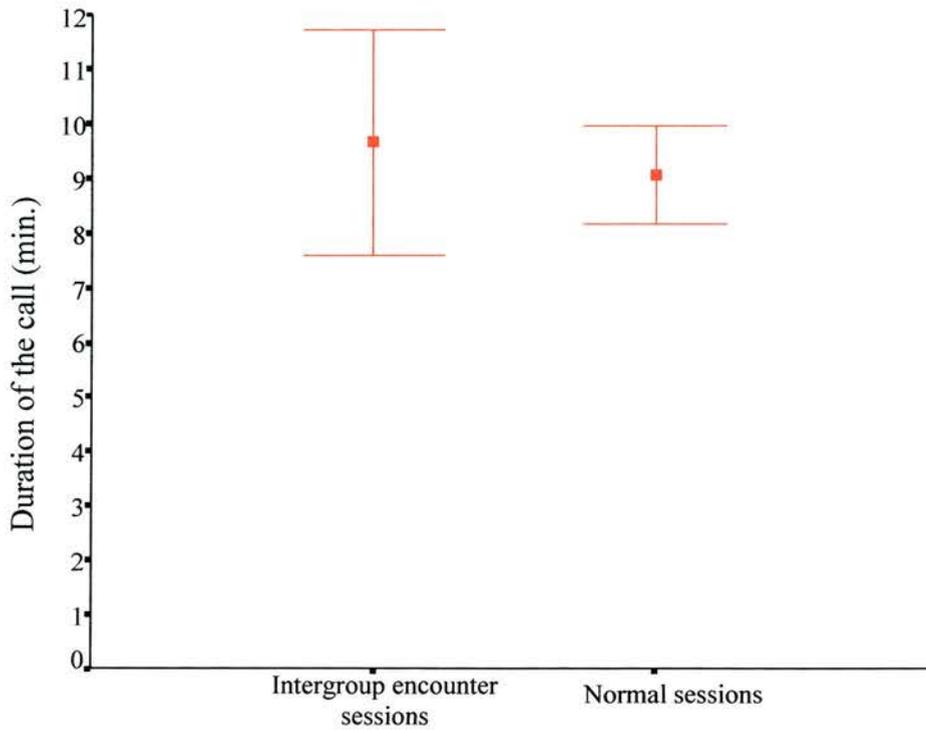
Despite the association between inter-group encounters and the *production* of loud calls, the former is not associated with the *type* of loud call

produced (Table 5.3- Pearson chi-square:  $\chi^2 = 0.997$ ,  $df = 1$ ,  $p = 0.468$  – exact significance, power = 0.9426 for a medium effect to be detected, test conducted excluding barks due to small expected values). Nonetheless, the study group never barked during inter-group encounters (anecdotal observations indicate that they can occur afterwards, especially with groups out of visual contact - see topic on natural inter-group encounters).

**Table 5.3 Occurrence of each type of loud call according to the presence or absence of a neighbour group nearby.**

|                      |                | Inter-group encounter |     | Total |
|----------------------|----------------|-----------------------|-----|-------|
|                      |                | Yes                   | No  |       |
| Type of<br>loud call | Roar           | 22                    | 103 | 125   |
|                      | Bark           | 0                     | 6   | 6     |
|                      | Incipient roar | 4                     | 10  | 14    |
|                      | Total          | 26                    | 119 | 145   |

As the duration of roar sessions emitted in both situations (inter-group encounters and all other emissions) met the necessary assumptions (Shapiro Wilk test for normality: sessions emitted in inter-group encounters - test statistic = 0.9526,  $df = 20$ ,  $p = 0.394$ ; remaining sessions - test statistic = 0.974,  $df = 99$ ,  $p = 0.05$ ; Levene's test of homogeneity of variance:  $F_{1,117} = 0.097$ ,  $p = 0.756$ ), no transformations were necessary for further comparisons. Roar sessions emitted during encounters did not differ in duration from the remaining sessions (independent samples t test  $t = 0.547$ ,  $df = 117$ ,  $p = 0.586$ , power = 0.6491 to detect a medium effect, see Figure 5.14).



**Figure 5.14 95% confidence interval of duration of roar sessions in intergroup encounters and in the absence of nearby groups.**

Participation by an individual on a given session was not contingent with the situation (Table 5.4 – Pearson’s chi-square, individual 2  $\chi^2 = 0.71$ ,  $p = 0.473$ ; individual 3  $\chi^2 = 2.6$ ,  $p = 0.14$ ; individual 4  $\chi^2 = 2.73$ ,  $p = 0.18$ ; individual 5  $\chi^2 = 0.13$ ,  $p = 0.742$ ; individual 6  $\chi^2 = 0.417$ ,  $p = 0.725$ ;  $df = 1$  in all cases, and significance values are for exact tests, in all cases power  $> 0.99$  to detect a large effect). Number of participants in roar sessions also did not differ among the two situations (Mann-Whitney  $U_{19,84} = 753.5$ , exact significance  $p = 0.697$ , Table 5.5).

**Table 5.4 Participation of each individual in roar sessions according to the context.**

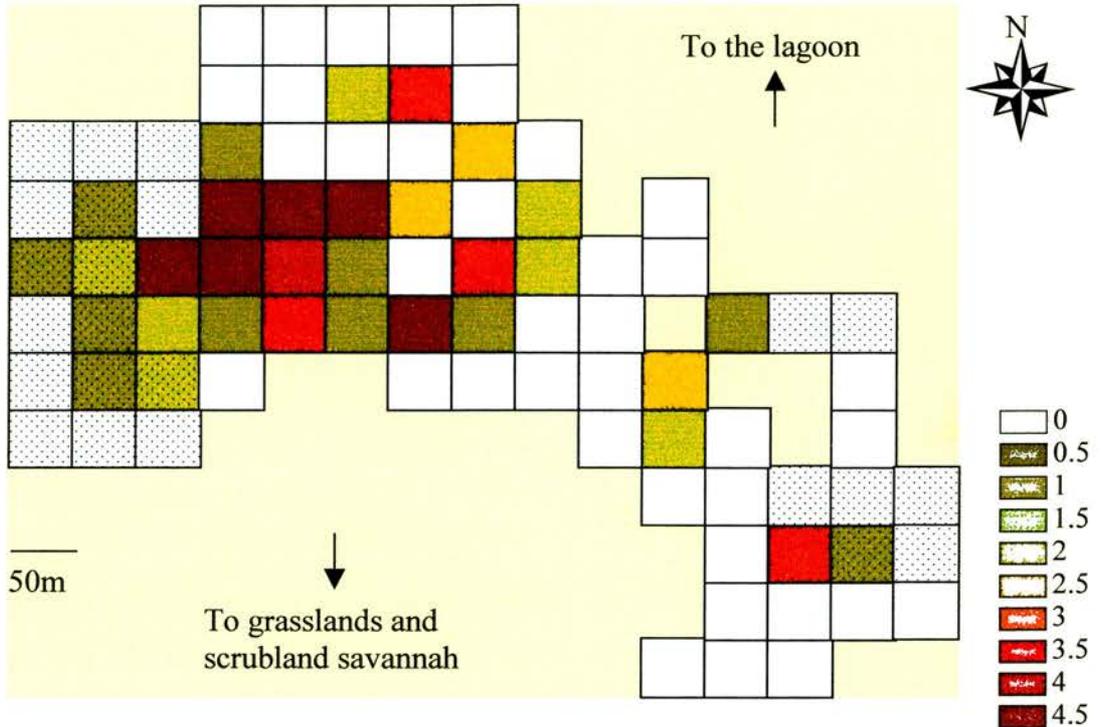
| Caller       | Participation | Inter-group encounter |    | Total |
|--------------|---------------|-----------------------|----|-------|
|              |               | Yes                   | No |       |
| Ind. 2 (AM)  | Yes           | 15                    | 68 | 83    |
|              | No            | 1                     | 11 | 12    |
| Ind. 3 (SAM) | Yes           | 8                     | 23 | 31    |
|              | No            | 7                     | 50 | 57    |
| Ind. 4 (SAM) | Yes           | 6                     | 14 | 20    |
|              | No            | 10                    | 61 | 71    |
| Ind. 5 (AF)  | Yes           | 11                    | 59 | 70    |
|              | No            | 4                     | 17 | 21    |
| Ind. 6 (AF)  | Yes           | 2                     | 16 | 18    |
|              | No            | 12                    | 57 | 69    |

**Table 5.5 Frequency of roar sessions with different number of participants according to the context.**

|                        |   | Inter-group encounter |    | Total |
|------------------------|---|-----------------------|----|-------|
|                        |   | Yes                   | No |       |
| Number of participants | 1 | 4                     | 12 | 16    |
|                        | 2 | 1                     | 9  | 10    |
|                        | 3 | 6                     | 37 | 43    |
|                        | 4 | 4                     | 11 | 15    |
|                        | 5 | 2                     | 10 | 12    |
|                        | 6 | 2                     | 5  | 7     |

#### 5.3.4 Distribution of calling in the home range

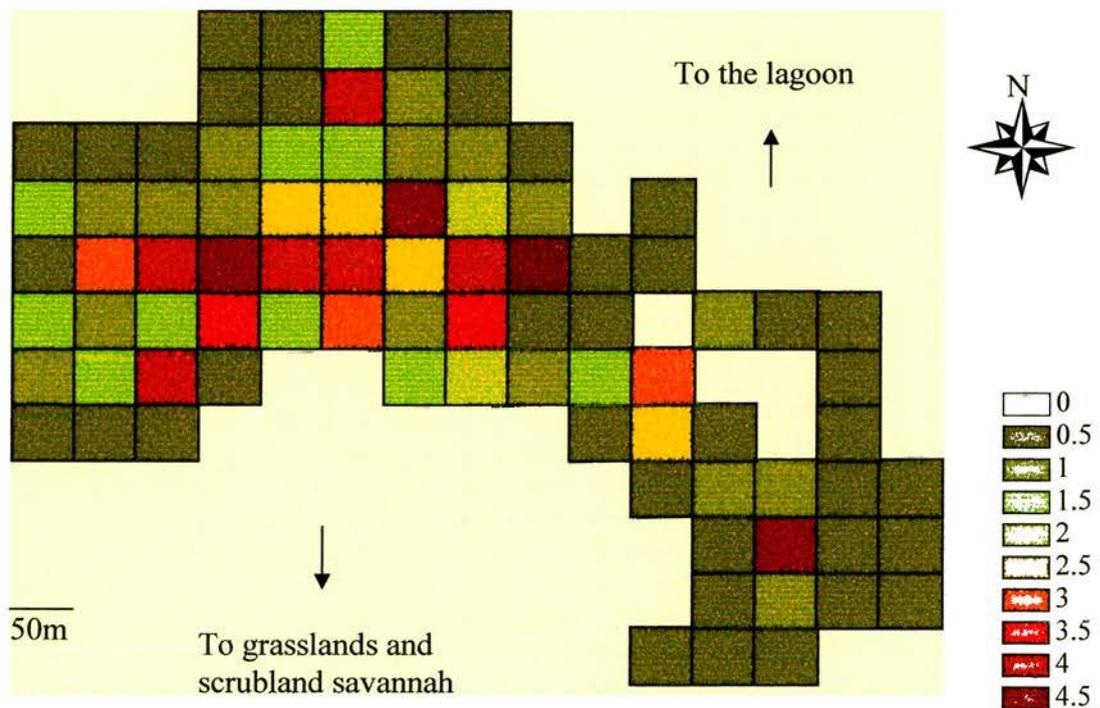
Looking at the distribution of calling sessions in the home range (Figure 5.15), two facts attract our attention. First, the study group called from a variety of locations, including core areas, areas towards the border and overlap regions. Second, calling was not uniformly distributed over the area. Two factors can help explain heterogeneity in calling: location and intensity of use. Animals might concentrate calling in specific regions of the home range (overlap or border areas, for example). On the other hand, if the animals simply call in proportion to the time they spent on a given location, and if there are differences in the intensity of use of different areas, the result is also a lack of uniformity.



**Figure 5.15** Percentage of the total number of roars produced by the study group (October 2001 through February 2003 plus July/August 2003) that were emitted on a given quadrat. Calls given during inter-group encounters, extreme weather events and after experiments were excluded. Dotted areas represent quadrats where neighbour groups were spotted or must have been used in order to get to areas where they were seen. Colour codes indicate the lower limit of the class.

As expected, the group did not use their range uniformly (Figure 5.16), and visually comparing the patterns of use with the one of calling there seems to be a good agreement. Indeed, effecting a non-parametric correlation (since both data are proportions) shows that the two variables (intensity of use and percentage of calls) are significantly correlated (Spearman  $r = 0.65$ ,  $p < 0.001$ ,  $n = 85$ ). Please note that one must be careful in drawing interpretation from this result. The reason is that the two data sets are different in their nature and coverage period. The data on loud calls were computed using all roars registered for the study group during the whole of the main study plus the two extra months. The intensity of use data, however, were collected only from May 2002 to February 2003, and the extra months (July and August 2003). The values of intensity of use of each quadrat were computed using an average of monthly

values, to account for differences in data collection time between different months, and the fact that two months (July and August) had data from 2 different years. Additionally, the correlation seems to be mostly due to the large number of quadrats with no calls, which mainly correspond to poorly used quadrats. Excluding the areas with no calls from the analysis render the correlation non-significant (Spearman  $r = 0.24$ ,  $p > 0.05$ ,  $n = 32$ ). Thus, to the extent allowed by the limitations of the data, it seems that the animals did not call in infrequently used areas, but there was no correlation for the remainder of the home range.



**Figure 5.16 Percentage of use of each quadrat along the year. Frequency calculated averaging monthly values. Data collected from May 2002 to February 2003, plus July/August 2003. Colour codes indicate the lower limit of the class.**

The pattern of calling could also be determined by the concentration of calling locations in specific areas of the home range. To address this possibility, I classified the quadrats into 3 categories: east border, west border, and core. The first two comprise the areas which both the study and a neighbour group were seen to use (dotted areas in Figure 5.15) either at the east or west of the home

range respectively. The remaining quadrats comprise the core region. Then, I calculated the intensity of use of these broad regions (summing up the individual values of their component quadrats), and used these figures to compute expected number of calls in each region. I then compared these expected values with the actual number of calls in each of these regions through a chi-square test. The test showed that the animals did not call in proportion to the time spent on each of these regions ( $\chi^2 = 8.39$ ;  $p < 0.05$ ; power = 0.855 to detect a medium effect). They called less than expected at the border areas (recall that I did not include in the analysis calls produced during inter-group encounters) and more than expected at the centre of the range. Given the limitations mentioned above in comparability of the data, I conducted a separate test on a different body of data. For the frequency of use, I employed the raw data, that is, not computing an average of monthly values. These values of frequency of use represent the proportion of time the group actually spent on each quadrat while I was with them, instead of an estimate of their overall use of the range. For the number of calls, I used only those calling sessions produced after the start of data collection on intensity of use, to make the data sets more comparable. The idea here was to compare the time they actually spent on an area with the proportion of calls produced in the same period (though with a much reduced sample size). Contrary to the previous analyses, the test conducted with these data was non-significant ( $\chi^2 = 1.25$ ;  $p > 0.05$ ; power = 0.484 to detect a medium effect), showing that the group did call in proportion to the time they spent on each of the three areas. Thus, the test on the effect of location also has conflicting and inconclusive results. However, one feature seems to be clear: in none of the analyses the group called more than expected at the border regions.

## 5.4 Natural inter-group encounters

In this section, I consider the few close inter-group encounters between the study group and neighbouring ones (west – W – and east – E – according to the location of their home ranges with respect to the study group) that I observed, concentrating on behaviours relevant to the discussion of the spacing pattern and system, and to the function of roars and barks. Spontaneous inter-group encounters provide a natural “experiment”, allowing the researcher to observe the behaviour of the animals under a variety of conditions. The drawbacks are the unpredictability, the lack of control of many variables, and the limited sample size. Nonetheless, these encounters constitute a crucial piece of additional information, as well as a rich source of guidance for future playback experiments.

Thus, according to the main events that took place, I divided the inter-group encounters into categories, which I describe next.

### **No visible reactions**

On five different occasions I observed the groups close to each other, but neither was performing any behaviour with reference to the other. Admittedly, two of these instances (closest animals separated by approximately 20m on both cases), both involving the W group, were already in progress when I found the study group in the middle of the day. Therefore, it is not possible to rule out previous interactions. In another episode, the study group slept circa 80m apart from the W group, and I did not register any vocal interactions or approximations between the groups at the late afternoon and at next dawn. The fourth instance involved the east group and took place in a region of the east border rarely used by the study group. Troops got within 50m of each other, and the neighbour group retreated without chases or calling taking place. The next morning the study group called from a place close to where they had met, and the neighbour group called an hour later from 200m away. Finally, the group once encountered an isolated female invading a core area (after the expulsion incident described below). The invader retreated to the overlap area without any chases or calls from the study group.

**Only one group calls, no chases**

On at least six occasions I observed the groups close to each other but only one of them loud called and neither chased. Four of the incidents involved the west group, and minimum distance between animals varied from 10 to 100m. The W group clearly retreated in one of the events, and the study group in another. In five of the cases the loud call was a roar, and in one a bark. On a separate case, the W group barked with no response from the study group and they were separated by approximately 160m. I arrived in the middle of the day with the situation already in place, and could not reject the possibility of previous interactions.

**Simultaneous or sequential calling**

Under this category I grouped those instances in which both groups called, either at the same time, or one soon after the other, but no chases were observed. I registered twelve such cases, eight of those being after dawn. One of the groups usually called much less than the other. In only one of the cases the groups employed different call types, with the neighbour group barking along a roar from the study group. Both groups retreated in at least two occasions, while in another one only the neighbour group retreated. Three extra cases were observed with the groups between 100 and 150m (recall that the criterion for an inter-group encounter was a maximum distance of 100m).

**Chasing over overlap areas**

Under this heading I grouped the five instances whereby one group chased the other over an overlap area. In all cases one or both groups emitted loud calls, preceding or following the chases. In three cases the chaser group emitted calls after the pursue (one bark and two roar sessions).

Some inter-group encounters, especially when the groups were close to each other, were particularly interesting due to the intensity of the interaction and I describe two in detail below.

25 September 2002

5:20-5:40 roar session close to the east overlap area. Some time after group went further east.

6:29-6:42 and 6:44-6:54 two roar sessions. Did not leave the vicinity after.

8:35-8:37; 8:44 -9:07 and 9:09-9:12 three roar sessions. Presence of neighbour group detected circa 35m away on the session started 8:44. Incipient roars at 9:14; 9:16; and 9:17.

11:00 neighbour group now 70m away. Study group did not leave.

After, the study group went a bit more to the east, and soft sounds were heard.

Then neighbour group approached to around 10m.

Incipient roars at 12:30.

12:33-12:39 roar session. Neighbour group emitted incipient roar during this session.

13:00-13:40 – distance between groups varied between 10 and 20m.

13:50 – groups within 5m, and later on 2m or less. Piloerection, staring and pivoting between males of both groups. Not many sounds. Study group backed up a few meters.

14:01 – incipient roar. Neighbour group retreats a few meters. Later kept retreating at a slow pace.

14:30 – neighbour group 30m away.

14:40 – study group starts to retreat to the core area, but adult males and one sub-adult male stayed behind. Only after 15:00 they finally joined the rest of the group.

