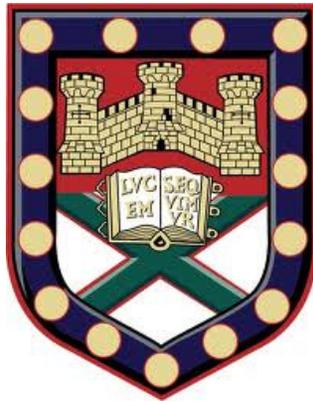


**Howl vocalisations of captive black and gold howler monkeys  
(*Alouatta caraya*); acoustics, function and applications for welfare.**



Submitted by Holly Lavinia Antonia Farmer, to the University of Exeter  
as a thesis for the degree of Doctor of Philosophy in Psychology  
in July 2011

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## ABSTRACT

This thesis aims to determine the function of howl vocalisations performed by the black and gold howler monkey, *Alouatta caraya*, and to examine the connections between howling, welfare and breeding in captivity. Comparisons of the behaviours performed during natural howling bouts and during howling bouts in response to experimental playbacks provide evidence for a range of howl functions including regular advertisement of the caller's occupancy and mate defence and attraction. Detailed analyses of howl call acoustics provide the first evidence of both individuality and context-specificity in the calls of *A. caraya* males. These findings further support the functions of intergroup spacing, mate defence and attraction and suggest that howling may act as an honest signal of male quality. Experimental playbacks of conspecific calls stimulated howling by captive male *A. caraya* and affected other behaviour patterns suggesting that playbacks are an effective form of environmental enrichment to enhance captive welfare. However, the efficacy of conspecific call playbacks as a form of enrichment were not reflected in the opinions of *A. caraya* keepers surveyed: responses to the use of this type of enrichment were unenthusiastic, and the routine use of auditory enrichment for captive primates was limited. Analysis of the European studbook found that individuals housed in a family group rather than a pair, and those which are regularly exposed to the calls of conspecific males had higher reproductive success. Also, males who performed higher rates of howling had higher reproductive success providing the first evidence of a link between howling and breeding rates. These findings contribute to the knowledge of howl vocalisations in *Alouatta* species and the influence of captivity on a highly vocal primate species. From thesis results it is recommended that captive *A. caraya* be housed in social groups containing more than one male and one female and that the playback of conspecific

male howl calls be introduced into the husbandry of groups to provide a more naturalistic auditory environment.

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## ACKNOWLEDGEMENTS

Firstly I would like to thank my supervisors, Dr. Lisa Leaver and Dr. Joah Madden, for their encouragement, advice and support throughout my thesis. Especially Lisa who since I started my PhD has had two beautiful sons and now knows more about howler monkeys than she ever thought she would. Thank you for being a fantastic supervisor and friend. I would also like to thank Prof. Stephen Lea who was my second supervisor until 2008, whose overwhelming knowledge of animal behaviour helped shaped my thesis.

I am exceptionally grateful to Dr. Amy Plowman from the Whitley Wildlife Trust who acted as an external advisor throughout my PhD and was always there to ask for advice, help on statistics and to support my work. Thank you to the Whitley Wildlife Conservation Trust who co-funded my studies and for my part-time job as an Assistant Zoo Research Officer alongside my PhD. Without this support I could not have gained the experience and knowledge of zoo-based research and management. Also, to my colleagues in the Field Conservation and Research Department who have always been encouraging and supportive.

This research was greatly facilitated by the helpfulness of the staff at each of the zoos that I visited: Paignton Zoo Environmental Park, Exmoor Zoo, Port Lympne Wild Animal Park, Bristol Zoo Gardens, Edinburgh Zoo, Hammerton Zoo, Twycross Zoo and Banham Zoo. Thank you for your support and for the cups of tea on the very cold days at Port Lympne and Twycross.

I would like to thank my fellow students at the University of Exeter, past and present, and the zoo PhD student group; Joanna Bishop, Andrew Bowkett, Kathy Baker

and Tracey Hamston, who were a great source of support and motivation and I look forward to celebrating their PhD successes in the next few years. Thank you so much to Kirsten Pullen who not only introduced me to the world of howler monkeys, being my MSc supervisor on the subject, but also for her support and advice in planning my PhD, encouraging words and cups of tea. I would also like to thank Kirsten for her fabulous description of howlers as ‘furry rocks with teeth’ which, after sitting in the rain and snow for 9 hours a day, I wholeheartedly agree with.

To my family, thank you so much for all your support throughout my academic career and my choice to be an eternal student. Mom and dad, I could not have done this without you, thank you so much for your love, encouragement and financial support throughout. To my wonderful sister Sophie, thank you for always being there for me to make me laugh and choosing wonderful places around the world to live so that I could enjoy fantastic holidays during my PhD. Soph it’s “not long now” and I’m “almost there”.

Finally to my best friend and fiancé Howard. Luckily you only had to endure the last two years of my PhD, but for this time you have been so supportive, kind, understanding, a shoulder to cry on and always knew how to make me laugh when I was having a bad day. I can’t wait to spend the rest of our lives together and enjoy trips to the beach in our campervan.

## **STATEMENT OF THE CANDIDATE'S CONTRIBUTION TO CO-AUTHORED PAPERS**

There are four studies included in this thesis, all of which have been written up as manuscripts for publication. As detailed below, the substantial contribution to the co-authored papers presented in this thesis was made by the candidate. However, while the candidate is fully responsible for the work presented in this thesis, where the first person is used it is in the plural (i.e., 'we' rather than 'I') as in the original peer-reviewed articles to reflect the collaborative efforts guiding the research process. All chapters that have been written up as manuscripts are presented in the format requested by the respective journal; since each manuscript is meant to stand alone, some information may be redundant.

**Paper 1:** Chapter 2

Farmer, H. L., Plowman, A. B. & Leaver, L. A. (submitted). **Individual and context-specific variations in howls of black and gold howler monkeys (*Alouatta caraya*)**. *International Journal of Primatology*.

The first manuscript, presented in this thesis as Chapter 2, was submitted to the *International Journal of Primatology* in May 2011. The manuscript was not accepted but the Editor invited a resubmission for consideration once all reviewer's comments were addressed. The paper was corrected and resubmitted in July 2011 and accepted with minor revisions in September 2012. The candidate collected the data, analysed the data and wrote the paper with supervisory support from Dr. Lisa Leaver and advice from Dr. Amy Plowman.

**Paper 2:** Chapter 3

Farmer, H. L., Madden, J. R., Plowman, A. B. & Leaver, L. A. (submitted). **An Experimental Investigation into Context Specific Variation in the Calls of the Black Howler Monkey (*Alouatta caraya*)**. *International Journal of Primatology*.

The second manuscript, presented in this thesis as Chapter 3, was submitted to the journal *Animal Behaviour* in November 2010, was not deemed novel enough but the reviewers gave great feedback and suggestions, thus the manuscript was corrected. The manuscript was then submitted to the journal *Ethology* in May 2011, again reviewers' feedback was positive, however it was recommended that the manuscript be submitted to a more specific primate journal. The manuscript was submitted to *International Journal of Primatology* in July 2011 and was accepted for publication subject to revisions and resubmitted in November 2011. The candidate collected the data, analysed the data and wrote the paper with supervisory support from Dr. Lisa Leaver, Dr. Joah Madden and advice from Dr. Amy Plowman.

**Paper 3:** Chapter 4

Farmer, H. L., Plowman, A. B. & Leaver, L. A. (in press). **Role of vocalisations and social housing in breeding in captive howler monkeys (*Alouatta caraya*)**. *Applied Animal Behaviour Science*.

The third chapter was submitted to *Applied Animal Behaviour Science* in March 2011 where it was published in November 2011. The candidate analysed the data and wrote the paper with supervisory support from Dr. Lisa Leaver and advice from Dr. Amy Plowman.

**Paper 4:** Chapter 5

Farmer, H. L., Plowman, A. B. & Leaver, L. A. (under review). **Auditory enrichment: efficacy, keeper opinion and it's future in husbandry practices for zoo-housed primates, particularly howler monkeys (*Alouatta caraya*).** *Zoo Biology*.

The fourth manuscript, presented in this thesis as Chapter 5, was submitted to *Zoo Biology* in June 2011 but was rejected. The candidate designed the questionnaire, collated responses, analysed the data and wrote the paper with supervisory support from Dr. Lisa Leaver and advice from Dr. Amy Plowman.

## **STATEMENT OF THE SUPERVISORS' CONTRIBUTION TO CO-AUTHORED PAPERS**

As outlined in the candidate's statement above, the substantial contribution to the co-authored papers presented in this thesis was made by the candidate. This includes the review of the literature presented in each paper, study design, statistical analyses and interpretation of the data, together with the write-up for publication. The supervisors contributed to the papers by advising on statistical analyses and interpretational issues, relevant literature, and writing style. Moreover, the theoretical framing of the empirical work in this thesis and the arrangement of the papers is a product of a concerted discussion of the thesis content between the candidate and supervisors.

Dr. Lisa Leaver (first supervisor)

Dr. Joah Madden (second supervisor)

## CHAPTER 1: Introduction

The focal species of this thesis, *Alouatta caraya*, is a member of the *Alouatta* genus, characterised by the production of loud roar or howl calls (Jones, 1980, 1983; Whitehead, 1995). Howling is an important component of the *Alouatta* communication system (Altmann, 1959; Hohmann and Herzog, 1985), but little is understood about the structure and function of these vocalisations in many howler species. There is limited research into the vocalisations of *Alouatta caraya*, the most common primate species in captivity, with only one study (Calegario-Marques and Bicca-Marques, 1995) providing a full vocal repertoire list for one wild group of the species. For howler species which have been well-studied, such as *Alouatta palliata* and *Alouatta seniculus*, the function of howling is still much debated.

This thesis includes detailed analysis of the howl calls of multiple captive *A. caraya* males, describing acoustic features from the full duration of howl bouts, not just roar components as in previous studies. From this and by studying the behaviours associated with howl performances, this thesis aims to provide the first comprehensive study of *A. caraya*, to improve the knowledge of howler calls and to determine the role of howling in communication. By conducting experimental acoustic playbacks, this thesis aims to further determine the proximate mechanism of howl calls and as studies were conducted in a captive environment, the link between social grouping and experience of conspecific male howl calls are also investigated in relation to howling and behaviour.

To determine the influence of captivity, detailed analysis of the European Studbook for *A. caraya* allowed for the assessment of both social and environmental factors on captive reproductive success in the species, allowing recommendations for the management of captive groups to be provided. Furthermore, this thesis includes

survey responses of the husbandry providers of captive *A. caraya*, to assess the current applications of auditory enrichment for the European captive population. I then compare responses to observational evidence from acoustic playbacks, to provide recommendations for the use of auditory enrichment for *A. caraya* and other captive primate species and to consider the welfare of the species in captivity.

In this thesis I provide an introduction to the *Alouatta* genus, focusing on *A. caraya*, animal vocal communication, the loud calls of *Alouatta* and their proposed functions, captive animal welfare and its influence on reproduction. Throughout this chapter I present the areas of research in this thesis and elucidate their importance. This introduction will also provide definitions for the terms discussed throughout this thesis and finally, clearly set out the aims of the thesis.

### **1.1. *Alouatta* taxonomy**

There are 15 recognised species of howler monkey in the genus *Alouatta*, which are among the largest of the New World primates (Crockett and Eisenberg, 1987). Previously classified in the family Cebidae, they are now placed in the family Atelidae (Groves, 2005) and divided into three main groups: *Alouatta palliata*, *Alouatta seniculus* and *Alouatta caraya* (Emmons and Feer, 1990; Eisenberg and Redford, 1999; Rowe, 1996). This thesis focuses on the black and gold howler monkey (*A. caraya*) which is one of the seven *Alouatta* species held in captivity, from an identified 15 species. These seven species are; *A. belzebul belzebul* (red-handed howler), *A. caraya* (black howler), *A. guariba guariba* (northern brown howler), *A. macconnelli insularis* (Guyanan red howler), *A. pigra* (Guatemalan black howler), *A. sara* (Bolivian red howler) and *A. seniculus* (Venezuelan red howler). Until recently, little was known about the black and gold howler monkey (*A. caraya*), although it is the most common

species of *Alouatta* in captivity worldwide (International Species Information System (ISIS), 2011).