What attract attention to this particular interaction are the length (more than six hours) and the amount of calling. After the neighbour group was noted, there were 3 sessions totalling 23 minutes. Before that, three sessions summed up to 45 minutes, generating a total of 68 minutes of calling on this day. Although the groups were quite close at times, no physical interaction or chases were observed. However, displays were quite common.

24/07/2003

During the extra field season in July/August 2003, I noticed that a pair of animals was using some quadrats well inside the home range of the study group. They never called when I was there, and seemed to behave quite inconspicuously. On 24/7, I witnessed an encounter between them and the study group, during which I observed many interesting behaviours:

Towards the end of the day, the group started to travel in the direction of the area where the invaders usually stayed. I did not notice anything unusual in the travelling session. When they came close to the invading pair, I heard *grunts* and *oodles* and the alpha male showed piloerection. Soon after a roar session started, lasting for eight minutes. All adult individuals, except female 9, joined the session, which then reached high amplitude. At the beginning there was a mild answer from the invading pair, which soon ceased. During the session, male 3 started chasing the invaders, and soon after was joined by males 1 and 4. Soon, the alpha male started to lead the chase, which was focused on the male. At some point the invading male went to the ground and so did the alpha male of the study group. The chase occurred for more than 100m, and took place until the limit of the forest on the direction of the chase. The invading female, which was not seriously chased, took a different route. Later on, a vocalisation was heard from the bearing of the female. Next morning an isolated female was found in the direction took by the invading female, but still in the core area. A small group (an adult male, two adult females and an infant) was found in the overlap area, in the region where the vocalisation heard the previous day came from, and it was not possible to ascertain if the invading male was the male of this group. The study group males, which had slept closer to the border than the other animals, later joined the rest of the group and a vocalisation session ensued close to the site of the encounter.

The relevant points of this interaction were the chase until the border (and partially on the ground); the non-involvement of the females in the chase, and also the focusing of the chase on the invading male; the tolerance of the vocalisation of the end of the day after the chase, emitted from the overlap area; and the next morning roar session at the encounter site.

## 5.5 Results - Playback experiment

### 5.5.1 *Effect of location: loud call responses*

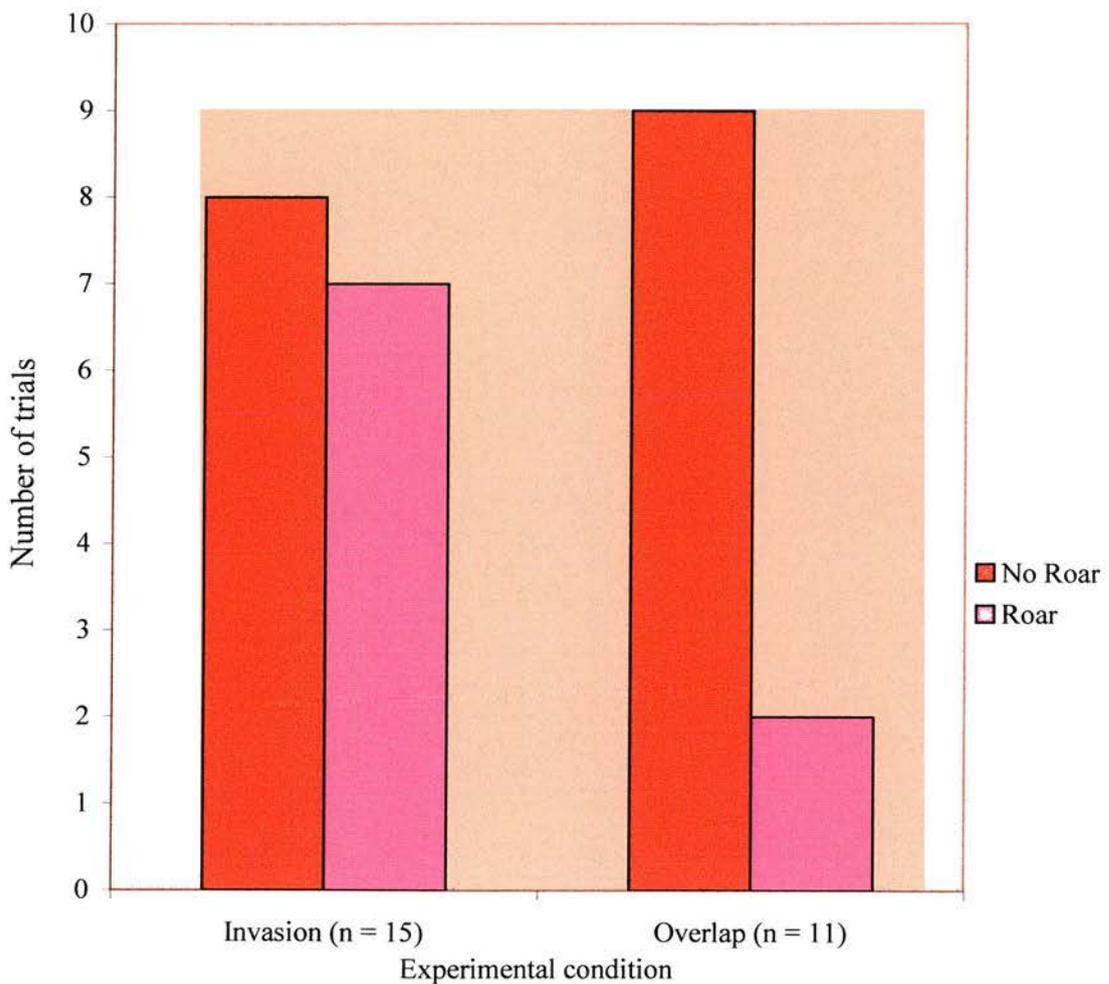
In this section I consider the behaviour of the alpha male after the playback trials taking into account the different location conditions (invasion, overlap, and outside). I first look at variables related to the loud calling behaviour to see if there was any difference between the conditions with respect to the: (1) number of sessions (both in absolute terms and with respect to the expected number of calls given their baseline behavioural patterns); (2) timing of the calls; and (3) location of the calls with respect to the speaker. If loud calls are used in the regulation of use of space (the basic working hypothesis), then one would expect different patterns of calling according to the possible systems of regulation (e.g. animals are expected to approach and counter-call in the overlap condition in systems involving border definition and defence, but not in mutual avoidance systems).

To analyse data involving loud call variables, I first excluded trials in which I did not stay continuously with the animals until the end of the day (2 instances). Then, I excluded from analysis vocalisations after the playback that were apparently caused by weather events or by inter-group encounters, and which were of the bark type (one case each). Trials with these calls were classified as having no calls after the playback. Incidentally, all of the calls in these trials occurred at least 5 hours after the playback, which makes less likely that they bore any relation to the broadcasting. I also applied this restriction in the analysis of the effect of the intensity of use of the playback site. Finally, I was able to conduct only three trials for the outside condition. Therefore, they were excluded from the statistical analysis, being considered only as anecdotal supporting evidence.

#### **Call occurrence**

In nearly half of the invasion trials (7 out of 15) the study group roared after the broadcasting, whereas this occurred in only 2 out of 9 border ones

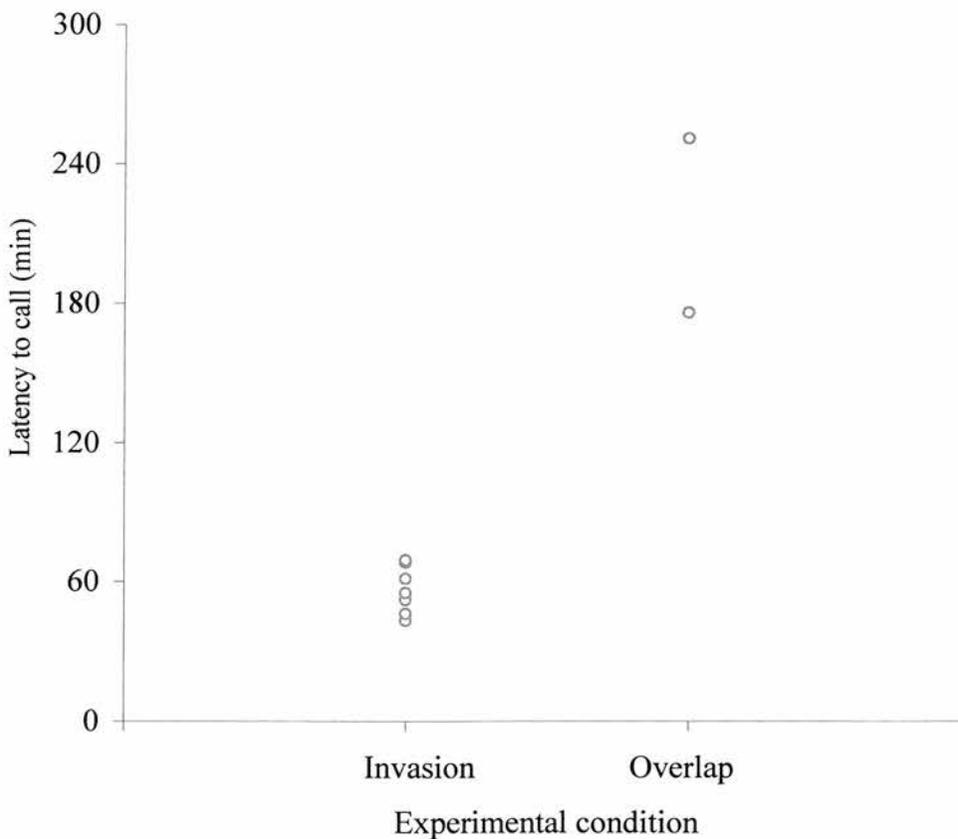
(outside trials were never followed by a call). To test the significance of this difference, I performed an association test between occurrence of a roar after the playback and experimental condition, excluding overlap trials due to small expected values. In spite of the apparent difference, there was no association between the variables ( $\chi^2 = 2.275$ ;  $p = 0.217$  exact significance; power = 0.7223 to detect a large effect, see Figure 5.17). However, due to the small sample sizes, other sources of data should be looked at, given that there seems to be a trend towards loud call responses in invasion trials, but not in overlap ones.



**Figure 5.17** Number of trials that were followed by a roar from the study group and in which they remained silent, according to the experimental condition.

## Latency to call

Looking at the timing of production of those calls with respect to the broadcasting (Figure 5.18), a clear difference between conditions emerges. All the invasion trials had their sessions starting less than 70 minutes after the playback, while the only two calls after overlap trials occurred much later. As these sample sizes do not allow a direct comparison between conditions, I resorted to a simpler alternative. As the sample of latency to call in the invasion trials is not significantly different from a normal distribution (Shapiro-Wilk  $W = 0.935$ ,  $df = 7$ ,  $p = 0.59$ ), I calculated what were the chances of getting each of the latencies observed in overlap trials from a population with the parameters of the invasion ones. In both cases the probability was smaller than 0.001.



**Figure 5.18** Scatterplot of latency to call in invasion and overlap trials.

### Probability of observing a session

All loud calls emitted after playbacks occurred in periods of the day in which the basal probability of calling was generally smaller than 5% (considering 10-minute points with respect to sunrise, see Figure 5.9). Individual invasion trials had a null probability of possessing at least one call after the playback that ranged from 0.06 to 0.21 (recall that these values vary due to differences in the time of the day in which a trial was conducted, and on the amount of time I remained with the group afterwards, see Methods section). Observing roars in 7 out of 15 trials (as registered in the invasion condition) by chance alone is unlikely under these conditions (binomial test, using the conservative value of 0.21 as the probability of success,  $p = 0.046$ ). On the other hand, for overlap trials, the null probabilities of calling varied from 0.07 to 0.18<sup>3</sup>. The probability of getting calls in 2 out of 9 experimental days by chance alone is virtually 1 when using the null value of 0.18 and 0.354 using the smallest figure (0.07). These results combined with the timing results above, lend strong support to the claim that roar sessions after invasion trials were produced as a response to the playback situation, while the ones after border trials were part of the normal pattern of calling behaviour.

Anecdotal data also support this interpretation. First, on one of the two border trials in which I registered a roar after the playback, the animals were involved in an inter-group encounter less than an hour after the emission of the call. Thus, apart from the longer latency to call, there is the possibility that the other group had already been detected, and the loud call was related to that. In an excluded invasion trial (due to the different experimental design of playing back twice to the animals), I registered a roar session 87 minutes after the first playback (57 minutes after the second, and the animals did not move between the two playbacks), a value well within the range observed in invasion trials.

### Location of the sessions

Considering the location of the tree in which roar sessions occurred after the playback, there is no association between this variable and experimental condition (Table 5.6,  $\chi^2 = 5.143$ ;  $p = 0.25$  - exact significance,  $df = 2$ , power = 0.2495 for a large effect to be detected). Significance is approached after combining the categories “PL site” with “overshoot”, as both seem to represent a response with reference to the playback site ( $\chi^2 = 5.143$ ;  $p = 0.083$  - exact significance,  $df = 1$ , power = 0.323 for a large effect to be detected). However, bear in mind that one of the very reasons for a small sample size for the border trials (which influences both the results and the power of the analysis) is the fact that the group emitted fewer calls on this condition. Also, only one of the responses to invasion trials was on a neutral location while the only two border responses were neutral (see Table 5.6).

**Table 5.6 Location of the places where the group emitted the first loud call after a trial with respect to the placement of the speaker and according to the experimental condition.**

|        |          | Placement of the call |         |           | Total |
|--------|----------|-----------------------|---------|-----------|-------|
|        |          | Neutral               | PL site | Overshoot |       |
| Design | Invasion | 1                     | 3       | 3         | 7     |
|        | Overlap  | 2                     |         |           | 2     |
|        | Total    | 3                     | 3       | 3         | 9     |

#### 5.5.2 Effect of location: movement data

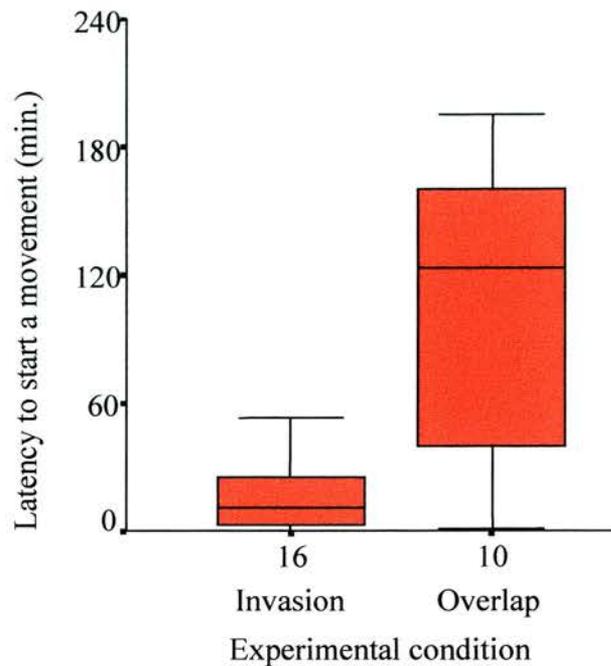
In this section, I analyse the variables related to the movement pattern of the alpha male, comparing the conditions with respect to: (1) the latency of the alpha male to start moving; (2) the total time of the of the resting session in the middle of which the playback was conducted; (3) the direction of the first movement session; (4) the position of the end point of the first movement session with respect to the speaker; (5) the latency to approach the speaker; (6) the occurrence of travel on the ground; and (7) the occurrence of patrolling

<sup>3</sup> Excluding an extreme value of nearly 0, due to a single trial performed very late in the day and after which I stayed only 1 hour 30 min.

behaviour. For the analysis of movement variables no trials had to be excluded. The rationale for studying the movement behaviour of the alpha male is that his reaction to the simulated presence of an invader group is expected to vary according to both the location of the invader and the inter-group spacing system, and this study can thus help in sorting out the alternatives. For example, if the groups mutually avoid each other, the alpha male should retreat or move neutrally in both conditions. If the groups defend boundaries, the alpha male should approach the speaker in both conditions (although maybe more intensively in the invasion condition since it represents an unlikely and unwanted event).

### **Latency to move**

As the latency to start a movement was not normally distributed in the invasion condition, I applied a transformation (cubic root) that yielded the best results in restoring it (invasion trials - Shapiro-Wilk  $W = 0.913$ ,  $df = 16$ ,  $p = 0.128$ ; overlap trials - Shapiro-Wilk  $W = 0.846$ ,  $df = 10$ ,  $p = 0.052$ ; Levene's test  $F_{1,24} = 0.397$ ,  $p = 0.535$ ). Then, the latency of the alpha male to start a movement proved to be significantly different between conditions (independent samples t test  $t = -3.6$ ,  $p < 0.01$ , power = 0.48 to detect a large effect, see Figure 5.19).



**Figure 5.19** Box-plot of latencies to start a movement on each of the experimental conditions. Above the experimental condition labels is the sample size for each condition. Please note that the graph represents the raw data.

### Total resting time

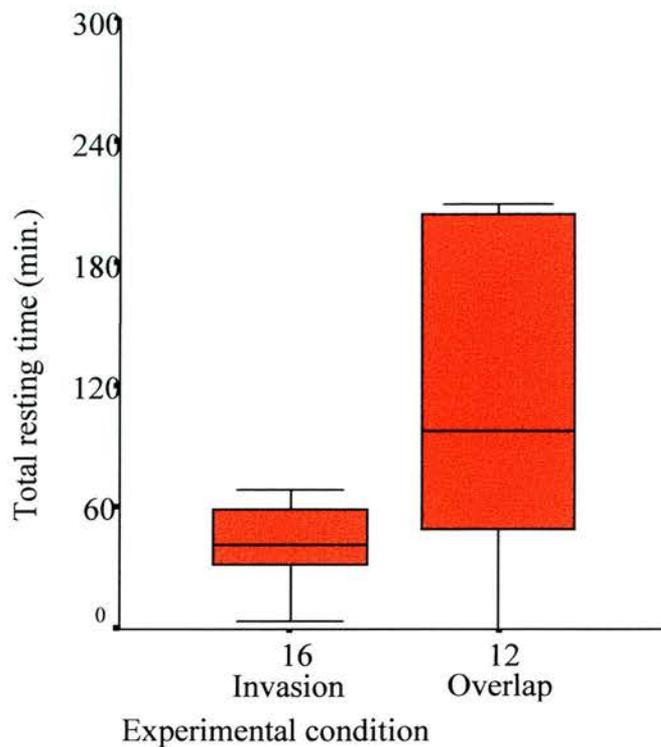
As time goes by during a resting session, the probability of its termination and the animals start moving presumably increases. Therefore, consistent biases between the conditions in the timing of the broadcast with respect to the start of the rest session could generate spurious differences with respect to the latency to move. There are two ways in which this interference might happen:

1 - if none of the experimental conditions influence the latency to start a movement, a difference between them might appear merely if one of the conditions have consistently longer time lags between the last movement and the broadcast (and thus have consistently shorter latencies to start moving again);

2 - if one of the conditions does influence the latency to move, the same consistent biases could result in a non-significant difference between conditions (or in an inflation of the differences).