### 1.1.1 *A. caraya* ecology

All howler species are native to South and Central America. *A. caraya* can be found in northern Argentina, Paraguay and Brazil (Crockett, 1998; Iwanaga and Ferrari, 2002), inhabiting a range of forest types including semi deciduous, semi evergreen, deciduous, gallery forests and savannah areas with small trees (see review, Crockett, 1998). The diet of howler species is classed as folivore-frugivore (Crockett and Eisenberg, 1987). *A. caraya* feed on leaves, fruit (Rumiz et al, 1986; Zunino, 1986), seeds, flowers, bark, stems and lichens (Bicca-Marques and Calegario-Marques, 1994a, b; Bravo and Sallenave, 2003). In common with *Alouatta fusca*, *A. caraya* is sexually dimorphic (Bicca-Marques and Calegario-Marques, 1998; Crockett, 1998). Male pelage changes from yellow/brown to black at maturation between 4 and 6 years (Bicca-Marques, 1991), the rate of colour change varying between populations (Bicca-Marques, 1990). Females of both species remain yellow/brown throughout their lifetime (Thorington et al, 1984). In the wild, from tooth wear observations, the oldest adult male *A. caraya* that has been recorded was approximately 20, and the eldest adult female recorded was 18 years of age (Thorington, Ruiz and Eisenberg, 1984). The European Studbook (ESB) of *A. caraya*, with data current to the end of 2009, records the oldest male to be held in captivity as 27, the oldest female as 31 years of age. The subjects in this thesis are all of reproductive age; over three years of age in both females (Thorington et al, 1984) and males (Shoemaker, personal communication, in Jones, 1983) and are all held in breeding groups. In the population investigated in Chapter 4,

concerning the factors influencing the breeding success of *A. caraya*, the oldest male to sire offspring is 20; the oldest female is 22 years of age.

As with other howler species (see Thorington et al, 1984; Neville, Glander, Braza and Rylands, 1988; Chapman and Balcomb, 1998), *A. caraya* group size and composition is highly variable. Studies report group sizes ranging from 3 individuals (Eisenberg and Redford, 1999) up to 19 group members (Thorington et al, 1984), however groups of just two individuals have been reported in fragmented areas of forest (Zunino et al, 2007). Group size can be related to habitat type and a positive correlation between group size and density of fruiting trees has been reported (Zunino et al, 2001).

Howler monkey groups, including *A. caraya*, can be uni or multimale (Eisenberg, 1979; Thorington et al, 1984; Calegario-Marques and Bicca-Marques, 1996; Zunino et al, 2007, Aguiar et al, 2009) and the number of females in *A. caraya* groups is typically greater than the number of males in a group (Thorington et al, 1984; Aguiar et al, 2009). Males of the same age are not found within one group, most groups are composed of unrelated adults of both sexes due to natal emigration (Thorington et al, 1984; Glander, 1992).

All *Alouatta* species exhibit bisexual emigration, where almost all males and females (79% and 96% respectively) leave their natal group (Crockett and Eisenberg, 1987; Rumiz, 1990; Glander, 1992; Zucker and Clarke, 1998, Fedigan and Jack, 2001). In *A. caraya*, group emigration is most commonly performed by females (Calegario-Marquez and Bicca-Marquez, 1995) which is linked to intrasexual breeding competition. Calegario-Marquez and Bicca-Marquez (1996) report that three of six observed female emigrations were by the oldest immature females from the group and that group females were seen to force these females out of the group through threat displays and chases. Male *A. caraya* leave the group at around five years of age

(Thorington et al, 1984; Calegario-Marques and Bicca-Marques, 1996). The emigration of male group members is also suggested to be related to intragroup competition for mates; however, males may leave their natal group when attracted away by females from a newly formed group (Calegario-Marquez and Bicca-Marquez, 1996). Those individuals which emigrate from the natal group may become solitary for a time or join other groups (Rumiz, 1990). When entering a new group, *A. caraya* males have been observed to kill the small offspring of a rival dominant male (Calegario-Marquez and Bicca-Marquez, 1996; Bicca-Marques and Calegario-Marques, 1998) since male-male competition in *Alouatta* species is high (Crockett and Eisenberg, 1987). Intrasexual competition in howler species is high, as would be expected in a polygynous species, therefore it has been suggested that the movement of individuals between groups is a reproductive strategy (Neville et al, 1988) facilitating increased reproductive success (Agoramoorthy and Rudran, 1995). In a study of three wild populations of *A. seniculus*, it was found that females which leave their natal group form coalitions with other migrating females. Through genetic analysis, the study reports that female coalitions between kin had higher reproductive success than females which formed coalitions with unrelated females. Also, those coalitions which contained more daughters produce a higher number of offspring (Pope, 2000). This finding reinforces the hypothesis of natal emigration as a reproductive strategy, however further research and genetic analysis of other *Alouatta* species would be beneficial to determine similarities, as the adult composition and sex ratio of groups varies dramatically between species (see Crockett and Eisenberg, 1987, Neville et al, 1988 for reviews of group composition).

### **1.1.2. Reproduction**

Reproducing groups of wild *A. caraya* contain up to three adult males, one to four adult females and a number of subadults and infants (Calegario-Marques and Bicca-

Marques, 1993; Peker et al, 2009). It is suggested that wild female howlers are highly promiscuous, mating with both resident group and extra-group males (*A. caraya*, Kowalewski and Garber, 2010; *A. palliata*, Jones, 1985; Jones and Van Cantfort, 2007). However, there is conflicting evidence about which females within a group produce offspring. In *A. seniculus*, Crockett and Eisenberg (1987) suggest that almost all group females produce offspring, but do not provide scientific evidence for this statement. Studies of *A. palliata*, suggest that offspring are only born to the socially dominant female of the group (Jones, 1985; Pope, 2000; Ryan et al, 2008). The dominant adult female of the group was also confirmed as the dam in a captive study of one group of *A. caraya* and it was also suggested that during the one birth noted, the lowest ranking female may have experienced reproductive suppression during gestation (Shoemaker, 1979). However, in another captive study on *A. caraya* conducted over only 2 weeks, Jones (1983) reported copulation occurring between two different male-female pairings within the group, a finding which contributes to the uncertainty of parental identity in howler species, which may only be determined through genetic investigation and long-term study.