Thus, one needs a compound time measure that takes into account both latencies (last movement to playback and playback to first movement) and that is able to deal with the two possibilities mentioned above. In other words, this measure should differentiate between a true reaction and an artefact caused by systematic bias in the timing of the broadcast (condition 1) and should be able to pick up a difference despite possible biases (condition 2). The total resting time (defined as the sum of both latencies) should be able to distinguish between these possibilities. If the trials fall in the first situation above, there should be no more difference between experimental conditions than the normal variation in total resting times. On the second situation, the total resting time should be smaller for whichever condition that stimulated an earlier termination of the resting session.

Data on total resting times were normally distributed but the variances were not homogeneous (Shapiro-Wilk test: invasion trials –  $W = 0.939$ ,  $df = 16$ ,  $p = 0.339$ ; overlap trials -  $W = 0.876$ ,  $df = 12$ ,  $p = 0.078$ ; Levenne's test  $F_{1,26} = 31.52$ ,  $p < 0.001$ ). Comparing the experimental conditions shows that there is indeed a difference between them (independent samples t test not assuming equal variances  $t = -2.9$ ,  $p < 0.05$ , power = 0.65 to detect a large effect, see Figure 5.20). Invasion condition had shorter values than the overlap.



**Figure 5.20** Box-plot of the total resting time<sup>4</sup> (time between the last movement before the playback and the first movement after it) on each of the experimental conditions. Above the labels is the sample size of each condition.

### Movement direction

Experimental condition was not significantly associated with the direction the alpha male set off when he started moving (Table 5.7,  $\chi^2 = 2.769$ ; exact significance  $p = 0.13$ ; power = 0.74 to detect a large effect). During the outside trials the alpha male always moved in neutral directions. Since these trials were always conducted close to the border, they might be considered as akin to the overlap condition. Adding overlap and outside data points indicates a trend towards significance ( $\chi^2 = 4.82$ ; exact significance  $p = 0.066$ ; power = 0.78 to detect a large effect). Although an association chi-square does not allow determining precisely where the association lies, the data indicates that invasion

<sup>4</sup> To compute this variable I used the first movement of the alpha male after the playback, irrespective of the distance moved.

trials seem to be positively associated to approaches, while the other conditions were associated to neutral movement directions.

**Table 5.7 Direction of the first major movement of the alpha male after a trial with respect to the placement of the speaker and according to the experimental condition.**

|                        |          | Movement direction |                      | Total |
|------------------------|----------|--------------------|----------------------|-------|
|                        |          | Approach           | Neutral <sup>a</sup> |       |
| Experimental condition | Invasion | 11                 | 5                    | 16    |
|                        | Overlap  | 4                  | 7                    | 11    |
|                        | Total    | 15                 | 12                   | 27    |

<sup>a</sup> I joined neutral and retreat responses, given that there was only one of the latter

### Displacement position

To examine the position of the end point of the first movement session after the broadcast (displacement variable), I decided to combine several categories. This reduction both made the data more comparable between conditions (for example, overshoots might be less likely in overlap trials) and decreased the number of empty and low expected value cells. Thus, I joined ‘neutral’ and ‘to the back’ responses into ‘neutral’; and the categories ‘before’, ‘at the site’, and ‘overshoot’ under the heading ‘advance’. The last category combines movements with (apparent) reference to the speaker, while the first one represents movements not related to the speaker. Retreat movements could be related to the speaker position in a negative way, but the only one observed case argues against that, as it was a single response, not a consistent trend. Considering the data thus combined, there was a borderline significant association between displacement and experimental condition (Table 5.8,  $\chi^2 = 4.03$ ; exact significance  $p = 0.061$ ;  $df = 1$ , power = 0.74 to detect a large effect). Invasion trials led to a displacement towards the speaker, something that did not occur in the overlap condition (outside trials showed only neutral displacement). Also, of the twelve ‘advances’ of invasion trials, one was a “before” (recall that this is when the alpha male did not get to within 20m of the speaker), 4 were “at the site” and 7 were “overshoots”. However, 1 of the 4 advances in overlap trials was a “before”, and the remaining 3 were “at the site”, with no overshooting.

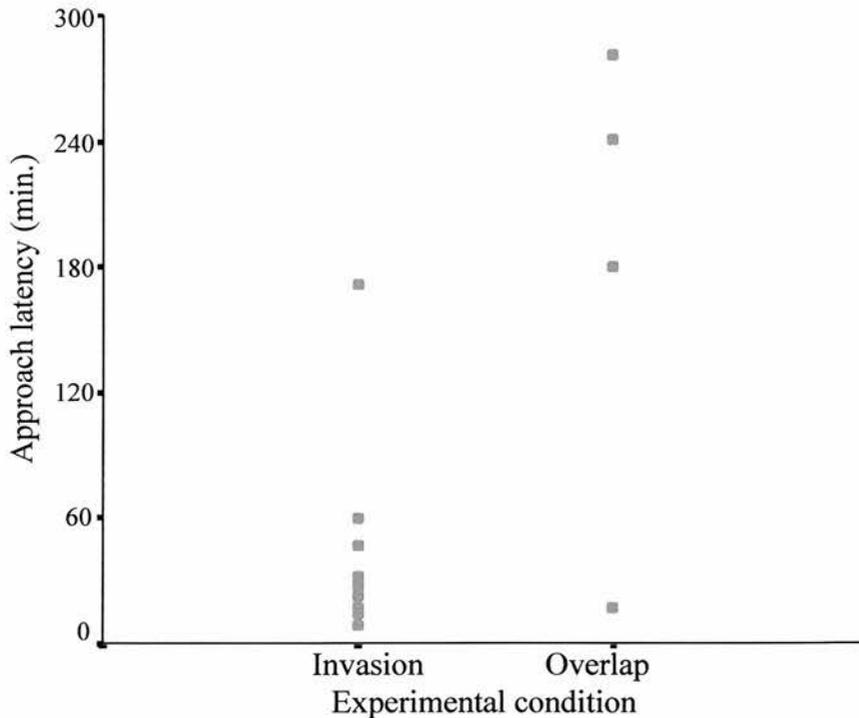
**Table 5.8 Location of the end point of the first major movement by the alpha male after a trial with respect to the placement of the speaker and according to the experimental condition.**

|                           |          | End point of movement |             |       |
|---------------------------|----------|-----------------------|-------------|-------|
|                           |          | Neutral               | Approximate | Total |
| Experimental<br>condition | Invasion | 4                     | 12          | 16    |
|                           | Border   | 7                     | 4           | 11    |
|                           | Total    | 11                    | 16          | 27    |

### Latency to approach the speaker

Considering only those cases in which the alpha male approached within 20m from the speaker, latency to do so was shorter during invasion trials (mean  $\pm$  SE: =  $23.6 \pm 3.94$  min.,  $n = 9$ ), than in the few border ones in which approaches occurred (mean  $\pm$  SE: =  $179.26 \pm 57.84$  min.,  $n = 4^5$ ). These data were normally distributed after the exclusion of a single outlier (Shapiro-Wilk test: invasion trials –  $W = 0.915$ ,  $df = 10$ ,  $p = 0.320$ ; border trials -  $W = 0.906$ ,  $df = 4$ ,  $p = 0.460$ ), but the variances were not homogeneous (Levenne's test  $F_{1,12} = 11.1$ ,  $p < 0.01$ ). Difference between conditions was borderline significant (unequal variances t-test  $t = 2.618$ ,  $p = 0.078$ , see Figure 5.21). As power is low (0.2382 for a large effect to be detected), and the significance is borderline, rejection of the null hypothesis should be treated with caution.

<sup>5</sup> Data calculated excluding the outlier on the invasion group (value well above the others, see Figure 12), as this made both groups normally distributed.



**Figure 5.21** Scatterplot of latency to approach in the invasion and border conditions. Note the outlier of the invasion condition (value close to 180 min.), excluded from analysis.

### Travel on the ground

While conducting the trials, I observed two unusual behaviours: travelling on the ground and patrolling. During all three field seasons, I observed animals on the ground, for the purpose of travelling, less than ten times exclusive of experimental days (on a few other occasions they came to the ground to feed or play). Thus it is striking that this behaviour occurred after five trials, and always in travel sessions that initiated shortly after the playback; I observed yet another case of travel on the ground after an invasion trial excluded from analysis (due to broadcasting twice to the animals). Testing for association between occurrence of travel on the ground and experimental conditions failed to achieve significance (Table 5.9,  $\chi^2 = 0.608$ ;  $p = 0.61$ , exact significance; power = 0.7536 to detect a large effect). However, the only overlap trial in which I observed ground travelling seemed to be a very unusual one. On this session, the alpha male exhibited almost the whole suite of behaviours displayed in many invasion trials: short latency to move, heading towards the speaker, short latency to get to the

playback location, travel on the ground and patrolling behaviour. This trial was conducted near one of the most intensively used areas of the east border and on an important sleeping site. Thus it remains to be seen with larger sample sizes if this response is associated to simulated invasions.

**Table 5.9 Occurrence of travel on the ground according to the experimental condition.**

|                        |          | Travel on the ground |    | Total |
|------------------------|----------|----------------------|----|-------|
|                        |          | Yes                  | No |       |
| Experimental condition | Invasion | 3                    | 13 | 16    |
|                        | Overlap  | 1                    | 11 | 12    |
|                        | Total    | 4                    | 24 | 28    |

### Patrolling

Travelling sessions led or initiated by the alpha male were a common occurrence throughout the study. I also observed “rushing ahead”, in which the alpha male speeded in front of the rest of the group, and sometimes these sessions terminated in roaring bouts. However, outside foraging contexts, I rarely witnessed individuals departing from the group. Therefore, this behavioural pattern was strikingly unusual: the alpha male setting off in a travelling session, not being followed by the whole group, not for feeding purposes, and returning later. Comparing the occurrence of patrolling across conditions also failed to achieve significance (Table 5.10,  $\chi^2 = 1.3$ ;  $p = 0.36$ , exact significance; power = 0.7536 to detect a large effect). I observed patrolling in yet another invasion trial, but this had to be excluded from the analysis. The only border trial with this behaviour is the same unusual one mentioned in the analysis of travel on the ground.

**Table 5.10 Occurrence of patrolling behaviour according to the experimental condition.**

|                        |          | Patrolling |    | Total |
|------------------------|----------|------------|----|-------|
|                        |          | Yes        | No |       |
| Experimental condition | Invasion | 4          | 12 | 16    |
|                        | Overlap  | 1          | 11 | 12    |
|                        | Total    | 5          | 23 | 28    |

### 5.5.3 *Effect of intensity of use: loud call responses*

Next, I study the effect of the intensity of use of the quadrat in which I placed the speaker on the occurrence, timing and location of loud call responses. The objective was to verify if the alpha male reacted more intensely (called more often or was faster to start calling) when the playback was conducted in areas used more intensively. This analysis mainly allows testing one possible spacing system (or maybe a part of a system), namely, that the animals defend (or react more intensively) favoured patches in their range.

#### **Call occurrence**

Tests of association between categories of intensity of use (defined in several different ways) and loud call occurrence failed to achieve significance in all but one case (Table 5.11). The test was significant only when classifying the trials using two categories (high and low frequency of use) defined by the median of intensity of use of all quadrats in the home range along the whole year. In this particular classification, trials conducted in the low intensity use quadrats showed no cases of loud call response. However, organising the trials in an array of increasing intensity of use of the quadrats in which the speaker was located shows some potentially interesting results (see Figure 5.22). Looking at the data referent to the whole year, although the more intensively used quadrats do not seem to be particularly related to positive responses, the six less-used ones had no loud calls produced after the broadcast; but note that five of those trials at the bottom end were of the border condition. This finding could be a confounding factor, both in the analysis of effect of speaker location (if intensity has primacy over location in determining the response) and in the analysis of intensity of use, if location has primacy. Although it remains a possibility that the animals ignore poorly used areas, there is definitely no tendency towards stronger responses in intensively used quadrats. The non-significant results here might also be due to a definition of categories that fails to grasp the reality (that is how the monkeys perceive a favoured patch) or to a lack of adequate sampling. Future researchers should bear in mind the possibility of an influence of the intensity of use in mind and attempt to address this problem. The arrangement concerning intensity of use

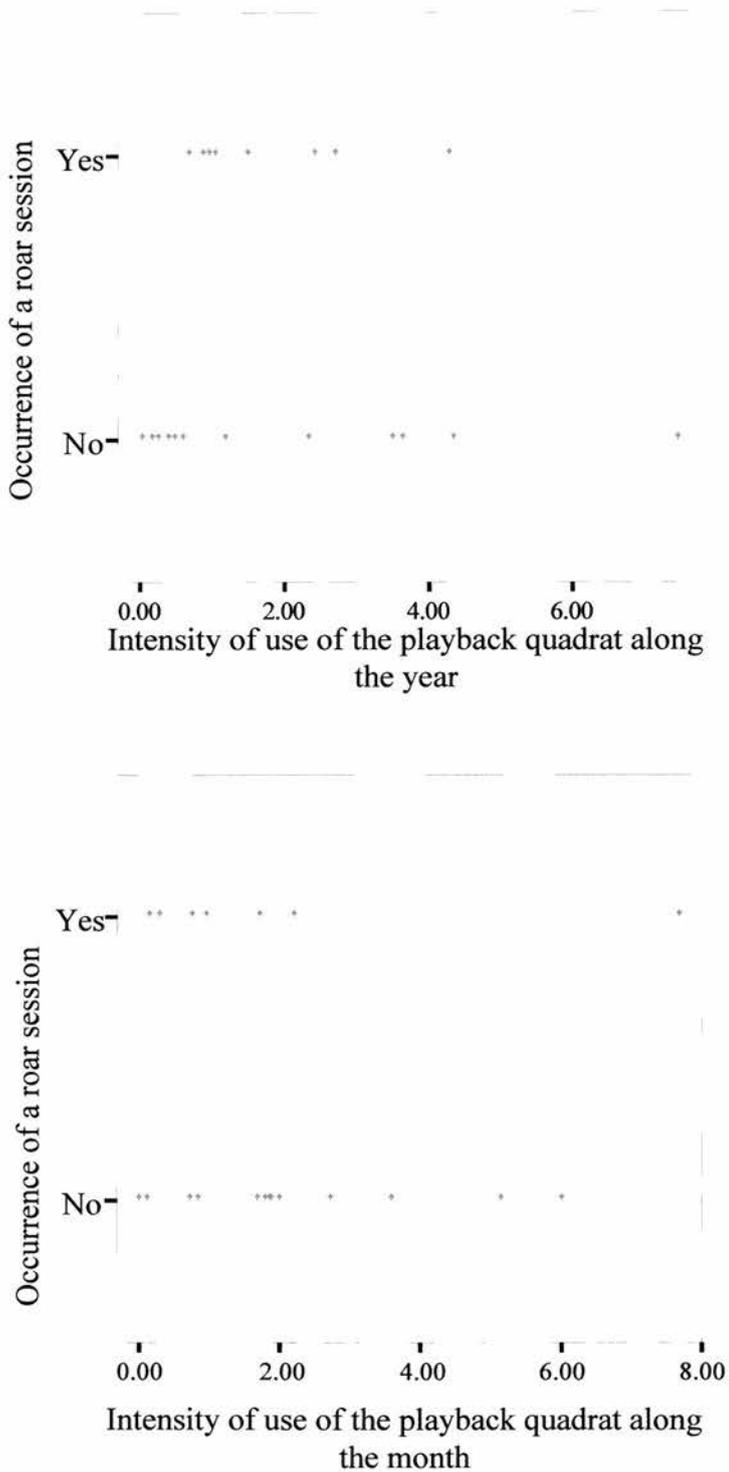
during the month in which a trial was conducted shows no signs of any trend whatsoever, indicating that the resources immediately available do not seem to influence the occurrence of roars after the playback.

**Table 5.11 Results of tests of association between categories of intensity of use defined through different methods and occurrence of a loud call after a trial.**

| Categorisation method <sup>a</sup>                                     | Pearson chi-square | DF       | Exact sig. (2-tailed) |
|--|--------------------|----------|-----------------------|
| Internal/Month/3 categories  | 0.042              | 2        | 1                     |
| Internal/Month/3 categories (but using only the extremes) <sup>b</sup> | 0                  | 1        | 1                     |
| Internal/Month/2 categories  | 0.170              | 1        | 1                     |
| Internal/Year/3 categories   | 3.418              | 2        | 0.264                 |
| Internal/Year/3 categories (but using only the extremes)               | 2.492              | 1        | 0.294                 |
| Internal/Year/2 categories   | 0.17               | 1        | 1                     |
| External/Array/Year/3 categories                                       | 1.194              | 2        | 0.712                 |
| External/Array/Year/3 categories (but using only the extremes)         | 1.039              | 1        | 0.542                 |
| External/Array/Year/2 categories                                       | <b>6.118</b>       | <b>1</b> | <b>0.023</b>          |
| External/Cum perc./Year/3 categories                                   | 0.503              | 2        | 0.846                 |
| External/Cum perc./Year/3 categories (but using only the extremes)     | 0.495              | 1        | 0.587                 |
| External/Cum perc./Year/2 categories                                   | 0.155              | 1        | 1                     |

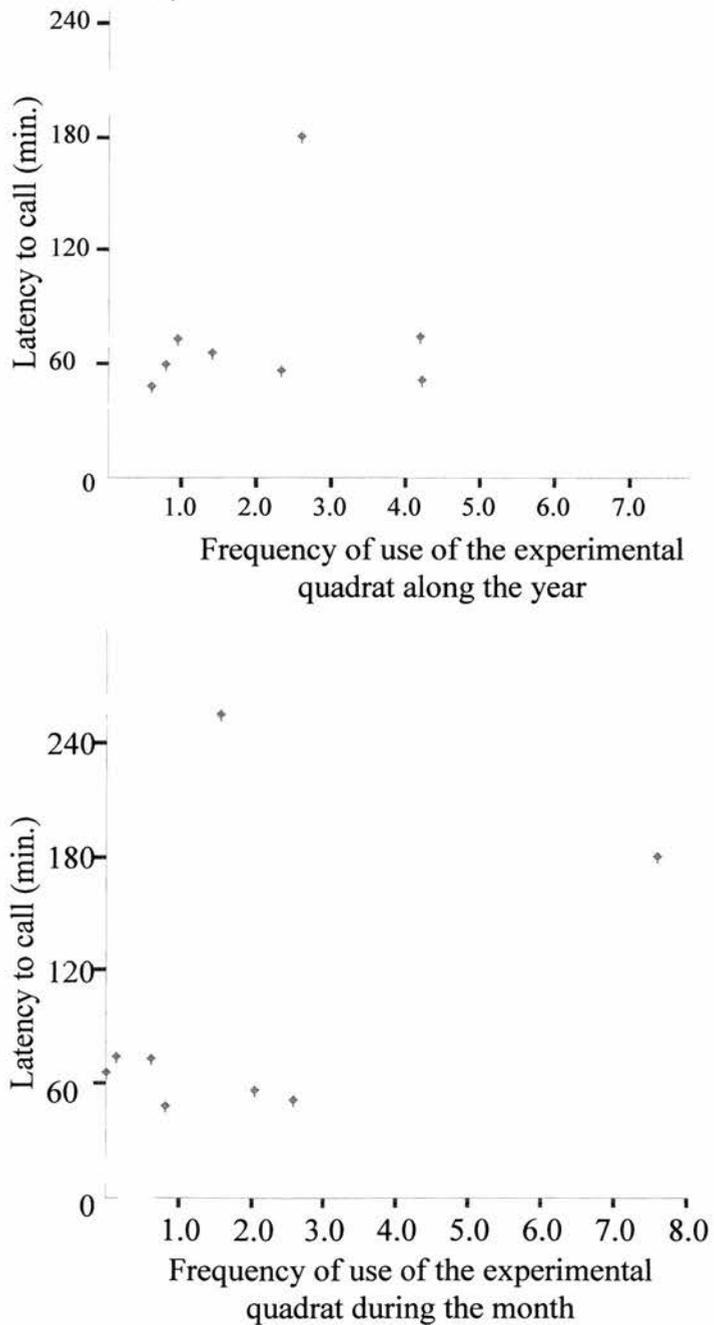
<sup>a</sup> Internal or External refers to the general approach to classification. Month or Year means analysis conducted using intensity of use during the month in which the playback was conducted or over the whole year. Array and cumulative percentage (Cum. perc. in the table) refers to the method of external classification (see Methods).

<sup>b</sup> Using the extremes means dividing the data into 3 categories, but excluding the middle one of the analysis, thus retaining the more and the less intensively used quadrats.



**Latency to call**

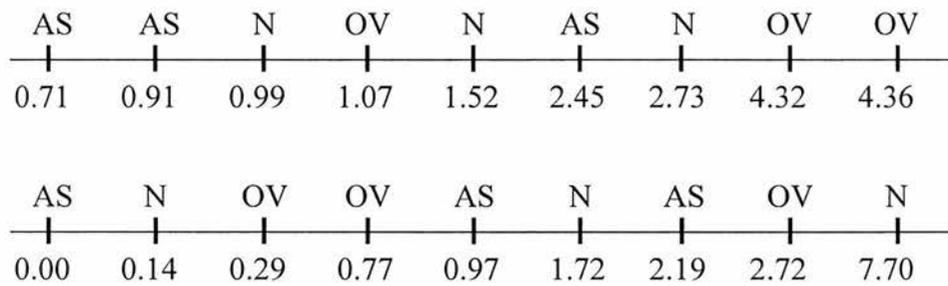
Although evidence was at best tenuous for an association of intensity of use of the playback quadrat with occurrence of a loud call, there could be still a relation between the latency to call and the frequency of use of the playback area. That is, animals might be expected to react faster to more valued areas, if defending specific resources. The arc-sine transformed data on intensity of use was normally distributed (Shapiro-Wilk test: intensity during the year –  $W = 0.880$ ,  $df = 9$ ,  $p = 0.156$ ; intensity during the month -  $W = 0.954$ ,  $df = 9$ ,  $p = 0.734$ ). However, the data on latency to call was not, exclusively due to the joint consideration of invasion and overlap trials (Shapiro-Wilk  $W = 0.684$ ,  $df = 9$ ,  $p < 0.001$ ). Thus, I resorted to non-parametric correlation which showed no relation between latency to call and intensity of use of the quadrat in which the speaker was located (Spearman's rho, year data:  $r = -0.133$ ,  $p = 0.732$ ,  $n = 9$ ; month data:  $r = -0.033$ ,  $p = 0.932$ ,  $n = 9$ , analysis conducted on non-transformed data; see Figure 5.23). The graphs show instead that, when a loud call response occurred, the latency was quite constant (apart from the two data points with longer latencies, which not coincidentally represent the overlap trials).



**Figure 5.23** Scatterplot of latency to call according to the intensity of use of the quadrat in which the speaker was positioned either during the whole year (top graph) or on the month of the trial (bottom graph). Each dot represents a separate trial.

### Location of the sessions

For the trials that had a roar after the playback (excluding inter-group encounter and “weather” calls), it was not feasible to test the influence of the frequency of use of the speaker quadrat on the location of the calling place due to the size of the samples involved. So, I resorted to a graphical display of the data in order to inspect for possible trends worth investigating in the future. Looking at Figure 5.24 indicates that the intensity of use of the playback quadrat seems to have no discernible influence on the location of the calling place.



**Figure 5.24** Location of the first roar session after a trial (excluding outside condition) with respect to the speaker position (categories above the lines), according to the intensity of use of the quadrat in which I placed the speaker (figures below the lines). Categories: AS – at the site; N – neutral; OV – overshoot. Diagrams for intensity of use either during the whole year (top) or during the month in which the trial was conducted (bottom).

#### 5.5.4 Effect of intensity of use: Movement responses

Under this topic I analyse the relation between the intensity of use of the quadrat in which I placed the speaker and the latencies to start moving and to approach the speaker location. As above, the purpose is to verify if the alpha male defended primarily the most favoured patches.

As nearly all movement variables were not normal (Table 5.12), I turned to non-parametric statistics, to avoid data manipulation of a large number of variables. Testing for correlation between frequency of use of the quadrat in which I conducted the trial and movement variables failed to achieve significance in all cases. Latency to move does not correlate with intensity of use

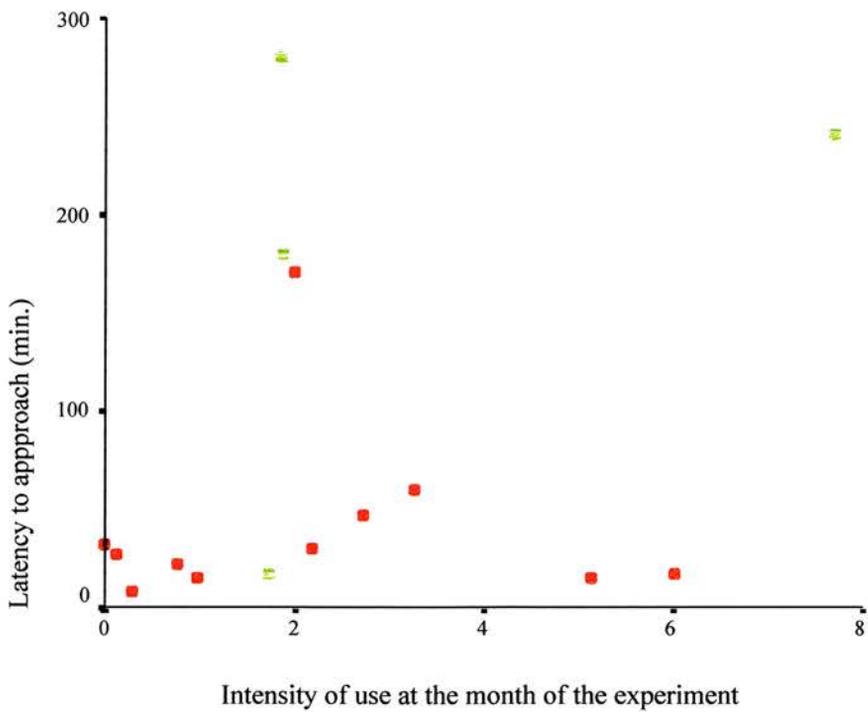
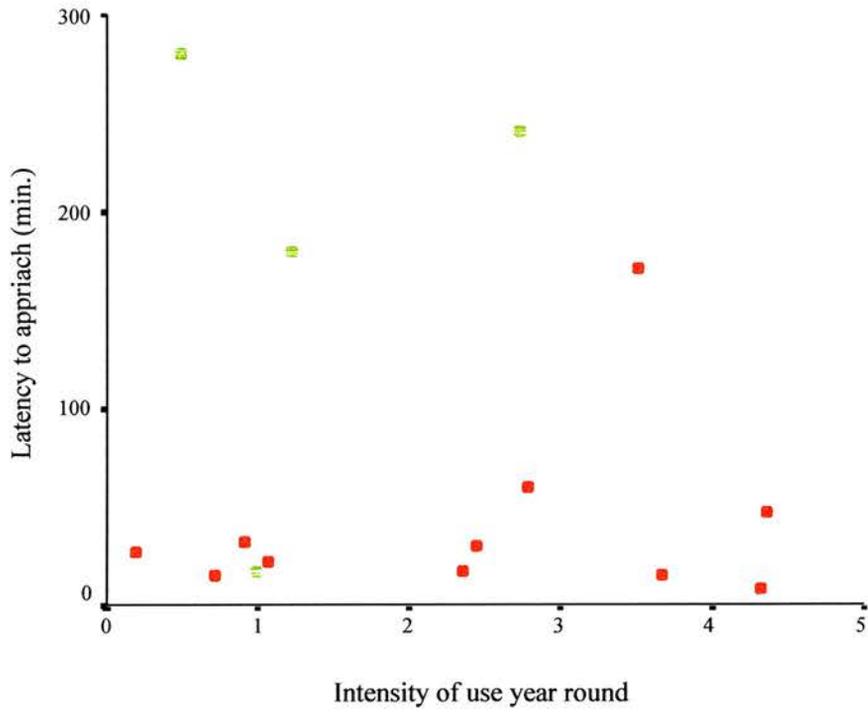
of the speaker quadrat, either using yearly values or only during the month of the trial (Spearman's rho  $r = -0.084$ ,  $p = 0.684$ ,  $n = 26$  and  $r = 0.099$ ,  $p = 0.632$ ,  $n = 26$ , respectively, Figure 5.25). The main difference between trials seems to be due to the location of the speaker. Repeating the analysis with invasion trials only does not alter the results (Spearman's correlation  $r = 0.152$ ,  $p = 0.575$ ,  $n = 16$  and  $r = -0.228$ ,  $p = 0.395$ ,  $n = 16$ , for the yearly and month data on intensity of use respectively). On those instances in which the alpha male approached the speaker, latency to do so did not correlate with intensity of use of the speaker's quadrat (year data: Spearman's correlation  $r = -0.061$ ,  $p = 0.830$ ,  $n = 15$  and month data:  $r = 0.264$ ,  $p = 0.341$ ,  $n = 15$ ). Conducting the analysis only on invasion trials did not alter the results (year data: Spearman's correlation  $r = 0.127$ ,  $p = 0.709$ ,  $n = 11$  and month data:  $r = 0.073$ ,  $p = 0.832$ ,  $n = 11$ , Figure 5.26). Again, the main difference seems to reside between the different location conditions, with no signs of any trend with regard to intensity of use.

**Table 5.12 Test of normality for movement variables**

| Variable                                      | Shapiro-Wilk statistic | DF | Significance |
|---|------------------------|----|--------------|
| Latency to a major mov. (pooled) <sup>a</sup> | 0.814                  | 26 | ***          |
| Latency to a major mov. (invasion)            | 0.684                  | 16 | ***          |
| Latency to a major mov. (overlap)             | 0.940                  | 10 | NS           |
| Latency to approach (pooled)                  | 0.728                  | 15 | ***          |
| Latency to approach (invasion)                | 0.641                  | 11 | ***          |
| Latency to approach (overlap)                 | 0.906                  | 4  | NS           |

<sup>a</sup> Pooled means combining invasion and overlap trials.





**Figure 5.26** Scatterplot of the latency to approach the speaker after a playback trial according to the intensity of use of the quadrat in which the apparatus was positioned either during the whole year (top graph) or on the month in which the trial was conducted (bottom graph). Data from invasion (●) and overlap (=) trials.

## 5.6 Discussion

I first summarise the main findings reported in the previous section. Next, I propose a hypothesis for the function of roars in the inter-group spacing system of *A. caraya* and show how my results provide evidence that supports the proposal. Then, I evaluate the evidence (or lack of it) concerning other possible functions that have been proposed in the literature for loud calls.

### 5.6.1 Summary of results

Observational data showed that the groups in the vicinity of the study site had a clear dawn peak in emission of roars, but the profile of calling during the day seemed to vary among months, with a smaller dawn peak during the winter. The timing of roaring was significantly influenced by the time of sunrise. Minimum temperature of the day may explain a small amount of the variation in the timing of the dawn session, and it certainly influenced its occurrence. Groups called less often on cold days, and possibly slightly later than expected, but no warm day without morning calls was observed. Calling behaviour was also influenced by extreme weather events: the study group tended to produce incipient roars or significantly shorter roar sessions during these occasions. Inter-group encounters clearly stimulated the occurrence of loud calls, particularly roars, but the duration of these sessions was not longer than spontaneous sessions, nor was recruitment of callers higher. Calling was distributed throughout the home range and the frequency of calling was related to the intensity of use of a given area, but only because the animals did not call from poorly used areas. The animals called less than expected in border areas, and more in the centre of the range. Caution is necessary with this result given a series of limitations in the data: an analysis conducted on a subset of data showed no association between calling and particular regions (borders x core) of the home range.

Observations during natural inter-group encounters showed a variety of behaviours. Neighbouring groups at medium distances could: (1) show no visible reaction; (2) call simultaneously or sequentially; (3) present an asymmetrical

response, with one of the groups calling and the other showing no response. Closer encounters were usually accompanied by counter-calling, and occasionally one of the groups chased the other. Some encounters were particularly protracted, and a deep invasion on the home range of the study group was repelled with high intensity.

After experimentally simulated invasions of the home range, the alpha male of the study group started a roar session significantly more often than would be expected given the normal pattern of calling. However, the same did not occur after playbacks on the overlap areas. Not only that, but also the roar sessions of the invasion condition were much closer in time to the playback than the ones of the overlap condition. There was a trend for association between the condition and the location of the roar session after the playback. Responses to the invasion condition were produced at the speaker location or at an overshoot location (with a single exception), while the only two cases of roar responses to the overlap condition were emitted from neutral locations. Contrasting the invasion with the overlap conditions with respect to movement variables showed that, in the first, the alpha male started moving earlier, presented a shorter resting time, and approached the speaker faster. Additionally, there were indications that, after simulated invasions, the alpha male tended to move towards the speaker and end up at or beyond the speaker location, whereas it moved neutrally in the overlap (and outside) condition, ending in neutral locations. Occurrence of travel in the ground and patrolling behaviour were not associated with experimental condition, but occurred chiefly during invasion broadcasts (the single outside trial in which these behaviours occurred was highly unusual). There was no relation between the intensity of use of the quadrat where I placed the speaker and call or movement variables.

### *5.6.2 Function in inter-group spacing*

Before proceeding with the discussion, let me clarify that, given the peculiarities of howlers' loud calls, I am going to consider here roars as synonymous with group sessions, and will not distinguish male and female emissions, since the majority of sessions includes calls from both sexes. However, this does not necessarily mean that males and females have similar

engagements, interests or even that the function is the same for both sexes. And although I consider here the functions of the sessions, as they are obviously led by males (and when one sex does not participate, it is always the female), it can be argued that the proposed functions apply for males only. I will discuss the issue of sex differences in more detail later on (topic 5.6.3).

The pattern of use of space by my study group consisted of exclusive use of a large portion of the home range, with relatively small overlap regions with neighbouring groups. A similar arrangement is found in a range of primate species, such as titi monkeys (Robinson, 1979, 1981 b), indris (Pollock, 1986), black and white colobus (Marler, 1969, 1972); Thomas langurs (Wich et al., 2002 a, b), and various hylobatid species (Chivers, 1975; Gittins, 1980; Mitani, 1985 a; Raemaekers & Raemaekers, 1985; Sommer & Reichard, 2000; Tenaza, 1976), besides at least one other howler species (*A. fusca*, pers. obs.; unclear in Chiarello, 1995). However, spacing patterns can be brought about by different spacing systems (Waser, 1977; Waser & Wiley, 1980), which is confirmed by the variety of systems (with more or less involvement of loud calls) in the studies just mentioned.

Based on the data of this chapter, I advance the hypothesis that roar sessions work in the regulation of use of space, through a dual mechanism of advertisement of occupancy and a complementary role during territorial encounters/disputes. On these occasions, I suggest that roars constitute a ritualised aggressive display, to reinforce occupancy, functioning to enable some disputes to be settled without costly chases and fights. Active defence of space backs up the system when necessary.

### **Advertisement of occupancy**

Concerning advertisement of presence or occupation of an area, several lines of evidence support this mechanism for the regulation of space use in the study group. First, there is the high frequency of calling, and the large number of calling sessions that seemed to be spontaneous, not connected with inter-group encounters or distant exchanges. Loud signals with these features are traditionally interpreted as related to the maintenance of distance between individuals/groups (Marler, 1972), e.g. the type 1 loud calls of Old World

monkeys (Gautier & Gautier, 1977). Contagion in call production is another characteristic of such signals, although evidence in my study was ambiguous. The clear dawn peak of emissions for all groups in the vicinity of the study group, which would normally be interpreted as a sign of contagion, may merely indicate a convergence of calling in a time of the day with plenty of natural triggers (circadian clues, other species' behaviour, etc.). Thus, the confluence could be caused either by contagion/mutual stimulation, or by an overall tendency to call at this time of the day caused by a common stimulus. A much stronger proof of contagion would be the occurrence of daytime bouts of different groups starting sequentially, and at no particular time of the day: I did not observe such a pattern in this study.

The regulation of use of space by signals that are loud, frequent, spontaneous, and contagious (besides stereotyped and discrete) can be achieved through a system of mutual avoidance or reciprocation of movements, leading to the maintenance of distance between groups (Gautier & Gautier, 1977; Marler, 1972; Mitani, 1985; Waser, 1977; Whitehead, 1987). However, the same characteristics are also compatible with a mechanism of *defining* a territorial area (as opposed to *defence* of a territory, see Pollock, 1986) through constant advertisement of occupancy as defended here. By calling frequently from all over the home range, a group defines its ranging area to others in the vicinity.

Data on distribution of calling places could in some cases help to further differentiate between the alternatives of mutual avoidance (or reciprocation) and territorial definition. Both hypotheses are consistent with an even distribution of calling throughout the home range, with measures of calling (frequency of sessions, total duration, etc.) proportional to the intensity of use of an area. However, disproportionate calling at borders could also provide definition of the territory to nearby groups (see Pollock, 1986), but is not expected under the avoidance hypothesis. Data on the location of spontaneous calling sessions of my study group and on the relation between their intensity of use and calling behaviour shows a mixed picture. Although the group called from a wide variety of places in the home range, the frequency of sessions in different areas did not clearly correlate with their intensity of use. With respect to placement of the calls in the home range, the results are also ambiguous, but it was at least clear that calling sessions not triggered by inter-group encounters were not associated with

border regions. Apart from the problem with this analysis mentioned above, there are three further potential confounding factors whose influence on the distribution of calling places need to be addressed in future studies. First, since the majority of calling is done at dawn, one has to consider the distribution of sleeping trees. Second, animals might have preference to call in certain kinds of trees with features that help the propagation of sound (e.g. tall, emergent or more exposed trees). Third, the distribution of trees used for calling might be related not to the intensity of occupation per se, but to the location of important food sources/patches, either seasonal or annual. The distribution of each of these three kinds of resources need not be related to the overall pattern of use of the home range, and might be better or auxiliary predictors of the distribution of the calling places. The nature of the interaction with different neighbours might also influence the relation between frequency of calling and specific places in the range, as one might expect different proportions of spontaneous and counter-calling sessions in “disputed” versus “settled” borders. In the former, the amount of spontaneous calling will be smaller than expected, as the sessions are likely to happen during inter-group encounters. Overall, the spatial patterns of calling behaviour analysed with respect to intensity of use do not help in differentiating possible alternative hypotheses supported by the data considered so far. Nonetheless, the occurrence of calling over the whole range is compatible with the hypothesis proposed.