Howler monkeys are not strictly seasonal breeders; they are able to reproduce throughout the year (*A. palliata*, Carpenter, 1934; Rowe, 1996, *A. caraya*, Rumiz, 1990; Zunino, 2004), sometimes giving birth in 'clusters' (Crockett and Eisenberg, 1987). They are iteroparous breeders with a litter size of one and adult survivorship is low (Stearns, 1976; Millar and Zammuto, 1983). Reproductive capacity is reached before maximum adult body weight; at one year for females, two for males (Crockett and Pope, 1993). In wild *A. caraya*, climatic conditions and food availability may influence the onset of oestrous cycles or neonatal survival (Shoemaker, 1979). A positive correlation between rainfall, temperature, birth patterns and conception has also been reported for the species (Zunino, 1996), suggesting that howler monkeys adapt their

reproductive activity to their environment and pattern of food availability (Kowalewski and Zunino, 2004).

Mating behaviour in the howler monkey is highly coordinated (Jones, 1985). The female oestrous cycle is usually signalled by close proximity between mating pairs as a courtship period (Crockett and Eisenberg, 1987). In *A. caraya*, the estimated gestation periods for two females from one wild group were estimated to be between 152 and 195 days (Calegaro-Marques and Bicca-Marques, 1993). Other gestation length estimates for the species, calculated during captive studies, reported a period of around 187 days for one birth, but subsequent keeper reports suggested a shorter gestation length of 139 days (Shoemaker, 1979). Data from both wild and captive studies suggest the inter birth interval of *A. caraya* to be between 17 and 23 months (Shoemaker, 1982; Calegaro-Marques and Bicca-Marques, 1993). At 31 days of age, nursing was seen to be supplemented by independent feeding in *A. palliata* (Altmann, 1959; Jones, 1997), while in a study of captive *A. caraya*, it was presumed that the offspring had weaned as its mother began to ignore it (Shoemaker, 1979); however, precise dates were not provided.

Allomaternal care, performed by non-maternal group females, has been observed in only a few wild *A. caraya* groups, where other group females were observed suckling infants which are not their own and carrying young or recently independent juveniles (Calegaro-Marques and Bicca-Marques, 1993; Bravo and Sallevave, 2003) and also on one occasion captivity (Shoemaker, 1979). This behaviour, only carried out by females suggests that it may be an important experience for immature females, learning to care for infants (Calegaro-Marques and Bicca-Marques, 1993), which may improve a female's reproductive success. Sires do not actively contribute to parental care (Smith, 1977; Bolin, 1981) but tolerate the infants to a high degree (Neville, 1972; Baldwin and Baldwin, 1976; Bolin, 1981). This finding may be

related to the occurrence of natal emigration and that related females form coalitions which may help to improve future reproductive success.

## 1.2. Vocal communication

In the natural world, the production of vocalisations is an important component of animal communication which can be defined as the transmission of a signal from one organism to another, where the receiver may or may not respond appropriately (Pearce, 1997). Throughout mammalian and bird species, the information conveyed through vocal signals can vary greatly; from broadcasting general information allowing for individual recognition (primate species, see review Cheney and Seyfarth, 1990), to conveying specific information to conspecifics, warning them of the threat of predation by performing acoustically distinct calls in response to different predator species (for example vervet monkeys, *Cercopithecus aethiops*, Seyfarth et al, 1980a, b; Campbell's monkeys, *Cercopithecus campbelli*, Zuberbühler, 2001, diana monkeys, *Cercopithecus diana*, Zuberbühler et al, 1997; Zuberbühler, 2000; white-faced capuchin, *Cebus capucinus*, Marler, 1955; see Zuberbühler et al, 1999).

For many social primate species which inhabit densely vegetated areas, natural selection has favoured the performance of vocal signals which transmit over large distances (see Whitehead, 1989) as visual communication is often not possible. Terrestrial species, inhabiting open areas, do not perform long-distance calls (Wich and Nunn, 2002) as it is known that vocalisations performed at ground level do not propagate as successfully (Waser and Brown, 1986). In a study concerning Old World monkey vocalisations, Brown, Gomez and Waser (1995) played the calls of two rainforest and two savannah primate species, re-recorded these calls at different distances from the source and measured distortion rates in the two environments. Savannah monkey calls were distorted when played in both habitats whereas rainforest

primate calls were less distorted when played in a rainforest habitat than a savannah habitat. These findings reinforce that rainforests are the more favourable environment for long-distance vocalisation propagation.

### 1.2.1. Long-distance calls

Long-distance calls, also termed long or loud calls, are vocalisations with energy concentrated at less than 500Hz or a broadband energy between 500 and 2000Hz (Byrne, 1982), which allow for the propagation of sounds to carry over large distances (Waser and Waser, 1977). These vocalisations are characteristically low frequency, which allows for long-distance transmission and minimal environmental influence (Mitani and Stuht, 1998). In New World primate species, groups occupy forest habitats and as such, perform long-distance calls (for review see Oliveria and Ades, 2004). Long-distance calls characterise the *Alouatta* genus (*A. caraya*, da Cunha and Byrne, 2006) and are common among many primate species (for example orangutans, *Pongo* spp., Delgado, 2007; gibbons, *Hylobates* spp., Geissmann, 2002; great ape spp., Hohmann and Fruth, 1995; see Waser, 1982; Zimmerman, 1995, see Delgado, 2006 for review of male primate long calls); it is suggested that such calls function in both extra-group and intragroup signalling such as mate competition and resource conflict, alarm calling and group coordination (for review see Oliveira and Ades, 2004).