Natural and experimental evidence gathered in this study argues against a mutual avoidance/reciprocation system in this case. First, the large home range overlap frequently encountered in such systems was lacking. Second, during experimentally simulated invasions of the home range, the group not only failed to show any signs of retreat, but rather tended to move *towards* the speaker. Differently from the classic grey-cheeked mangabey study (Waser, 1976, 1977), the whole group followed the alpha male in the majority of cases. Patrolling, somewhat similar to the rapid-approach behaviour of mangabey alpha males, occurred in only 5 trials. This strongly suggests intolerance towards invaders, reinforced by the behaviour of the group in the only clear-cut natural invasion event registered (obviously not a case of mutual avoidance).

The apathetic responses to experimentally simulated incursions to overlap regions, particularly with respect to movement variables, also contribute

evidence against a mutual avoidance system driven by roar sessions. In such systems, the same responses are expected to occur independently of the location of the neighbour group in the range. Groups should avoid each other or merely ignore the neighbour's presence, if too far away. Quite to the contrary, after invasion trials the alpha male started moving at a time significantly closer to the playback, tended to move towards the speaker, and, when he did so he tended to approach the speaker area faster. As a final possibility, a mutual avoidance system could be compound by a defence of favoured areas, in which case some heterogeneity on the response to the playbacks might be expected. Failure to demonstrate any relation between intensity of use of the speaker quadrat and alpha male response argues against this. In fact, location remained as an apparently confounding effect in such analysis.

Before proceeding to the second part of the argument, let me elaborate on some possible confounding factors. Looking at the details of the playback procedures, the sceptic might argue that the observed responses were caused by the fact that the test tapes contained loud calls from strangers, and that lack of acquaintance with the caller was the prominent factor in the response. However, the design was planned to contrast the response to the *location* of the stranger. By playing back the same category of individuals (i.e. strangers) in different locations, I controlled for the potential. Furthermore, if the observed reactions occurred merely to the fact that the playback calls were from strangers, then one would expect similar reactions to trials conducted inside or in overlap areas. After all, overlap areas are also part of the home range, some of the quadrats in these areas were intensively used, and actually dispute over some of them seemed to have occurred. Under the mutual avoidance/reciprocation hypothesis one would expect similar reactions regardless of the level of acquaintance with the calling group. In fact, none of the test groups studied by Whitehead, 1987 (who proposed a mutual reciprocation system based on loud calls) was immediate neighbour with the group that was the source of the test tapes (which lived on an forest islet). One of the groups actually lived more than 1km from the source (based on figures in Whitehead 1987). Nonetheless, the responses to the trials led him to propose the mutual reciprocation hypothesis, which can not be defended with my results.

However, it remains true that a definite proof requires another experimental series, where one contrasts the response to trials playing back calls from immediate neighbours with trials broadcasting strangers.

### **Aggressive display**

I propose that roars also play a complementary role during territorial encounters and disputes. On these occasions, my hypothesis is that roars constitute a ritualised aggressive display that would provide either a way of reinforcing the occupation of an area or an assessment mechanism that can provide a way to settle disputes without chases and fights. Evidence supporting the reinforcement of occupancy idea comes from the behaviour after chases, the vocal exchanges at medium distances, and from calling behaviour in the experimental series. In chases, as one of the groups involved in the incident was already withdrawing, there would be no need for the successful group to spend energy in a calling session. By doing so, however, they may be reinforcing the occupation of the area and/or of the location of the border, thus discouraging further encroachment. Vocal exchanges at medium distances remind neighbours of a group's occupancy of an area, without dragging them together to a close encounter, as far as there is no dispute. The calling behaviour of the group in the experimental series also provides support for a reinforcement of occupation function. Although not all the calling variables showed a significant difference between invasion and overlap conditions, the difference was always in the same direction. To be precise, all timing and call location variables pointed to a pattern of calling after simulated invasions clearly related to the playback. On the other hand, calling in the overlap trials seemed to be part of the natural calling behaviour, that is, not influenced by the experimental situation. Thus, during invasion trials calling was more frequent than during overlap ones (but not significantly so), significantly closer in time to the playback, and much more frequent than the baseline probability of calling would predict. It also showed a tendency to occur closer or overshooting the speaker location. Calling after a presumed invasion, even when the invaders are not visible anymore, conforms to the notion of reinforcing occupation through a display.

Territorial disputes can arise if a group expands its home range or if a neighbour group ignores the territory definition through constant calling. In such cases, I hypothesise that roars are part of an assessment mechanism as a first approach to settle the contest without escalating. Whichever the information transmitted through the call (proximate function), all observed outcomes in natural encounters can be explained by an assessment hypothesis. In fact, there is no alternative left for such a prolonged display in close encounters, the problem lying more on the proximate function. There are two kinds of basic information that can be transmitted by an aggressive display: resource holding potential (RHP) or threat. The first corresponds to any trait of the individual/group (size, weight, condition, status, numbers, etc.) related to its ability to defend the resource under dispute. Alternatively, a threat signal indicates merely the willingness to engage in an escalated contest over the resource under dispute. In this case, a consideration of the costs of the escalation against the benefits accrued from the exclusive use of the resource becomes important. Under the RHP hypothesis, one can expect either protracted disputes, if the groups are matched on their RHP, or shorter ones followed by chases from the group with higher RHP in asymmetric contests (or quiet retreats by the group with lower RHP). As described in the section on natural inter-group encounters, I observed all these situations. In case of advertisement of threat, one can also expect both outcomes. If both groups are announcing their intention to escalate, the costs are presumably the same (although visual information on numbers may be important), although the benefits might vary. Then, there may be an asymmetry in how much one is willing to escalate. If one of the groups has more to gain in escalating, it could attempt doing so and chase. If both groups are matched in terms of costs and benefits, one would expect a protracted encounter.

The alternative hypothesis for the use of loud calls in inter-group encounters is the mutual reinforcement of the boundary limits (e.g. as proposed for titi monkeys and gibbons). This hypothesis may be criticised on the grounds that it might require an underlying group selectionist reasoning. Without a detailed consideration of costs of escalated disputes and what could be gained from them, it is not clear why should both parties “agree” on a mutual boundary, and why neither side should attempt to invade. It seems, especially because of the words mutual and conventional used in these cases, that on this view the

animals are following a “contract” because it is good for both sides, a group selectionist approach. On an individual selection view, it would be expected that the boundary would only be arrived at after extensive testing and challenge. In any case, this hypothesis does not seem to apply to my group calls because the groups are not regularly drawn to a common boundary at which counter-calling might occur. The paucity of both vocal and movement responses to overlap trials, especially when compared to invasion ones, also supports the view that mutual reinforcement is not part of the inter-group spacing system of black howler monkeys. Although I was able to conduct only three valid outside trials, their results can be considered as a supporting source of evidence, since the speaker location, though outside the home range, was usually close to the border. If the howlers’ spacing system was one of conventional reinforcement of boundaries, one would expect at least an approach to the nearest border and probably counter-calling as well, which did not happen. This lack of evidence for conventional mutual reinforcement is for the moment the best argument for the function of roars as an aggressive display, to assess opponents and settle a dispute without escalating.

### **Apparent exceptions**

Some of my results may seem contradictory at first and at odds with the hypotheses proposed. On one side, there is the neutral response to experimental trials located at border and outside regions, which apparently conflicts with the observations of the long contests during natural encounters at boundary regions with neighbour groups. At the same time, I also observed some counter-calling at medium distances in bordering areas, or even only one group calling close to the border, and in both cases no further reactions were observed. The last observation at least lends support to the notion that the playback results of overlap trials were not artificial.

All these observations can be explained through a refinement of the model. The drawn-out contests may require other factors to happen (e.g. distribution of seasonal resources), which would be in accordance with the ideas advanced here, as mutual reinforcement of boundary location would not be a necessary result of a neighbour group at a bordering area. Also, for a protracted

encounter to occur, the real presence of the neighbour group close by is obviously necessary, and not a mere 30 s playback. Additionally, the encounters may not be actively sought, but only occur if the two groups happen to be drawn to a common border by their usual activities or when a conflict of interest ensues. This alternative is compatible with all the apparently contradictory observations. Another possibility is that my definition of the overlap regions (i.e. areas used commonly by two neighbouring groups) may differ from the one of the monkeys. Neighbour groups can encroach and use areas regarded by the study group as exclusive. When this happens *and* the resident group detects it, then a conflict results. The strong reaction to one of the overlap trials (the same one mentioned all along the results section), located on an intensively used area, indicates that such incongruity may happen. But without a more objective criterion to define the real and the perceived exclusion zones, this explanation can not be called upon, as it is a post-hoc dismissal of results that do not fit into the general scheme. Finally, as the amplitude of playback roars seemed to be smaller than natural calls, they might have been perceived by the animals as coming from a more distant place than the actual speaker location. For the overlap trials this would mean sounds perceived as coming from inside the neighbour group home range. This explanation, besides being in contradiction with the results of the invasion trials, also faces the problem that amplitude may not be the main indicator of distance for loud calls (Whitehead, 1987).

After reading the previous paragraph, the sceptic might counter-argue that it was necessary to add post-hoc features in order to rescue the hypotheses put forward and accommodate apparently contradictory features. However, note that the only thing that it was necessary was to advance further conditions under which the hypotheses must operate. More importantly, none of the results is compatible with the alternative hypotheses of mutual avoidance/reciprocation, mutual reinforcement of boundaries or territory definition through boundary calling.

## **Repulsion of invaders**

An active defence of the space, following the detection of an invasion, complements the dual role of roars in the inter-group spacing system. The timing and the direction of movement during invasion trials and the behaviour during the natural invasion observed shows that the tendency is to quickly approach invader(s) and eventually chase them out of the home range. The use of roars in these cases can be seen either as a reassurance of the occupation (if the invader retreats, as in the observed cases in the border) or as an aggressive display functioning to avoid chases (if the invader does not retreat immediately, as in the natural invasion witnessed).

## **Travelling on the ground and patrolling**

Finally, I briefly consider the unusual behaviours of travelling on the ground and patrolling in the context of the suggestions above. There seemed to be an association between these behaviours and invasion trials, although it was not statistically reliable. I registered both behaviours in only one overlap trial, and that was a very unusual one, having the nearly complete suite of behaviours displayed in invasion trials; moreover, the playback was on an intensively used area and an important sleeping site. I tentatively suggest some non-exclusive hypotheses for travel on the ground, assuming for the moment that it is related to invasions. Travel on the ground might be a strategy for a more silent approach to an invader; however, as for most of the year walking in the ground is at least as noisy as jumping between branches this hypothesis is weak. Alternatively, ground travel may be a swifter way to approach an invader, as presumably the ground offers less deviation from a straight line. Finally, travel on the ground might represent a surprise mechanism, as an invader could be expecting a canopy approach, or be less vigilant towards the ground. The relatively short tracts travelled on the ground also do not seem to agree with the swiftness and surprise hypotheses, as the alpha male did not go all the way on the ground to the speaker location. With respect to the hypotheses proposed, it is interesting to note that Katherine Milton provide an anecdote (Byrne & Whiten, 1990) in which a male spider monkey used the ground for a furtive copulation with a female. This

behaviour was interpreted as a deceptive behaviour, fitting with the silence and surprise hypotheses.

Patrolling behaviour, also assuming that it is indeed related to invasions, can be seen both as an extension of approach, one in which the alpha male is looking for the invaders, or a situation where the group merely did not follow the alpha, but took another route.

### *5.6.3 Sex differences in production and function of loud calls*

Production of loud calls is an eminently male phenomenon among primates (Gautier & Gautier, 1977). However, there are a number of species, particularly platyrrhines and hylobatids, in which females regularly produce loud vocalisations (Hohmann & Fruth, 1995). When analysing the occurrence of female calls and possible differences in function between sexes, the first obvious aspect to consider is the function attributed to the loud calls. Concerning functions not related to defence or control of access to resources (e.g. alarm, predator deterrence, contact, etc.), one could expect emission by both sexes. However, analysing the situation more carefully, males and females could still show differences, given different strategies employed in the different circumstances. For example, when dealing with predator calls, females might refrain from calling as a strategy to remain inconspicuous. When one considers the functions most commonly ascribed to loud calls, that is, defence or control of access to resources, then one might also expect to see variation, given differences in patterns of migration, and different interests of males and females. When the resources in dispute are reproductive partners, it is obvious that sex differences should emerge. Here, the migration pattern becomes important. Hohmann and Fruth (1995, p. 175) argue that “it is conceivable that loud calls are directed towards those individuals who are most likely to transfer between groups”. The corollary to the argument is that the sex that transfers should be the sex that calls, since the natal members of the group would lose tenure or rank after a successful take-over. The authors showed that in the catarrhines (group in which loud calls are male business), most of the species have only male migration or a male-biased migration (Hohmann and Fruth, 1995). Accordingly, they showed that, for the species possessing female loud call, migration is female-biased towards or

both sexes migrate. They point out four limitations of their findings: (1) none of the sexes call in a few species with female-biased migration; (2) the philopatric sex may also call in some species; (3) there are no species in which only the female calls; (4) females, even being the migrant sex, refrain from calling in some species.

When the resource in question is space (whole home range or parts of it), it could equally be argued that the philopatric sex is the one that has more to lose from encroachments and losses in the home range, although the migratory sex also loses in a short term basis. Members of the migratory sex that stay in the natal group or have already transferred into the group also have long-term interests. This argument alone could help to explain points two to four above. A third hypothesis can be proposed for the cases in which only male calls for defence of space when females are the sex that migrates (belonging to point 4 above). The reasoning is that females may use the potential of males to secure their home range as a sexual selection mechanism, by choosing the males with the highest potential for defence (and inciting male-male competition).

Having briefly depicted this complex issue, it comes at no surprise that males and females call in the study species, since in howler monkeys both sexes migrate (Kinzey, 1997). However, it remains to be explained why the sexes have different involvement in calling. This difference was not only in terms of number of sessions (alpha male participated in all sessions, and the beta male in nearly all, while females participated in a smaller number of sessions), but also within a session as well. The alpha male was the initiator of the session in *all* cases observed, and females and sub-adult males usually dropped their participation first, followed by the beta male, and the alpha male was the last one to give up calling. Furthermore, female calls do not seem as continuous as the male, bearing more resemblance to the barks, and females sometimes called from a sitting position, not with the typically tense quadrupedal posture of males. These differences may relate to lower motivation and thus lower energy expenditure in females. Intriguingly, I had the clear impression that female calls are a stimulus for the alpha male. In waning sessions, the emission of a female call (and of other supporters as well) generated an invigoration of the alpha male emissions. Another further difference between male and female engagement comes from the fact that females were not involved in the natural chase observed. Also, recall

that in the invasion condition of the playback experiments, the alpha male performed a patrolling behaviour in five occasions, and was not followed by the whole group. In three of those he was alone and in two was followed by the second male, but a female never followed him.

It would be interesting to contrast this pattern of differential investment with precise data on the migratory patterns. Under the possibility, raised below, that loud calls of black howlers could have an additional role of dissuading immigrants, one could verify if males are more prone to migrate than females. The sexual selection hypothesis should also be tested. Another relevant point here is the distinct costs and benefits of the migration into a group of a member of a given sex. Concerning male migration, the resident alpha male stands to lose its rank or even a place in the group, while the females might perhaps lose the offspring of the moment, if the invader is infanticidal. Regarding female migration, the male has nothing to lose, and maybe can gain increased opportunities for mating, while the females have nothing to gain, and lose in having to share their resources with additional females and their future offspring.

#### *5.6.4 Energy expenditure of roar emissions*

It is generally assumed that the emission of loud calls by howler monkeys is energetically costly, although this has never been confirmed with physiological studies. One result in this study might point in this direction. Minimum temperature of the day, which usually occurs just before dawn, was shown to affect the occurrence of the early morning sessions. The animals were less prone to call on cold mornings, whereas they nearly always do on warm ones. It seems though, that the animals attempted to avoid calling on days on which it was necessary to expend more energy to keep up body temperature. This limitation would not be necessary if the energy expenditure during calls was negligible. It would be interesting to pursue this idea further, to verify if the energy expenditure of the calls could serve as an honest indicator of the animal resource holding power. In this respect, it is possible to suggest that one of the reasons for the early morning peak could be that it is the time of the day in which it is more *costly* to call. Therefore, if the calls are an honest indicator of RHP, animals

could have been selected to call at the time of the day which is more costly for them to do so.

#### 5.6.5 Proximate function of roars

Concerning the specific information being transmitted by the roars, that is, the proximate function, my data do not allow even to speculate. Possibilities include, but are not restricted to, information on numbers (Kitchen, 2004), size (Bee et al., 1999; Wilczynski et al., 1993), weight (Reby & McComb, 2003), fighting ability (McComb, 1991), willingness to contest (Poole, 1999), competitive ability/rank (Kitchen et al., 2003), age, health status, physical condition, etc. The only possibility that can be excluded is advertisement of location, the only information necessary in systems of mutual avoidance/reciprocation of movements. The hypotheses I advance in this chapter for the function of roars require that the signal announces either RHP or threat. All the possibilities just mentioned fit in one of these alternatives.

#### 5.6.6 Alternative proposals

Apart from a role in an inter-group spacing system, other hypotheses have been put forward for the function of primate loud calls. Next, I consider evidence for or against the application of these hypotheses to explain *A. caraya* loud calls based on my observations, starting with functions suggested for other howler species.

#### **Access to reproductive partners**

Sekulic proposes that *A. seniculus* males use roars in assessment of opponents for access to females (Sekulic, 1982 c; Sekulic & Chivers, 1986). The main evidence is a significantly higher roaring frequency “on days when a competing male was in the troop than on days when no such male was present” (Sekulic, 1982 c, p.44). Also, during inter-troop encounters, “the troop with the larger number of adult/sub-adult males called less frequently than expected by chance than did the troop with the smaller number of males” (Sekulic, 1982 c, p.

45-6). As I have regular data on only one group, it is not possible to test her working hypothesis with my data. Nonetheless, some of my observations are in contrast to her predictions. Apart from the alpha male, the study group had three other adult/sub-adult males. According to Sekulic's proposal, the study group's own males would be the main competitors and the alpha male should direct his aggressive efforts towards them, and not call very often. However, he engaged in frequent calling, and apparently more so than males in the immediately neighbouring troop (pers. obs.). Not only that, but I never observed intra-troop aggression from the alpha male towards the other adult/sub-adult males, even when they constantly harassed the troop females that came into oestrus.

These observations could still be compatible with the hypothesis of assessment of opponents for access to females under a different set of conditions. In some primate species, the main threat towards tenure comes exclusively from outside (Steenbeek et al., 1999; Wich et al., 2002 a, b). In this case, one would expect frequent calling by the dominant male, regardless the presence of other troop males, which would be in accordance with the observed data. However, a similar and strong reaction of the alpha male to the playback of a stranger group independently of the speaker location would be also expected, since the threat would be equal in all places (Wich et al., 2002 b). I observed exactly the opposite in playback experiments. It still remains the possibility that constant calling by a dominant male that counts with subordinate support might be a means of dissuading emigrating males to attempt a take-over. Carefully designed playback experiments could provide a test for this hypothesis.

### **Defence against infanticide**

Results of playback experiments carried out with Thomas langur groups, coupled with natural observations, led researchers to propose that male behaviour, including calling, can be best explained as providing infant defence against infanticide (Wich et al., 2002 a, b). In many respects my results mimic their findings. For example, they also report shorter latency to call and move, and shorter latency to approach the speaker in centre trials compared to border ones. The authors did not find any difference between edge trials carried out in food-containing trees against non-food trees; this is somewhat similar to my result of

lack of difference between trials conducted in quadrats with different intensity of use. Equally, some of their results are also compatible with a resource (territory) defence hypothesis, advocated here to occur during invasions. Remember, however, that I propose that the calling behaviour in such cases does not relate to the defence *per se*, but the approaches and chases are. Although infanticide does occur in *A. caraya* (Rumiz, 1990), I have no information from the study area, and in several species of primate this behaviour is known to vary between different populations. Therefore, to properly evaluate this hypothesis, one has to await detailed, longitudinal data on the study area and/or playback studies specifically aimed to test it.

### **Communication to predators**

Primates also produce loud calls in the presence of a potential danger, e.g. the vocalisations for leopards and eagles of Diana and Campbell's monkeys (Zuberbühler, 2000 a, c, 2001; Zuberbühler et al., 1997). In this case, the researchers proposed a double function for these calls: predator deterrence (by advertising ambush hunters that they have been spotted: see also Byrne 1981) and warning conspecifics of the particular danger. Potential predators, including dogs and humans, can elicit loud calls in howler monkeys, although this is clearly not its commonest usage (Altmann, 1959; Baldwin & Baldwin, 1976; Carpenter, 1934; Sekulic, 1982 c). The predator deterrence hypothesis can almost certainly be ruled out for *A. caraya* roars and barks in this study. Predator presence was neither a necessary nor a sufficient condition for elicitation of loud calls. Despite the high number of loud calls registered during the study, none of them occurred with a potential predator in view. Also, ocelots, which are potential predators of howlers (Carpenter, 1934, Braza, 1980 quoted in Asensio and Gómez-Marín, 2002), were underneath the group in four separate occasions. The monkeys did not produce loud calls in any of these instances, and the same during a possible sighting of a jaguarondi *Felis yaguaroundi*, (a cat smaller than an ocelot). However, the predation pressure from these species is probably very low in the study area, and there is plenty of terrestrial prey. Therefore, these anecdotes must be seen with reserve, and await studies in places with higher predation density. Additionally, I carried out playback trials with various groups,

broadcasting puma and ocelot calls (unpublished data). None of the tested groups produced a single loud call after the playback. It could be counter-argued that the low density of these predators would not expose the animals frequently to their calls, so that the monkeys could know the predator's vocalisations. Despite being a negative argument, it is also very difficult to assess without specific studies, given that many felids (including ocelots) have nocturnal (or cathemeral) hunting habits.

However, I noted an incipient roar in an incident involving a tayra, a potential predator of howler monkeys (Asensio & Gómez-Marín, 2002). In this event, some animals were mobbing the tayra, and on its attempt to escape it went through a route where other members of the group were. A *mêlée* ensued, with many animals vocalising (including vocal types never heard before), and I noticed incipient roars in the confusion. As all animals were aware of the presence of the tayra, the incipient roar was probably a by-product of the excitement caused by the incident. Disturbances to the environment seemed to trigger barks on a few occasions. I observed these calls after startling, caused by cattle running in the forest floor, and in the presence of dogs and humans, and maybe even deer. In some cases an unhabituated group that was roaring switched to barking after spotting a human. As not all these situations represent a potential danger to the animals, and are in contradiction to the lack of calling in the presence of possible predators, it is difficult to interpret the functional significance of the emissions. An alerting function, drawing the attention of the group to an environmental disturbance, does not seem likely. Bark sessions are extremely drawn out, lasting up to an hour and a half, and this length is clearly unnecessary for an alerting signal.

Despite all the counter-arguments and lack of detailed information on predation at the study site, combined evidence from various sources seems to indicate that loud calls, or roars at least, are not particularly used in predation contexts or do not have a function related to predation. Looking at the scant evidence in the literature, it would seem that loud calls are indeed produced in the presence of potential predators. Disturbance by man or dogs is quoted as a common eliciting factor, particularly of barks (Altmann, 1974; Baldwin & Baldwin, 1976; Carpenter, 1934; Sekulic, 1982 c, 1983 b; Thorington et al., 1984). However, the evidence is much more inconclusive when it comes to real

predators. Carpenter (1934) described unusually intense roaring following an ocelot attack, and interprets it as a means of scaring and chasing away the predator. The key point here is that the call was produced during the context of the attack, and therefore was not effective in preventing it. As loud calls are also described to occur in other situations of disturbance (rain, thunder, low flying airplanes, gun shooting, horses, etc.), it seems that the calls during the attack event could well be interpreted as being caused by an extreme disturbance. And despite the fact that the genera is one of the most studied ones, with field studies being conducted in a variety of different places (Kinzey, 1997), as far as I am aware, there has been no report of a clear association of loud calls and presence of predators.

Another possible role for loud calls in relation to predators is honest information on number of adult males in the group, and thus of its capacity to defend against predators (e.g. nocturnal volleys of Guinea baboons, Byrne, 1981), in which case the emission does not need to occur in the immediate presence of the threat. Some conditions need to be fulfilled to advance this suggestion: high predation pressure; potential for defence against predators and variation in the number of males (or in group size) among the troops (Byrne, 1981). Predation risk is certainly low in my study site. Jaguars are practically absent and pumas are quite rare in the area. None of the raptors that prey on monkeys - harpy eagle, crested eagle (Gil-da-Costa et al., 2003; Julliot, 1994)- occur in the Pantanal region. Ocelots and tayras are the only possible predators with a reasonable abundance. Additionally, I did not observe a single predation attempt during the whole study. However, not too much strength should be put on the low predation pressure, as this might be an evolutionarily recent phenomenon, and the behaviour of the animals might reflect their adaptation to original conditions of higher predation pressure. Regarding the second condition, it seems reasonable to assume that howlers have capacity to defend themselves from a few of their possible predators, such as tayra, ocelot, and foxes. Finally, there is variation in the number of males and group size in the study area. I observed troops varying from 1 to 14 animals, with 1 to 4 adult/sub-adult males. Although the conditions seem to be satisfied, this function does not seem to apply to black howlers' loud calls. Predator calls failed to elicit loud vocalisations in the playback trials mentioned, although in the baboon study

predator calls readily elicited loud calling (Byrne, 1981). On the other hand, the extremely long barking sessions are suggestive of an honest indication signal. What is being informed and if it is a message to conspecifics or predators is left open for even further speculation, as barks could be triggered by a variety of events, including, but not restricted to, potential predators.

However, in a discussion of potential functions related to predation, it is necessary to remember that the environment in which most primates live nowadays is impoverished (sometimes heavily so) with respect to predator fauna. This phenomenon at the Neotropics is extremely recent in evolutionary terms, always less than two or three hundred years and often only a matter of decades. Therefore, caution is needed when arguing against a predator-related function. It could be the case that the motivation of animals to call, once including predator presence, was substituted or restricted to other stimuli, given the lack of exposure to predators. Careful playback studies should be conducted, coupled with observations in areas with higher predation density, before more firm conclusions are advocated. Nonetheless, it seems equally plausible to advocate that if an eventual function related to defence against predators is found, this role would be in addition to the one proposed in this study. In addition, one should remember that the vocalisations recorded in this study were mostly spontaneous, which decrease the strength of the argument of stimuli substitution.

## 5.7 Barks

Little can be said with respect to barks, given their rarity: only eight emissions were registered along the main *and* the extra field seasons. As it was the case for the roars, bark emission did not seem concentrated in particular places in the home range. A few of the emissions apparently started spontaneously, whereas others seem to have started after a startling event or the sudden presence of people to whom the group was not habituated. In this respect, it is interesting to note that, when I was recording calls from non-habituated groups, the roar sessions usually turned into barks once the groups noticed my presence. Finally, there seems to be a continuum between staccato calls and barks. Staccatos usually precede and follow bark sessions. When emitted in

isolation, the situation is usually one of surprise, a possible threat or the presence of another animal. The most common eliciting situation for staccatos was when the distance between a human and the animals was too short. Thus, there are some grounds to believe that the call might somehow be related to possible threats to the animals. On the other hand, their extremely long duration points in the direction of an honest indication. Of what and to whom remain open questions.

## 5.8 Conclusion

In this study, I was able to propose some hypotheses on the function of *A. caraya* roars, and also to determine which functions can *not* be played by these calls. In this way, I have greatly narrowed the range of possible functions, providing a solid basis for future studies.

Observational, anecdotal and experimental data point to an inter-group spacing pattern of exclusive use of most of the home range with a small overlap zone. In this context, I propose that roars provide a mechanism for advertisement of occupancy, and an aggressive display during encounters to reinforce occupancy, and provide a way of settling disputes without chases and fights. In contrast, there is enough evidence to suggest that roars do *not* function in a system of mutual avoidance (or reciprocation of movements) nor they operate in conventional and regular reinforcement of border locations.

Among alternative proposals, *A. caraya* do not seem to use roars in assessment of opponent for access of females, but still may help to discourage male immigration and take-overs. Female roars, always produced as an accompaniment to the male emissions, may play a role in reinforcing the pair-bond, and helping to prevent infanticide, but are not used in female-female competition for access to males. An infanticide prevention hypothesis has to await more extensive data collection or experiments designed specifically to test this possibility.

Emission of incipient roars during strong winds and rains may serve as an auditory beacon for the group. Apart from this option, co-ordination of intra-group cohesion is not a possible function for the roars and barks. The following functions are also excluded for roars: broadcasting information on resource localisation; initiation and direction of group movement; predator deterrence; warning co-specifics of predator presence; and honest advertisement (to predators) of the troop defensive potential. *Oodles*, a component of roar sessions, when produced in agonistic contexts, may be indicators of dominance, but other loud calls cannot be.

However, the reader must be cautioned that these results and, more importantly, their interpretation, derive from the study of a single group. Also,

there were many results not easily comprehensible at first and that forced me to develop an explanation that was also not straightforward. Therefore, the hypotheses above should be tested, refined, and modified if necessary, with the study of additional groups, in the study area and in other sites, under different socio-ecological conditions. Only then we can achieve a complete explanation of the function of roars in black howler monkeys.

The variety of functions attributed to howlers loud calls in the literature, to which I added one more example, points to an extraordinary richness and flexibility of usage of a single behaviour. It is particularly striking the diversity of proposals related to a general category of functions, that is, inter-group spacing. It would be interesting to verify if the inter-specific variation is mimicked within species. Regardless, it seems that the genus *Alouatta*, once considered uniform, is showing as much variability as exhibited by Old World monkey genera, and in diverse aspects of its behaviour and ecology.

## CHAPTER 6: GENERAL DISCUSSION

### 6.1 Importance of vocal behaviour

Howlers, as every group living species, encounter many situations during their daily activities in which communication is highly advantageous. Given their usually cohesive nature, such that the visual channel could in principle fulfil many of their communicative needs, we might expect vocalisations to be relatively less prominent. However, the howler monkeys observed in this study proved to be highly vocal animals, even without including loud calls. Considering only the soft vocalisations that I analysed (*moos* and *screech* complex calls), the group produced nearly 17000 calls, and this figure (probably underestimated, given the limitations mentioned along the thesis) gives an average of a call at approximately every 5 minutes of daylight. If we add up two call types commonly emitted and not analysed (*mutterers* and *snarls*), this figure would be much higher. And since howlers spend a great deal of the day actually sleeping, the frequency of vocal emissions during active hours is even higher. This fact alone indicates the importance of the acoustic channel in the communication system of howlers, and in their natural history.

### 6.2 Soft calls

One of the problems every group-living animal must face to a more or less intense degree is the one of maintaining the cohesiveness of the group. For that end, some mechanism must be in place that helps animals to maintain contact with each other, or to regain lost contact. For *Alouatta caraya*, one of their most commonly emitted call types (*moo*) seems to be part of such a mechanism. Individuals capable of independent travel produced this call in a variety of circumstances. However, the call was emitted significantly less often during feeding and with a trend towards higher frequency during travel. Furthermore, group diameter during call emission was significantly larger than baseline values, and group spread decreased after emissions much more often than it increased. These results indicate that the call is produced during

circumstances in which keeping in contact is more essential, not emitted when it contact is not critical, and that it might help to bring the group to a more cohesive state. A series of anecdotal observations also added evidence towards a contact function for this call. In many cases, it looked as if only the animals needing to re-establish contact were producing the call, which would agree with the findings in baboons (Cheney et al., 1996; Rendall et al., 2000). However, in some other cases I also had the impression that they could be answering to the calls of other animals.

The possibility of a contact function opens exciting avenues for investigation. First, one could address the possibility of the existence of *moo* variants. If these are found, then it would be possible to focus on the relation between specific contexts or situations and the variants. If however the call is indeed a single type, then it would allow investigating which particular suite of circumstances stimulate call production. This is especially relevant for contact calls, given the possibility to study intentionality and the mechanisms through which the contact function is achieved. For the study of these issues, the use of playback experiments (on the lines pursued with the baboon studies quoted above) would be particularly interesting.

Immature animals also produced *moos* in a completely different set of circumstances. Individuals at the early stages of development face different problems than older animals and also some similar ones but with a different perspective (e.g. being fed, instead of finding food). Many of these differences relate to their status of dependency in many spheres of their everyday lives (feeding, travelling, etc.). It is thus obvious that for immatures being able to communicate their needs or their status is highly advantageous, as it allows the mother or other care-takers to take appropriate action or respond in positive ways.

Immature individuals, in particular completely dependent infants and infants starting independent travel, emitted *moos* in situations indicative of distress or anxiety. In fact, *moos* were significantly associated with the period in which anxiety was presumed to be higher. This occurred (1) before the solution to the problem of facing a gap between branches too wide to be crossed by their own means; (2) before riding the back of a carrier; and (3) after a conflict of interest (i.e. when they were prevented from attaining a goal or had an action or

stable state interrupted). However, I found no difference in call production before and after another potential context of anxiety: when mothers left their infants. Several *ad libitum* observations corroborate the association with “gap problems”. My informal observations also suggested that emissions occurred with a particular temporal pattern (after a series of *screeches* or in the build up to such a series). This pattern, together with *moos*’ lower amplitude than *cries*, and their lower rate of emission when compared to *screech* sessions, combine to suggest that the call is triggered by lower levels of anxiety, and maybe with a degree of context specificity.

Given the context with which the calls were most clearly associated in immatures (“gap problems”), I speculate here that there might be a similar motivational state behind call production in gap situations and the more typically adult emission. When facing a wide gap, the infant might be attempting to maintain contact, or might fear losing contact with other animals, which are not within reach or may be actually distancing themselves. Similarly, older animals attempting to maintain or regain contact might be experiencing similar emotional states of anxiety to an infant attempting to cross a gap. Admittedly, testing this hypothesis is not easy. Maybe the ontogenetic study of the production and usage of the call from individuals since they are born until they reach adulthood could provide some hints, particularly during transitional phases.

But the youngsters did not emit just *moos* during distressful situations. A set of structurally related calls (*screeches*, *cries*, and *screech-cries*) was also associated with these contexts, but each in a slightly different way. Like *moos*, all three vocalisations were also uttered more often before than after the solution to “gap problems”. However, only *screeches* occurred significantly more often after conflicts of interest. When studying the event “invitation to play”, the time from the start of the invitation to the first call after it was significantly shorter than the time since the previous call, for all three vocalisations. However, *screech-cries* were the calls emitted more often in this context. Along with anecdotal observations, these results indicate that each of the call types relates to a slightly different set of circumstances, and performed somewhat different roles. Thus, *screeches* seemed to be emitted in situations where the individual needed or wanted help or care, or in which access to a desired item was hindered; *cries* appeared to be particularly produced during more intense or prolonged stress;

and *screech-cries* seem to represent mild or defensive threats or submissive signals. However, transitions seemed to exist between most of these types, including the *moos*, and it was also common to have more than one call type produced on a given situation. Given this ambiguity between the specificity and generality of call production and also the existence of transitional types, these vocalisations constitute a good model to study call perception, that is, if the animals perceive them categorically or continuously. It would also be worth investigating if there is some simple syntactic rule behind their production.

Whichever the case regarding their production or perception, the fact is that the four call types produced in distressful situations all possess an important role in the natural history of howlers. In the case of immatures (responsible for the vast majority of emissions), these calls signal to the mother (and to other care-givers), that the individual is in a state of distress or discomfort. In many cases this seemed to be due to a physiological need (e.g. hunger), or to a more practical one (wide gap). The action taken by the care-taker can be informed either through a more specific relation between call type and situation, or, if the calls are non-specific, through supplementary information provided by the context itself. The advantage of this kind of signals is such that, as far as I am aware, similar calls have been found in every species of primate whose vocalisations have been described.

However, some emissions of calls of the *screech* complex occurred in circumstances that allowed me to conclude that they could also indicate uneasiness, submission or an ambivalent state (mild threat/submission). The contexts included: sequences of *screeches* during begging (particularly when an infant/juvenile was attempting to interact with a newborn being held by the mother) and emissions of *screech-cries* during invitations to play and approaches by a dominant (the last one the most common circumstance of *adult* call emission). Although still related to a potentially distressing context, however mild, these calls apparently performed a completely different social function than signalling a need. They belong to the group of signs that regulate social interactions. This class of signals is extremely important for the individuals to adjust their behaviour and prevent unnecessary risks of more serious agonistic interactions. For example, an individual can prevent an attack by indicating its submissive status when approached, or can warn that it is willing to escalate by

showing uneasiness during an interaction. If these additional ultimate functions are performed by calls which are structurally distinct and were here lumped under a single label, or if the difference in meaning is informed by the context is a matter for future studies.

### 6.3 Loud calls

Apart from such everyday, immediate problems, howlers also face longer term ones with which they must cope: control of access to resources, defence against predation or infanticide, etc. For many of these problems, the main interactants are usually outside the group, and it is in this arena that the functions of loud calls must be sought. Observational and experimental evidence gathered in this study indicates that the ultimate function of the roars of the studied group is to help regulating the use of space between troops.

The group was able to secure a large exclusive area, with overlap occurring at a narrow stretch at the borders. I proposed the hypothesis that the regulation was achieved through a dual mechanism: constant announcement of occupancy and a display providing an assessment mechanism during disputes.

The spontaneous sessions of calling, which comprised the bulk of the occurrences, would serve to define the territory area to neighbours via a constant announcement of occupancy. The evidence for that includes the frequent lack of a clear event that could trigger the call, and even when this was sometimes found (meteorological events), the events had nothing to do with the addressees themselves. Call production was also clearly related to dawn, with the first registered call in the vicinity of the group being strongly influenced by sunrise time. Furthermore, the group produced loud calls from quadrats situated at very different places in the home range, including core locations (well inside the range), border areas and places within the overlap regions. Calling frequency did not clearly associate with particular regions, but definitely was not concentrated at the borders. Thus, the calls were emitted spontaneously, or influenced by abiotic events, and from a variety of places within the home range. The production of loud calls after experimentally simulated invasions of their home range also supports the announcement of occupancy function. During these trials,

the animals called after the playback much more often than one would predict for the time of the day when the experiments were conducted, something that did not occur when the speaker was situated on the overlap area. Furthermore, in the invasion trials, the calls were significantly closer to the playback time, and tended to be emitted close or after the speaker location, when compared to the overlap trials. However, roars were not produced immediately after the playback, but at least 40 minutes after it. As the invading group was obviously not present, this pattern was interpreted as a sign of reassurance of occupation of an exclusive area.