The ability to identify individuals at a distance is very important (Rendall et al, 1996), especially in arboreal species. In small howler monkey (*A. seniculus*) groups, it is suggested that it would not be beneficial to advertise group movements to others in the surrounding area, informing neighbouring groups that another area is unoccupied since such groups may take advantage of that exposed area. Although informing neighbours of a caller's occupancy may reduce costs from inter-group interactions

because howlers mainly defend their location via vocal battles, groups may lose their resources in the process (Sekulic, 1982a).

In the natural world, many factors can influence acoustic signals such as the surrounding environment, caller morphology, physiology, phylogeny and health, sexual selection and predator presence (for review see Forrest, 1994). As acoustic signals must be recognisably transferred from sender to receiver over large distances, environmental conditions can strongly influence the transmission of sound through specific habitats and signals may be distorted during transmission. Long-distance calls are highly adapted to environmental conditions (for review see Oliveira and Ades, 2004) and contain precise structural characteristics allowing for propagation across large distances, to minimise environmental attenuation (Deputte, 1982). In arboreal species vocal signals can be affected by attenuation and influenced by physical factors of the environment such as absorption and scatter (Whiley and Richards, 1978) and degradation and masking (Leader et al, 2005). Sound may also be influenced by microclimatic factors such as temperature, relative humidity and wind gradients which can increase sound transmission in the upper canopy (Wiley and Richards, 1974; Henwood and Fabrick, 1979). The majority of loud calls are performed during the dawn chorus, between 7 and 9am (Waser and Waser, 1977). In the upper canopy, optimal sound transmission periods are during the early morning when temperatures are most favourable and signals are less affected by reflection, scatter and absorption from vegetation and surrounding objects (Marten and Marler, 1977).

The long-distance calls produced by the *Alouatta* genus are typically termed loud calls in the literature, perhaps due to their being heard up to 3km away through forest and 5km away over water (Snowdon, 1989). *Alouatta* loud calls are then further described as howls or roars; and hereafter they will be referred to as howl calls. Howlers also perform a range of close-contact vocalisations which communicate over short

distances, such as the ‘purr’ and ‘eh’, which are produced by younger group members (for review see Neville et al, 1988). It has been suggested that howlers and other forest primates perform howl calls during ‘sound windows’ each choosing a specific time to call when sound transmission is most favourable (Sekulic, 1983; Waser and Brown, 1986). The majority of howl calls are performed in the early morning, during the ‘dawn chorus’, before daily activities have begun (*A. palliata*, Collias and Southwick, 1952; Altmann, 1959; Bernstein, 1963; Chivers, 1969; Baldwin and Baldwin, 1976; Eisenberg and Redford, 1999; *A. seniculus*, Sekulic, 1982b; *A. caraya*, da Cunha and Byrne, 2006). The onset of the dawn chorus can vary significantly and is influenced by sunrise, moon phase and weather conditions (Chivers, 1969; Sekulic, 1982a). Howl calls may also be heard spontaneously throughout the day but at a lesser frequency than at dawn (Bernstein, 1963; Chivers, 1969; Sekulic, 1982a), in the late afternoon and at dusk (Sekulic, 1982a; Cornick, 1998). However, not all *Alouatta* species perform a dawn chorus. A bimodal pattern of calling has been reported in *Alouatta pigra* (Horwich and Gebhard, 1983; Cornick and Markowitz, 2002) and in this species vocal production can also vary throughout the year. During the dry season the majority of vocalisations are performed in the early morning, and midday and afternoon calling rates decrease (Cornick, 1998; Cornick and Markowitz, 2002), correlating with abiotic factors such as high temperatures and insolation (solar radiation). In *A. guariba*, no dawn chorus is performed; loud calls are performed in the mid-morning and mid-afternoon (Chiarello, 1995; Oliveira, 2002).

The reported howl rates and duration of howl calls produced by *Alouatta* species vary significantly. Evidence is limited in both the number of groups studied and sample sizes of studies conducted (Table 1.1). The work of Sekulic and Chivers (1986) report noticeably shorter howl durations for *A. seniculus* and *A. palliata* than other studies concerning these species. The study does not provide a clear definition or description of

howl calls and was unable to differentiate between callers, discussing data from a range of howls performed by adult males, subadult males and females. There may however be variation in the duration of howl calls performed by different group members. When the adult male of a group begins howling, both subadult males and females often join in (Altmann, 1959; Schön Ybarra, 1986; Whitehead, 1995; Steinmetz, 2000); therefore, they may not call for the full duration of the male's howl, which may influence the findings in this study. Only one study has compared the calls of multiple *Alouatta* species, contrasting acoustic features of the howl calls of seven species (Whitehead, 1995). Prior to the study it has been suggested that the physical environment influences the frequency and other acoustic characteristics of howl calls (Sekulic and Chivers, 1986). Whitehead (1995), determined that two patterns of vocalisations illustrate species adaptations of *Alouatta* to their surrounding environment, based on the relative duration of roars. The study analysed the recordings of howls performed by wild males of seven howler species and one captive group of *A. caraya*, taken by a range of researchers, the only publication to compare the acoustic characteristics of the majority of *Alouatta* species. The first group was suggested to contain only *A. palliata* howl calls, which are limited in duration and cannot be sustained in a long, continuous sequence which Whitehead (1995) suggests are adapted to the high levels of background noise associated with inhabiting areas near to rivers. All other howler species included in the study (*Alouatta belzebul*, *A. caraya*, *A. pigra*, *A. seniculus* and two subspecies of *A. fusca*) were classified into a 'non-*palliata*' group, stating that the howl call of these species are longer in duration and maintain roars for extended periods and that 'non-*palliata*' species appear to predict the frequency channel for producing long-distance calls with extended durations (Whitehead, 1995). In low audible environments, sound must be adapted to signal above the ambient noise level, with a loud volume and in specific frequency bands for successful propagation (Whitehead,

1995). At high frequencies, sounds may be more affected by vegetative distortion and degradation (Seyfarth, 1987). *Alouatta* species are hardy colonisers and are often situated along river systems, therefore long calls have been proposed to be highly adapted to travel through the noise along river channels (Whitehead, 1995).