When researchers observe patterns of loud call emission like the one in this study (i.e. spontaneous and spread over the range), they usually suggest a mechanism of regulation of space use by which the animals mutually avoid or reciprocate each other's movements, based on the locational cues of the signal. This system has been explicitly proposed for another howler species, *Alouatta palliata* (Baldwin & Baldwin, 1976; Chivers, 1969; Whitehead, 1987). Such system usually involves a considerable overlap in the home range, something not observed. Also, if a mutual avoidance system were in place, the animals should avoid or move neutrally with respect to the simulated presence of stranger groups, irrespective of the speaker location in the home range. Comparing trials conducted inside the home range (simulating an invasion) with ones conducted in overlap regions, the alpha male started moving sooner after the playback, and approached the speaker more often in the invasion condition. In contrast, after overlap trials, and also after the few trials conducted outside the home range, the group generally ignored the playback and kept sleeping. These results allowed me to discard another mechanism of regulation of space use, mutual reinforcement of boundary locations. Under that system, the animals would be expected to react strongly to the invasion condition, but also to approach and counter-call after overlap and outside trials, as this is the behaviour of species for which a system of mutual reinforcement of the boundary location was proposed such as titi monkeys and gibbons (Robinson, 1979 b, 1981; Tenaza, 1976).

However, inter-group encounters did occur, and some of these were protracted events accompanied by intense and various roar sessions. It was rare to observe neighbour groups close by that did not interact vocally. However, in a few instances, two groups were noted at medium distances, and then seemed to

ignore each other. As these events occurred in the border regions, they constitute further evidence against a system of constant mutual reinforcement of boundary location. The behaviour during different encounters seemed contradictory at first, as the animals sometimes just battled vocally, in other occasions there were chases followed or preceded by loud calls, in others still only one group called, apart from the occasional lack of interaction of groups at medium distances. However, the differences can be understood if the animals were using the loud call as display to avoid fights. It is true that in some of the cases, the behaviour is also consistent with reassurance of occupation (e.g. giving loud calls after a chase; and exchange of loud calls at medium distance), without necessarily implying a display to *settle* a contest. In others, however, the behaviour seems better interpreted as a display that can be used during territorial contests (particularly in close inter-group encounters), especially because the consequences were variable (one or both could retreat, chases could occur or not after a call). Variability is expected in display situations, as the interactants can vary either in the traits being assessed (if the call provides assessment of some characteristic of the resource holding power) or in the costs/benefits involved in the contest (in case of a call signalling threat of injury). For both of the mechanisms proposed (definition of the territory and displays during encounters), the data was insufficient to advance a hypothesis on the proximal function of the call, i.e., the information encoded in the signal.

#### 6.4 Relation with broader theoretical issues

In this topic, I will discuss the relation of my findings to broader issues, mentioned in the introduction. As dealing with these questions was not the main purpose of the thesis, the discussion will be speculative. I intend here merely to show possible avenues for investigation and stimulate further discussion and research.

#### 6.4.1 Informational content of vocalisations: affective or referential?

Looking at the soft calls that were studied (*moos* and the *screech* complex), it seems difficult to imagine that they are in any way referential. However, as we shall see, to consider this issue properly, more in-depth studies should be conducted. Considering first the suggested contact role for the *moo* calls, the scepticism might arise both from the observations themselves and from the literature. To start with, there was only a slight indication that sub-types of *moo* calls might exist, and no suggestion whatsoever of association with different circumstances. In fact, it was puzzling the range of circumstances and contexts in which *moos* (apparently a unitary call type) were emitted, something already noted in other studies of contact calls (see Caine & Stevens, 1990; Robinson, 1982). Additionally, none of the published researches on contact calls suggest a referential content to them. In fact, the issue is not even considered as a possibility. However, this very aspect shows that the question merits more careful consideration that has been given. Looking at the calls from the *screech* complex, as well as emission of *moos* by infants, the situation is rather ambiguous, and also deserves more careful investigation. On one hand, there are hints that the calls might reflect different distress levels, or even be indicators of different emotional states. However, there were also clues that there could be some degree of context specificity, as for example the seemingly stronger tendency towards emission of *moos* when immatures were facing a large gap, to the expense of the other calls. Given that it was very common the emission of more than one of these infant/juvenile calls on a given situation, it is interesting to consider together the issues of referentiality and syntax (see below).

To investigate the possibility of a referential content, it is recommended the classic paradigm of coupling a preliminary observational phase with playback experiments. In the observational stage, the purpose is to investigate first the existence of sub-types or clear boundaries between the types. Then, one can verify the occurrence of consistent association between these types and clearly defined referents, contexts or situations of use, so that listeners could obtain information solely on the basis of the calls. If the observational step is successful, then it is necessary to confirm the results with playback experiments, which can take a variety of forms. For example, one can verify if responses to the playbacks

mimic natural responses. Another possibility is the use of a habituation-dishabituation paradigm, using one sub-type in the habituation phase, and changing it to verify the reaction of the test subjects.

There are also two other kinds of vocalisations which have proved very fruitful in demonstrating referentiality: alarm calls and agonistic screams. With respect to alarm calls, nothing can be said on the basis of the present study. No predation attempts were ever observed, and very few potential predators were seen in the vicinity of the group. To investigate this possibility, one should look at a population of howlers, maybe even of another species of the genus, which lives on an area with a higher predator density. Not only that, but different categories of predators should be present, particularly felids and harpy eagles, so that one could unambiguously address the possibility of referential alarm calls and make a parallel with the African species (Seyfarth et al., 1980 a, b; Zuberbühler, 2000 b, c, 2001). Regarding agonistic screams, the problem lies on the low rate of overt aggressive interactions, and the only solution is the study of different groups for longer periods of time. Additionally, considering the tight nature of howler groups, maybe there was no “evolutionary need” to evolve a system of screams labelling different interactions as in rhesus monkeys (Gouzoules et al., 1984) or different roles as in chimpanzees (Katie Slocombe, pers. com.). After all, the animals usually have full visual access to the social interactions occurring within the group.

#### *6.4.2 Intentionality in call production*

The problem of intentionality has been particularly studied with contact calls, since in many cases there seems to be a system of call-and-answer in place. Nonetheless, to the moment, the evidence indicates that supposed responses are actually a consequence of the state of separation of the respondent itself, and not an answer (Cheney & Seyfarth, 1999; Cheney et al., 1996; Rendall et al., 2000; Seyfarth & Cheney, 2003). Then, it is concluded that the calls are not emitted with the intent of maintaining contact or informing the whereabouts of the group to the separated animal(s). However, contact calling may involve a first-order intentionality, which does not require theory of mind (Byrne, 2000).

As described in Chapter 3, with respect to the contact role of *moo* calls, there were anecdotal observations indicating the existence of a call-response system in place, and involving other call types as well (*mutters* and *oodles*). Although the data do not allow extrapolating and addressing the intentionality issue, these observations do indicate the potential to use this call type in studying the problem. Careful consideration of the situation of the first caller and the respondents, as well as playback designs similar to the ones used in baboon studies (Cheney et al., 1996; Rendall et al., 2000) are both important in such studies.

#### 6.4.3 Syntax, grammar and conversation rules

As briefly mentioned in Chapter 4, the calls of the *screech* complex, together with infant *moo* calls, provide the best case to investigate the possibility of simple grammar rules in the repertoire of black howlers. While conducting field work, I got the general impression that there was an ordering of emission in some drawn-out sequences. Thus, in many cases, a long string of *screeches* was punctuated by a *moo*. In other cases, the sequences seemed to evolve to a long *cry*, particularly when the infant/juvenile seemed highly distressed. Strings of *moos* also seemed to turn into *screeches* if the stressful situation was not overcome. Now the task for future studies is to confirm if there are in fact rules governing sequences of calls, and then investigate if there is an association of particular sequences or rules to specific contexts/situations/states.

With respect to conversational rules, I gathered a few anecdotal observations (on calls not analysed in this thesis) which are worth pursuing in more detail. Thus, for example, it was very clear the emission of volleys of *mutters* during feeding sessions. These volleys, however, were produced by different individuals. Each bout was triggered by the call of one animal, after which a couple of others would call in very close succession. Thus, the task here is to verify if there are “starters” and “followers”, and if there are rules for the sequences, similar to the ones observed for pigmy marmosets (Snowdon & Cleveland, 1984). Also interesting is the emission of *snarls* during playing bouts. When two individuals were playing, particularly the sub-adult males, they

usually emitted *sarls* continuously. To the human ear, the sounds seemed composed of pulses of different amplitude and tonal quality. Although very difficult to verify, it would be interesting to investigate if there are rules behind the production of such pulses. If confirmed, this rule could be hypothesised to regulate the play bout.

#### 6.4.4 Graded and discrete vocal repertoires

As emphasised in the introduction, this dichotomy may be a false one, but the distinction has given impulse to the discussion on how stimuli are perceived by animals. The repertoire of the black howlers, as a whole, seems composed of relatively discrete types, especially considering the disparity between the loud and the soft calls. However, looking at the situation more carefully, there seems to be gradations between many of the types. Thus, for example, there might be intermediate types between the different calls of the *screech* complex, and also with *moos*. Additionally, some long sessions of barks usually started with a soft call (*staccato*). These small amplitude vocalisations slowly gained intensity and at some point the animal started barking. Thus, even the distinction between soft and loud calls became blurred in these cases. These examples show the need for two kinds of studies. The first, which will be a follow-up from this thesis, is a very detailed description of the whole repertoire, performing discriminant analyses to check for the reality of the types. In passing, it will be also interesting to check for the existence of undetected sub-types. If some types do prove to lie along a graded continuum, then one could conduct a study on how the animals perceive the stimulus, if continuously or in a discrete way (see Snowdon & Pola, 1978).

#### 6.4.5 Honest signalling: the case of loud calls

Perhaps one of the topics to which howler monkey vocalisations could make an important contribution is the one on honest signalling. It has been suggested before that *Alouatta palliata* loud calls do provide honest information on distance and movement direction (Whitehead, 1987, 1989 a, b). However,

given the characteristics of howlers' loud calls, the anatomical commitment, and the functions most commonly ascribed to their roars and barks, I believe that there is much more to investigate on this question. Considering the ultimate functions most commonly ascribed to the loud calls of primates, there are three main possibilities (not mutually exclusive) for a proximate function: honest information of resource holding potential (RHP); announcement of threat of injury; and announcement of presence/location. Given the extremes of loudness, pitch (the very low pitch is even more impressive due to the size of howlers, which are not large animals), and duration, one is inclined to think that there is a high chance of them being honest indicators of RHP. But, apart from demonstrating that this is the case, it also remains to be investigated exactly which attribute is being informed and through which physical parameter(s) of the calls (see Bee et al., 1999; Kitchen, 2004; Kitchen et al., 2003; McComb, 1991; Poole, 1999; Reby & McComb, 2003; Wilczynski et al., 1993). The possibilities here are numerous, and to illustrate the point I outline some suggestions. For example, the pitch of the lower formant could provide an indication of the size of the caller, as in the case of red deer (Reby & McComb, 2003). The duration of the session might provide an indication of the stamina of the male (as in the baboons studied by Kitchen et al., 2003), or of its health condition. The intensity of the call could also give an indication of the stamina or health condition, or maybe even of the animal's strength, given the forces that are necessary to produce such loud calls.

## 6.5 Final remarks

In this study I was able to show the role that some soft call types play in the lives of a group of black howlers, and to suggest hypotheses for the function of their loud calls. Both aspects of the study demonstrate the vital importance of vocal communication in the natural history of the black howler monkeys, and the relevance of its study. Nevertheless, the results presented in the thesis and summarised here open more questions than they answer, and some were indicated along the data chapters. In the sections above, I also indicated further

questions and areas of research of a more broad nature which could profit from a more detailed study of a given call type.

I hope that the data presented on loud calls stimulate both further theoretical discussions, and observational and experimental work. The methodological approaches that I used with the soft calls were found useful in improving understanding of call function. If these methods, the study designs proposed and the lines of research just pointed also prove to be helpful for studies of soft calls of this and other species, in attempts to go further than the anecdotal description of contexts of use, that would be a major achievement.

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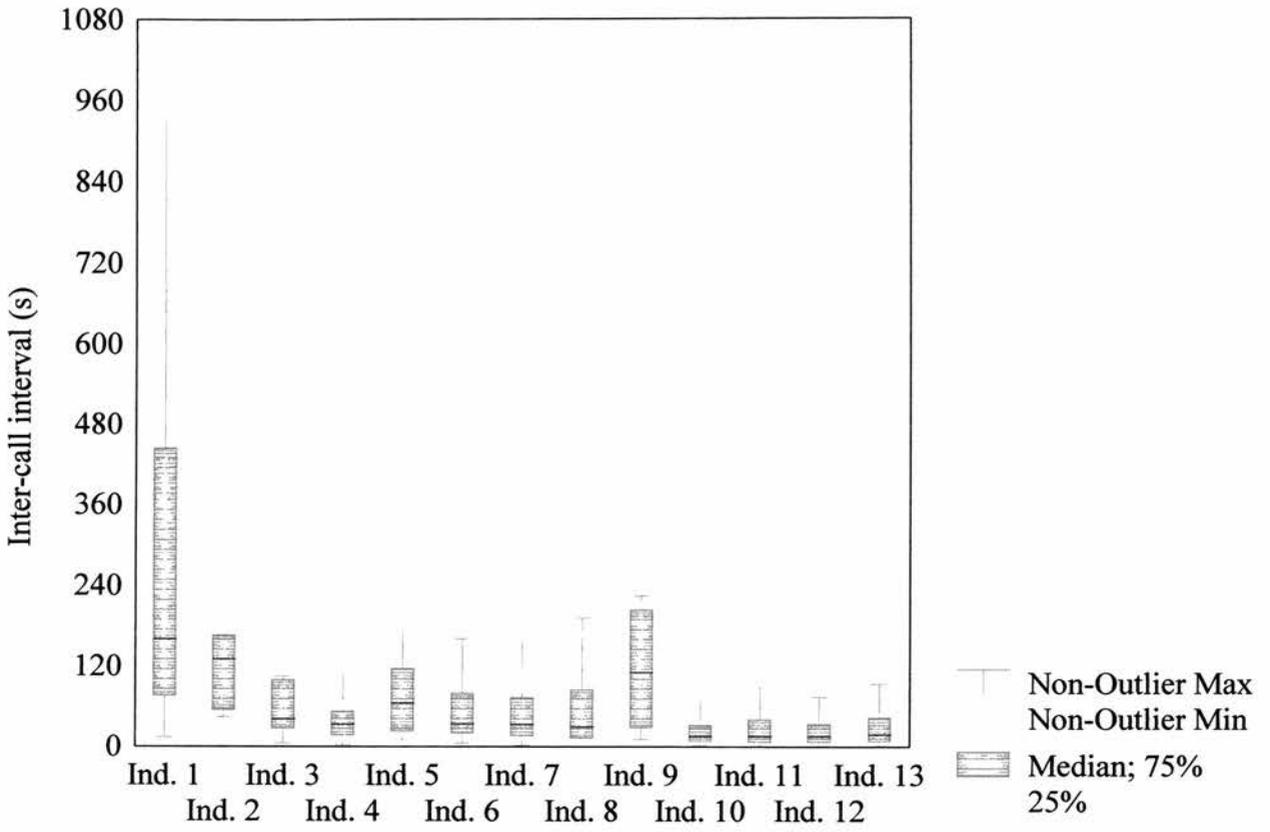
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## APPENDIX 1: INTERVAL BETWEEN SUCCESSIVE MOOS

On this appendix, I will present the data on intervals between consecutive emissions of moos that I used in for the establishment of the independence criterion for this vocalisation. Recall that the first step was the extraction of all inter-call intervals of each individual. I did this both considering their focal files only, and also using all data files. The risk of not registering a call of an animal is higher for non-focal individuals. Thus, the data extracted using all files might present a bias towards longer intervals, and generate a more conservative estimate of the independence criterion. After having a distribution of all intervals for each animal, the initial criterion I had chosen was to calculate the third quartile of each individual and then use the more conservative of the individual values. Starting with the data extracted from all data files, as the third quartiles varied considerably between individuals (Figure A-1.1), I adopted a compromise solution, choosing a value of 120s. This value was higher than the third quartile for almost all individuals (especially the ones with a high sample size) and it covers circa 40% of the inter-call intervals of male 1 (see Table A-1.1). Individuals 2 and 9 presented small sample sizes, and thus higher chances of biases. Nonetheless, the chosen value closely approximates the median for these individuals. Note that for the individuals with larger sample sizes (individuals 10-13), the independent criterion covers the majority of inter-call intervals, and the distributions is highly concentrated, which matches field observation of them having long bouts of calls in close succession. The data extracted from the focal files is very similar (see Figure A-1.2). Contrary to predictions, the distributions are more spread for the focal data. Still, the criterion used seems a good compromise and it is above the third quartile for the individuals with larger sample sizes (Table A-1.2). Note the considerable reduction in sample sizes, which gives more credit to the estimate using data from all files.

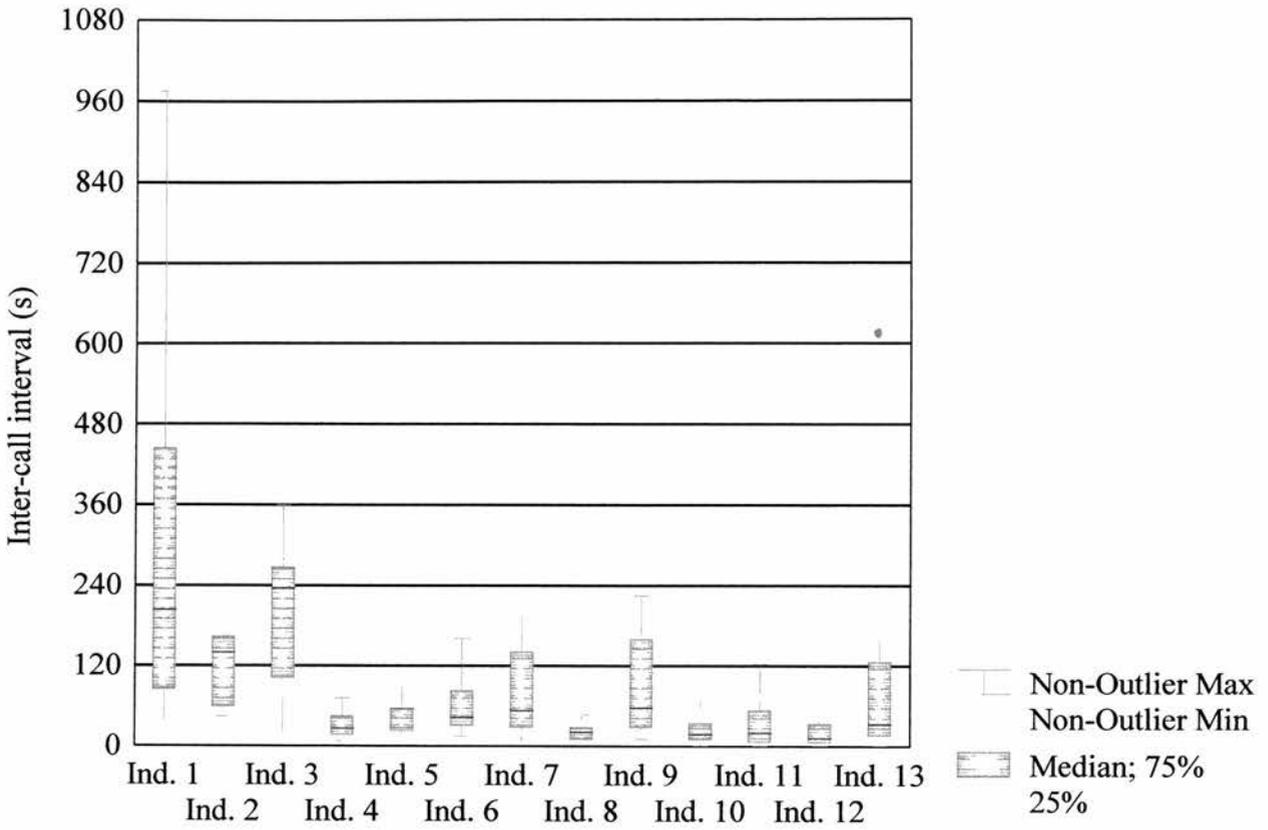


**Figure A-1.1. Box plot of intervals between consecutive emissions of moos of each individual, using data extracted from all files.**

**Table A-1.1. Descriptors of the distribution of inter-call intervals of each individual, using data from all files.**

| Individual        | Median (s) | 3 <sup>rd</sup> Quartile (s) | Percentage <sup>a</sup> | N    |
|-------------------|------------|------------------------------|-------------------------|------|
| 1 (Ad. ♂)         | 160        | 425.5                        | 40.4                    | 47   |
| 2 (Ad. ♂)         | 130        | 166                          | 46.7                    | 15   |
| 3 (Sub-ad. ♂)     | 40.5       | 99                           | 81.3                    | 32   |
| 4 (Sub-ad. ♂)     | 33.5       | 52.5                         | 87.3                    | 110  |
| 5 (Ad. ♀)         | 64.5       | 115.25                       | 77.8                    | 36   |
| 6 (Ad. ♀)         | 34         | 80                           | 83.3                    | 114  |
| 7 (Juv. ♀)        | 33         | 70.5                         | 82.6                    | 155  |
| 8 (Juv. ♀)        | 29         | 82.5                         | 77.5                    | 71   |
| 9 (Sub-ad./Ad. ♀) | 110        | 181.5                        | 53.3                    | 15   |
| 10 (Inf./Juv. ♀)  | 15         | 32                           | 91.4                    | 847  |
| 11 (Inf./Juv. ♀)  | 15         | 40.25                        | 90.0                    | 912  |
| 12 (Inf./Juv. ♂)  | 15         | 33.75                        | 91.6                    | 2478 |
| 13 (Inf. ♀)       | 18         | 43                           | 86.8                    | 402  |

<sup>a</sup> Percentage of inter-call values that fall below the criteria of 120s. N = sample size



**Figure A-1.2. Box plot of intervals between consecutive emissions of moos of each individual, using data extracted from focal files only.**

**Table A-1.2. Descriptors of the distribution of inter-call intervals of each individual, using data from focal files only.**

| Individual        | Median (s) | 3 <sup>rd</sup> Quartile (s) | Percentage <sup>a</sup> | N   |
|-------------------|------------|------------------------------|-------------------------|-----|
| 1 (Ad. ♂)         | 193.5      | 406.25                       | 34.6                    | 26  |
| 2 (Ad. ♂)         | 130        | 160.5                        | 45.5                    | 11  |
| 3 (Sub-ad. ♂)     | 169        | 267                          | 50.0                    | 4   |
| 4 (Sub-ad. ♂)     | 26         | 44.5                         | 88.0                    | 50  |
| 5 (Ad. ♀)         | 55         | 56                           | 100.0                   | 5   |
| 6 (Ad. ♀)         | 43         | 80.5                         | 80.8                    | 26  |
| 7 (Juv. ♀)        | 53         | 140.75                       | 71.4                    | 28  |
| 8 (Juv. ♀)        | 20         | 28                           | 100.0                   | 13  |
| 9 (Sub-ad./Ad. ♀) | 52.5       | 151.5                        | 60.0                    | 10  |
| 10 (Inf./Juv. ♀)  | 18         | 35                           | 88.3                    | 326 |
| 11 (Inf./Juv. ♀)  | 19.5       | 54                           | 86.1                    | 266 |
| 12 (Inf./Juv. ♂)  | 12         | 34                           | 88.2                    | 338 |
| 13 (Inf. ♀)       | 32.5       | 125.5                        | 75.0                    | 16  |

<sup>a</sup> Percentage of inter-call values that fall below the criteria of 120s. N = sample size.

## APPENDIX 2: INFORMATION ON EXPERIMENTAL TRIALS

Table A-2.1. Basic information about the experimental trials.

| Experiment number | Date      | Playback time | Condition | Potential problem <sup>a</sup>                      | Speaker quadrat | Intensity of use – year (%) <sup>b</sup> | Intensity of use – month (%) <sup>c</sup> |
|-------------------|-----------|---------------|-----------|---|-----------------|--|---|
| 1                 | 09-Aug-02 | 11:05         | Invasion  |   | F5              | 2.45                                     | 2.19                                      |
| 2                 | 22-Aug-02 | 7:30          | Invasion  | Longer playback (2 min.); short stay after playback | J7              | 2.78                                     | 3.28                                      |
| 3                 | 28-Aug-02 | 9:00          | Overlap   | Short stay after playback                           | O9              | 0  | 0   |
| 4                 | 05-Sep-02 | 11:31         | Invasion  |   | F6              | 0.71                                     | 0.97                                      |
| 5                 | 09-Sep-02 | 10:55         | Overlap   |   | A5              | 2.73                                     | 7.7                                       |
| 6                 | 15-Sep-02 | 11:10         | Overlap   |   | A6              | 0.5                                      | 1.85                                      |
| 7                 | 19-Sep-02 | 14:43         | Invasion  |   | C3              | 0.91                                     | 0   |
| 8                 | 27-Sep-02 | 11:59         | Outside   |   | A3              | 0.02                                     | 0   |
| 9                 | 01-Oct-02 | 11:50         | Overlap   | Double playback                                     | alfa7           | 0.57                                     | 2.33                                      |
| 10                | 08-Nov-02 | 11:08         | Invasion  |   | D5              | 3.67                                     | 5.15                                      |
| 11                | 12-Nov-02 | 13:15         | Invasion  |   | F4              | 4.36                                     | 2.19                                      |
| 12                | 23-Nov-02 | 11:00         | Overlap   | Double playback                                     | A4              | 0.62                                     | 1.68                                      |
| 13                | 25-Nov-02 | 12:31         | Outside   |   | A8              | 0.05                                     | 0   |
| 14                | 28-Nov-02 | 11:45         | Invasion  |   | K8              | 0.19                                     | 0.13                                      |
| 15                | 19-Dec-02 | 12:35         | Invasion  |   | E3              | 1.07                                     | 0.77                                      |
| 16                | 17-Jan-03 | 12:25         | Invasion  |   | J5              | 0.05                                     | 0   |
| 17                | 20-Jan-03 | 13:40         | Invasion  |   | F4              | 4.36                                     | 2.72                                      |
| 18                | 24-Jan-03 | 12:36         | Overlap   |   | L9              | 0.99                                     | 1.72                                      |
| 19                | 27-Jan-03 | 9:46          | Invasion  |   | G4              | 1.52                                     | 0.14                                      |

|    |           |       |          |       |      |      |
|----|-----------|-------|----------|-------|------|------|
| 20 | 30-Jan-03 | 9:11  | Invasion | C5    | 4.32 | 0.29 |
| 21 | 03-Feb-03 | 12:10 | Invasion | F4    | 4.36 | 2.72 |
| 22 | 06-Feb-03 | 12:26 | Invasion | D4    | 2.36 | 6.02 |
| 23 | 12-Feb-03 | 15:23 | Invasion | D5    | 3.67 | 0.72 |
| 24 | 16-Feb-03 | 11:55 | Invasion | B5    | 3.52 | 2.01 |
| 25 | 20-Jul-03 | 13:16 | Overlap  | alfa5 | 0.42 | 1.8  |
| 26 | 22-Jul-03 | 10:34 | Outside  | N9    | 0.41 | 0    |
| 27 | 24-Jul-03 | 11:30 | Overlap  | alfa6 | 1.21 | 3.6  |
| 28 | 26-Jul-03 | 13:42 | Outside  | O9    | 0    | 0    |
| 29 | 28-Jul-03 | 11:53 | Overlap  | alfa6 | 1.21 | 3.6  |
| 30 | 02-Aug-03 | 12:03 | Overlap  | alfa4 | 1.22 | 1.88 |
| 31 | 11-Aug-03 | 15:51 | Overlap  | N10   | 0.29 | 0    |
| 32 | 14-Aug-03 | 11:41 | Outside  | ?     | 0    | 0    |
| 33 | 19-Aug-03 | 12:30 | Overlap  | M9    | 0.44 | 0    |
| 34 | 21-Aug-03 | 13:55 | Overlap  | N10   | 0.29 | 0    |
| 35 | 23-Aug-03 | 15:18 | Invasion | H5    | 7.51 | 0.84 |

<sup>a</sup> Short stay after playback indicates that I did not stay continuously with the animals until the end of the day; Double playback indicates the instances where I played back twice to the animals. Use of commercial tape players indicate a change in the playback apparatus for commercial players due to malfunctioning of the main equipment.

<sup>b</sup> Intensity of use of the quadrat in which the speaker was positioned along the year (data corrected using an average of monthly values).

<sup>c</sup> Intensity of use of the quadrat in which the speaker was positioned during the month in which the experiment was conducted.

Table A-2.2. Information about the variables related to calling behaviour on each trial.

| Exp. number | Condition | Loud call before PL <sup>a</sup> | Latency from the last call (min.) <sup>b</sup> | Loud call after PL <sup>c</sup> | Special conditions <sup>d</sup> | Latency to the first call (min.) <sup>e</sup> | Location of the call after the playback <sup>f</sup> |
|-------------|-----------|----------------------------------|--|---------------------------------|---------------------------------|---|--|
| 1           | Invasion  | Roar                             | 299  | Roar                            |                                 | 52  | At the site  |
| 2           | Invasion  | No                               |  | Roar                            |                                 | 453   | Overshoot  |
| 3           | Overlap   | No                               | 162  | No                              |                                 |   |  |
| 4           | Invasion  | Roar                             | 213  | Roar                            |                                 | 43  | At the site  |
| 5           | Overlap   | Roar                             | 267  | Roar                            |                                 | 176   | Neutral  |
| 6           | Overlap   | No                               |  | No                              |                                 |   |  |
| 7           | Invasion  | Roar                             | 368  | Roar                            |                                 | 55  | At the site  |
| 8           | Outside   | No                               |  | No                              |                                 |   |  |
| 9           | Overlap   | No                               |  | No                              |                                 |   |  |
| 10          | Invasion  | No                               |  | No                              |                                 |   |  |
| 11          | Invasion  | No                               |  | Roar                            |                                 | 87  | At the site  |
| 12          | Overlap   | No                               |  | Bark                            |                                 | 343   | Neutral  |
| 13          | Outside   | No                               |  | Roar                            |                                 | 105   | Before   |
| 14          | Invasion  | No                               |  | Roar                            | Rain                            | 301   | Neutral  |
| 15          | Invasion  | No                               |  | Roar                            |                                 | 68  | Overshoot  |
| 16          | Invasion  | No                               |  | No                              |                                 |   |  |
| 17          | Invasion  | No                               |  | Roar                            |                                 | 46  | Overshoot  |
| 18          | Overlap   | No                               |  | Roar                            |                                 | 251   | Neutral  |
| 19          | Invasion  | Roar                             | 135  | Roar                            |                                 | 61  | Neutral  |
| 20          | Invasion  | No                               |  | Roar                            |                                 | 69  | Overshoot  |
| 21          | Invasion  | No                               |  | No                              |                                 |   |  |
| 22          | Invasion  | Roar                             | 245  | No                              |                                 |   |  |
| 23          | Invasion  | No                               |  | No                              |                                 |   |  |
| 24          | Invasion  | Roar                             | 372  | No                              |                                 |   |  |

|    |          |      |     |      |     |         |
|----|----------|------|-----|------|-----|---------|
| 25 | Overlap  | No   |     | No   |     |         |
| 26 | Outside  | No   |     | No   |     |         |
| 27 | Overlap  | Roar | 266 | Roar | 349 | Neutral |
| 28 | Outside  | No   |     | No   |     |         |
| 29 | Overlap  | Roar | 307 | No   |     |         |
| 30 | Overlap  | No   |     | No   |     |         |
| 31 | Overlap  | No   |     | No   |     |         |
| 32 | Outside  | No   |     | No   |     |         |
| 33 | Overlap  | No   |     | No   |     |         |
| 34 | Overlap  | No   |     | No   |     |         |
| 35 | Invasion | No   |     | No   |     |         |

<sup>a</sup> Indicates the occurrence and type of loud call before the playback.

<sup>b</sup> Time in minutes from the end of the call before playback, when emitted, to the start of the playback.

<sup>c</sup> Indicates the occurrence and type of loud call after the playback.

<sup>d</sup> Occurrence of circumstances that normally elicit loud calls during or before the loud calls produced *after* the playback

<sup>e</sup> Time in minutes from the playback to the start of the first loud call after it, when emitted.

<sup>f</sup> Location of the tree in which the group produced a loud call session after the playback with respect to the position of the speaker, according to the categories defined in Chapter 5.

Table A-2.3. Information about the variables related to movement behaviour on each trial

| Exp. number | Condition | Approach latency (min.) <sup>a</sup> | Latency from last movement (min.) <sup>b</sup> | Latency to the first movement (min.) <sup>c</sup> | Time rest (min.) <sup>d</sup> | Movement Direction <sup>e</sup> | Displacement <sup>f</sup> | Ground <sup>g</sup> | Patrolling <sup>h</sup> |
|-------------|-----------|--------------------------------------|--|---|-------------------------------|---------------------------------|---------------------------|---------------------|-------------------------|
| 1           | Invasion  | 30                                   | 14   | 2   | 16                            | Approach                        | Approximate               | Yes                 | No                      |
| 2           | Invasion  | 60                                   | 18   | 14  | 32                            | Approach                        | Approximate               | No                  | No                      |
| 3           | Overlap   |                                      | 26   | 383   | 27                            | Neutral                         | Neutral                   | No                  | No                      |
| 4           | Invasion  | 14                                   | 30   | 2   | 32                            | Approach                        | Approximate               | Yes                 | No                      |
| 5           | Overlap   | 240                                  | 0  | 195   | 0.5                           | Approach                        | Approximate               | No                  | No                      |
| 6           | Overlap   | 280                                  | 30   | 40  | 70                            | Approach                        | Approximate               | No                  | No                      |
| 7           | Invasion  | 32                                   | 31   | 3   | 34                            | Approach                        | Approximate               | No                  | Yes                     |
| 8           | Outside   |                                      | 30   | 165   | 195                           | Neutral                         | Neutral                   | No                  | No                      |
| 9           | Overlap   |                                      |  |   |                               |                                 |                           | No                  | No                      |
| 10          | Invasion  | 15                                   | 30   | 2   | 32                            | Approach                        | Approximate               | No                  | No                      |
| 11          | Invasion  | 63                                   |  |   |                               |                                 |                           | Yes                 | No                      |
| 12          | Overlap   |                                      | 66   | 160   | 79                            | Neutral                         | Neutral                   | No                  | No                      |
| 13          | Outside   |                                      |  |   |                               |                                 |                           | No                  | No                      |
| 14          | Invasion  | 27                                   | 30   | 13  | 43                            | Approach                        | Approximate               | No                  | No                      |
| 15          | Invasion  | 22                                   | 34   | 3   | 37                            | Approach                        | Approximate               | No                  | No                      |
| 16          | Invasion  |                                      | 48   | 21  | 68.5                          | Neutral                         | Neutral                   | No                  | No                      |
| 17          | Invasion  |                                      | 40   | 0   | 41                            | Neutral                         | Approximate               | Yes                 | No                      |
| 18          | Overlap   | 17                                   | 52   | 1   | 53                            | Approach                        | Approximate               | Yes                 | Yes                     |
| 19          | Invasion  |                                      | 35   | 19  | 54.5                          | Neutral                         | Neutral                   | No                  | No                      |
| 20          | Invasion  | 8                                    | 1  | 3   | 4                             | Approach                        | Approximate               | No                  | Yes                     |
| 21          | Invasion  | 47                                   | 34   | 30  | 64                            | Approach                        | Approximate               | No                  | Yes                     |
| 22          | Invasion  | 17                                   | 45   | 9   | 54                            | Approach                        | Approximate               | No                  | Yes                     |
| 23          | Invasion  |                                      | 15   | 53  | 68                            | Neutral                         | Neutral                   | No                  | No                      |
| 24          | Invasion  | 171                                  | 19   | 84  | 47                            | Approach                        | Approximate               | No                  | No                      |

|    |          |     |     |     |          |             |    |
|----|----------|-----|-----|-----|----------|-------------|----|
| 25 | Overlap  | 42  | 73  | 115 | Neutral  | Neutral     | No |
| 26 | Outside  | 22  |     | 253 | Neutral  | Neutral     | No |
| 27 | Overlap  | 76  | 133 | 209 | Neutral  | Neutral     | No |
| 28 | Outside  | 147 | 40  | 187 | Neutral  | Neutral     | No |
| 29 | Overlap  | 110 | 122 | 205 | Neutral  | Neutral     | No |
| 30 | Overlap  | 94  | 163 | 207 | Approach | Approximate | No |
| 31 | Overlap  | 37  | 25  | 45  | Neutral  | Neutral     | No |
| 32 | Outside  | 100 | 183 | 206 | Neutral  | Neutral     | No |
| 33 | Overlap  | 165 | 124 | 167 | Neutral  | Neutral     | No |
| 34 | Overlap  | 103 |     | 202 | Neutral  | Neutral     | No |
| 35 | Invasion | 38  | 131 | 109 | Neutral  | Neutral     | No |

<sup>a</sup> Time in minutes from the start of the playback until the moment when the alpha male arrived within 20m of the speaker location.

<sup>b</sup> Time in minutes from the until the start of the playback.

<sup>c</sup> Time in minutes from the start of the playback until end the performed by the alpha male in which it moved more than 50m (see Chapter 5 for details).

<sup>d</sup> Total resting time from the end of the last movement performed by the alpha male before the playback until the start of the first movement after the playback, *irrespective* of the distance travelled.

<sup>e</sup> Direction of the first travelling session (as defined in <sup>c</sup>) with respect to the relative positions of the speaker and the reception tree and according to the categories described in Chapter 5.

<sup>f</sup> Location of the end point of the first travelling session (as defined in <sup>c</sup>) with respect to the relative positions of the speaker and the reception tree and according to the categories described in Chapter 5.

<sup>g</sup> Occurrence of movement on the ground after the playback.

<sup>h</sup> Occurrence of patrolling behaviour after the playback, as defined in Chapter 5.