Table 1.1. Rates and duration of howling for *Alouatta* species from published studies

Author (year)	Species studied	No. of groups studied	Howl call rate	Howl call duration (seconds)
Sekulic (1982a)	<i>A. seniculus</i>	4	5.17-10.42/hour/troop/day (dawn chorus) 0.98-3.95/hour/troop/day (during day)	Not provided
Sekulic (1982b)	<i>A. seniculus</i>	4	Not provided	173-555
Drubble and Gautier (1993)	<i>A. seniculus</i>	1	5.2 (0-11 at night, 0-14 during day)	98-207 (mean 208, max 600)
Schon Ybarra (1986)	<i>A. seniculus</i>	15 adult males (no group numbers provided)	Not provided	2700 (approximately)
Baldwin and Baldwin (1976)	<i>A. palliata</i>	8	Not provided	1200-2700 (dawn chorus)
Chivers (1969)	<i>A. palliata</i>	4	1-76 howl calls over 54 days	Not provided
Bernstein (1964)	<i>A. palliata</i>	2	141 howl calls per day	Not provided
Sekulic and Chivers (1986)	<i>A. palliata</i>	4	Not provided	2.5-6 (median 3.5)
	<i>A. seniculus</i>	4	Not provided	6-26 (median 19)
Chiarello (1995)	<i>A. fusca</i>	1	47 howl calls over 30 days	Not provided
Da Cunha and Byrne (2007)	<i>A. guariba</i>	1	1-6 howls/day (179 over 91 days)	60-1440
Cornick and Markowitz (2002)	<i>A. pigra</i>	22-25	1.73/hour (rainy season)	< 60-2340 (in autumn)
			1.14 /hour (dry season)	330 (in spring)
Horwich and Gebhard (1983)	<i>A. pigra</i>	9	0.5 to 0.18/hour	Not provided

### 1.3. Vocalisations in *Alouatta*

#### 1.3.1. Vocal repertoire

A total of 23 vocalisations have been reported in the *Alouatta* repertoire, including the male bark, woof, scream and rumble (*A. palliata*; Carpenter, 1934; Collias and Southwick, 1952; Altmann, 1959; Baldwin and Baldwin, 1976; Whitehead, 1995, *A. seniculus*, Sekulic, 1982a; Schön Ybarra, 1986; *A. caraya*, Calegario-Marques and Bicca-Marques, 1995). Studies have suggested that there are two main types of vocalisation produced by adult males of the genus; barks or woofs and roars (*A. palliata*; Carpenter, 1934; Altmann, 1959; Baldwin and Baldwin, 1976; Whitehead, 1987, 1995, *A. seniculus*; Schön Ybarra, 1986). Barks are short, low-pitched loud vocalisations which are repeated in a variety of rhythms (*A. palliata*, Altmann, 1959; *A. seniculus*, Schön Ybarra, 1986, *A. caraya*, Calegario-Marques and Bicca-Marques, 1995). The other main vocalisation and one which has been the focus of studies in to the vocal behaviour of *Alouatta* is the roar or also known as the howl call vocalisation (*A. palliata*, Type 1, Carpenter, 1934, Type A1, Altmann, 1959; Baldwin and Baldwin, 1976, *A. caraya*, Calegario-Marques and Bicca-Marques, 1995) which is the focus of this thesis. Howl calls are the loudest, low-pitched call produced by *Alouatta* species. This vocalisation is primarily performed by adult males, with subadult males and females of the group often joining in (Altmann, 1959; Schön Ybarra, 1986; Whitehead, 1995; Steinmetz, 2000).

#### 1.3.2. Howl acoustics

There is limited knowledge of acoustic measures or variables in the calls of all howler species, the majority of studies concern *A. palliata* (Baldwin and Baldwin, 1976; Whitehead, 1987, 1989) and *A. seniculus* (Schön Ybarra, 1986; Drubbe and Gautier, 1993). In *A. palliata*, howl calls comprise a sequence of exhaled and inhaled syllables

(Baldwin and Baldwin, 1976) and involve three phases; an introduction or preface, the climax or crescendo, and the coda (Schön Ybarra, 1986; Whitehead, 1987, 1989; Drubble and Gautier, 1993). At the start of a roar, notes have weak amplitude due to inflation of the air sacs, as the roar progresses the amplitude of sounds increases, reaching a maximum during the climax and decreasing in amplitude during the coda, probably due to emptying of the air sacs (Drubble and Gautier, 1993). In *A. caraya*, male howls are formed from a succession of low grunts, which develop into barks, these barks then fuse into a roar (Thorington et al, 1984). Roars are produced as a continuous string of notes, alternating in frequency and producing what is described as a “sawing” sound (Whitehead, 1995).

Whilst producing their characteristic howls, *Alouatta* maintain a distinct body posture. Males usually stand in a quadrupedal position (but sitting occasionally) and orientate their heads upwards with their mouths forming a funnel-shape (Altmann, 1959; Schön Ybarra, 1986; Drubbel and Gautier, 1993). The lower jaw is dropped and the lips are flared out to perform the intense ‘climax’ phrase of the howl (Drubbel and Gautier, 1993; Whitehead, 1995). To produce the final section of the howl, the head is lowered (Whitehead, 1989). *A. palliata* howling behaviour includes neck extension and thyroid swelling (Schön Ybarra, 1988). Continuous sound production is achieved by the performance of high notes during inspiration and low notes during exhalation. This posture is not only a threatening stance but also, by maintaining this posture whilst performing howl calls, elongating the larynx and flaring the lips, howlers may increase their perceived body size (Fitch, 1977) contributing to the threat of their call.

Howl calls are performed in response to a wide range of stimuli including; intergroup confrontations (Carpenter, 1934; Baldwin and Baldwin, 1976; Chivers, 1969; Thorington et al. 1984; Calegario-Marques and Bicca-Marques, 1995; Chiarello, 1995; da Cunha and Jalles-Filho, 2007), intra-group aggression (Calegario-Marques and Bicca-

Marques, 1995; Sekulic, 1982a), the passage of aeroplanes (Bernstein, 1964; Baldwin and Baldwin, 1976; Carpenter, 1934), the passage of large birds (Baldwin and Baldwin, 1976), fallen young (Carpenter, 1934), the sound of a weapon firing (Lundy, 1954), disturbance by dogs, horses and goats (Sekulic, 1982a). Extremes of weather such as rain (Carpenter, 1934; Bernstein, 1964; Chivers, 1969; Baldwin and Baldwin, 1976; Horwich and Gebhard, 1983; Calegario-Marques and Bicca-Marques, 1995), strong winds (Carpenter, 1934; Baldwin and Baldwin, 1976) and thunder (Carpenter, 1934; Calegario-Marques and Bicca-Marques, 1995) also act as stimuli. If we view call context as the “external events preceding and surrounding the signal” (Partan and Marler, 2005), *Alouatta* howl calls are performed in a wide range of contexts. However, acoustic differences between howl calls performed in response to different external stimuli have not been studied; therefore, this is investigated in Chapter 2.

### **1.3.3. Functions of howl calls in *Alouatta* species**

The howl calls produced by *Alouatta* species have been described as having multiple functions (Table 1.2), however the majority of our knowledge is limited to three species of howler; the mantled howler monkey (*A. palliata*), the red howler monkey (*A. seniculus*) and the black howler monkey (*A. pigra*). Evidence for the functions of howl calls in howler monkeys varies both within and between species including roles in intergroup spacing, resource defence and opponent assessment. The majority of literature considers the function of intergroup spacing; however, many studies are not experimental and conclusions are often highly speculative.

Table 1.2. Proposed function of *Alouatta* howls from published studies.

Author (year)	Species studied	Field period	Purpose of study	No. groups studied	Were study subjects habituated?	Proposed howl function (proximate mechanism)
Carpenter (1934)	<i>A. palliata</i>	Dec 1931-May 1932	Behaviour and ecology	2	No	Intergroup spacing
Altmann (1959)	<i>A. palliata</i>	Oct-Dec 1955	Behaviour, social communication and ontogeny	1	Yes (Barro Colorado Island)	Intergroup spacing (territoriality)
Bernstein (1964)	<i>A. palliata</i>	Jan-Feb 1962	Responses and diurnal effects of activity	1	Yes (Laboratory group)	Intergroup spacing (territoriality)
Southwick (1962)	<i>A. palliata</i>	Jan-Apr 1951	Intergroup social behaviour	30	Yes (Barro Colorado Island)	Intergroup spacing (mutual avoidance)
Chivers (1969)	<i>A. palliata</i>	Jun-Aug 1967	Howling behaviour	14	Yes (Barro Colorado Island)	Intertroop spacing
Baldwin and Baldwin (1976)	<i>A. palliata</i>	Dec 1970-Feb 1971	Vocal repertoire	8	Yes (Barro Colorado Island)	Intergroup spacing (mutual avoidance)
Whitehead (1987)	<i>A. palliata</i>	May-Sept 1983	Playbacks; influence of distance on reverberation	5	Hacienda la Pacifica	Intergroup spacing (reciprocate group movements)

Whitehead (1989)	<i>A. palliata</i>	Aug-Dec 1980, May-Sept 1983	Playback, responses to caller location and female accompaniment	11	Hacienda la Pacifica	Intergroup (regulation of space use)
Sekulic (1982a)	<i>A. seniculus</i>	Aug 1979-Aug 1980	Diurnal and seasonal call patterns and intertroop interactions	4		Resource defence (defend food resources)
Sekulic (1982b)	<i>A. seniculus</i>	Aug 1979- Aug 1980	Function of howls	4	Yes (Hato Masagural)	Intergroup spacing (deter intergroup males) and opponent assessment
Sekulic (1983)	<i>A. seniculus</i>	Aug 1979- Aug 1980	Effect of female calls on male howling	4	Yes (Hato Masagural)	Intergroup spacing (deter intertroop male invasions) and opponent assessment
Sekulic and Chivers (1986)	<i>A. seniculus</i>	1969 and 1982, 1983	Howl call duration	8	Yes (Barro Colorado Island) and Venezuela	Intergroup spacing
Drubbe and Gautier (1993)	<i>A. seniculus</i>	Mar-Jun 1987, Dec 1988-Jan 1989	Loud call structure and diurnal and nocturnal occurrences	5	No	Intergroup spacing (spacing)
Horwich and Gebhard (1983)	<i>A. pigra</i>	Apr-Jul 1981	Howl behaviour	9	Yes (Bermuda Landing)	Intergroup spacing (territoriality)

Cornick and Markowitz (2002)	<i>A. pigra</i>	Sep-Nov 1996, Jan-Apr 1997	Vocal patterns	22-25	Yes and no, Lamanai	Intergroup spacing (alternative to physical conflict)
Kitchen (2004)	<i>A. pigra</i>	Jan-Jun 1995 and 1997	Playback, influence of numeric odds on responses to howl calls	12 males	Yes (Community Baboon Sanctuary)	Opponent assessment (convey information on group numbers)
Kitchen (2006)	<i>A. pigra</i>	Jan-Jun 1995 and 1997	Playback, female responses to howl calls	12 males	Yes (Community Baboon Sanctuary)	Opponent assessment (assess intertroop fighting ability)
Da Cunha and Jalles-Filho (2007)	<i>A. guariba</i>	Jun 1997-Mar 1998	Function of howls	1	Yes	Intergroup spacing (territoriality)
Da Cunha and Byrne (2006)	<i>A. caraya</i>	Oct-Feb, Jul-Aug 2003	Playback, role of loud calls	1	Yes	Intergroup spacing (constant advertisement)
Chiarello (1995)	<i>A. fusca</i>	Feb 1991-Feb 1992	Role of loud calls	1	Yes	Intergroup spacing (limits fighting) and resource defence (food resource defence)

### 1.3.3.1. Intergroup spacing

#### *Alouatta palliata*

Research into the vocal behaviour of *A. palliata* stems from work conducted on a population at Barro Colorado Island, Panama (Carpenter, 1934; Altmann, 1959; Bernstein, 1964; Southwick, 1962). Carpenter (1934) was the first researcher to propose a function of howl calls during behavioural observations of two groups of *A. palliata*, that of intergroup spacing through mutual avoidance, although these findings are limited to anecdotal evidence and are reported purely from behavioural observations.

Subsequent research at Barro Colorado suggested a territorial role of howling. A territory has been defined as any area which an animal defends (Nobel (1939; Burt, 1943). Maher and Lott (1995) have recently reviewed the definition of territory and have suggested that it may contain more than one criterion; including advertisement of location through scent marking and the behavioural responses of intruders such as physical avoidance. In this thesis, I include the performance of scent marking behaviours as an indicator of territorial demarcation in *A. caraya*. Subsequent studies, which will be presented in this section, discuss the defence of an animal's home range through the performance of howl calls. A home range is simply the area in which an animal lives, reproduces and travels to find food (Burt, 1943). Territoriality can occur in all or part of a home range (Maher and Lott, 1995) but as will be discussed, *Alouatta* home ranges often overlap, which is the reason that the idea of howler monkey territoriality is disputed.

In a study on one group of *A. palliata*, Bernstein (1964), found no overlap between the home range boundaries of neighbouring groups, claiming that group activities were limited to core areas. Since he noted that groups called when they came within close proximity of another group, he interpreted this as evidence for territoriality. Altmann (1959) also supported the idea that *A. palliata* maintain territories solely

through vocal contests. The author reported that loud calls were performed predominantly along the edge of a group's boundary, functioning as an active territorial defence. When neighbouring groups were detected at the boundary edge, groups approached each other, engaged in a vocal battle and then retreated, with no aggressive contact reported. However, contradicting Bernstein's findings, Altmann reported that the home ranges of neighbouring groups did overlap, negating the idea of territorial defence. Both papers were highly speculative; Bernstein's study only looked at two wild groups and Altmann's paper did not clarify the area which groups were actively defending, i.e. whether it was the home range itself or an area within the home range.

Further research into the behaviour of *A. palliata* confirmed that neighbouring group ranges do overlap (Altmann, 1959; Southwick, 1962; Milton, 1980; Whitehead, 1987, 1989) but that groups are not observed to share these overlap areas at the same time (Chivers, 1969; Whitehead, 1987). Chivers (1969) also suggested that home ranges vary due to changes in group ranging patterns each month. These reports all suggest that howling acts as a mechanism for intergroup spacing, but their conclusions differ greatly, as outlined below.

By performing loud calls in the morning, when groups are most likely to encounter one another and calling from an unspecified location within the home range, it is suggested that calls function to coordinate the ranging patterns of neighbouring groups. This mechanism of intergroup spacing via mutual avoidance has been reported in *A. palliata* in many studies (Carpenter, 1934; Southwick, 1962; Chivers, 1969; Baldwin and Baldwin, 1976; Whitehead, 1989). Mutual avoidance allows groups temporary, exclusive use of a small part of their present home range by providing information to neighbours on their relative location (Southwick, 1962; Chivers, 1969; Baldwin and Baldwin, 1976). When a neighbouring group is detected or heard calling, the resident male will stop his activity and reply (Southwick, 1962), initiating a howling

battle. It has been suggested that this mechanism allows groups to maintain a determined distance from conspecific groups (Chivers, 1969) and facilitates group avoidance of areas of overlapping home range which are used by a group during their daily activities (Burt, 1943), termed an activity field in the work of Whitehead (1987, 1989). However, Chivers (1969) and Southwick (1962) reported that howling competitions become more intense when the two groups approach each other and this increases the tendency for the groups to move apart (Southwick, 1962; Chivers, 1969). Chivers only states that 'groups' approached each other, but if in fact all members of the competing groups approach each other, this does not provide evidence for mutual avoidance and instead shows that groups are intolerant of each other and that groups are not actually avoiding each other. Also, neighbouring groups are known to enter the home range of another group which contradicts the idea of mutual avoidance; from Chivers' (1969) report of home range variation, these studies, which only followed groups for a limited period, are overstressing their findings. Howling may be functioning as a response to encountering other conspecific groups, which may advertise the caller's location, rather than maintaining spacing between groups.

Whitehead (1987) suggested that neighbouring males can estimate their distance from a caller and thus concluded that howling functions to reciprocate group movements. The author also proposed that howlers actively avoid confrontation with neighbouring groups and that howling may help to maintain a stable buffer zone between the home ranges of groups. To further investigate this idea, Whitehead carried out experimental playbacks on five wild groups and showed that male *A. palliata* responded vocally to the calls of conspecific males, even with no visual indication of their presence. Males approached the speaker when simulating the approach of a conspecific male and retreated from the playback of a retreating male, which it was suggested, minimised the cost of physical intergroup encounters. From these findings,

the author concluded that groups avoided each other through vocal cues alone. This is a highly speculative conclusion, as it is not known what information is conveyed in howl calls and that calling may simply function as a greeting call. Also, it is known that *A. palliata* call from all areas within their home range and therefore cannot be maintaining a buffer zone between home ranges. If this is the function, calling would only maintain spacing around the calling male.

A further form of intergroup spacing concluded by Whitehead (1989) is that of the regulation of space use. In this study, the author suggested that by notifying neighbouring groups of a caller's location through howling, the ranging patterns of groups with overlapping home ranges could be maintained, which is the same spacing mechanism described in Whitehead's previous study (1987). The study also concerned playback experiments on 11 groups from the same geographical site as his previous study, with results showing that males responded vocally to the presence of conspecific groups. Males approached the speaker more when simulating the presence of conspecifics in an intensively used area of a home range, rather than an area that was less frequently occupied. The author concluded that the function of howling was to defend a specific resource which it would be assumed is location-specific. However, Whitehead did not indicate whether more intensely occupied areas were in the overlap zones of the home ranges of neighbouring groups and defined intensively used quadrats as one which was used more than once, which does not seem a reliable criterion. Also, the author suggested that site-dependent responses were a form of territorial defence; however, there is no evidence for territoriality in this study and therefore it is not possible to conclude whether howling is playing a territorial role in this situation.

*Alouatta seniculus*

The loud calls of *A. seniculus* are suggested to function in a similar way to *A. palliata*, by maintaining intergroup spacing (Sekulic and Chivers, 1986). *A. seniculus* call in the morning, before the onset of group movement notifying nearby groups of the caller's location, discouraging neighbours and solitary individuals from moving that way during the day (Sekulic, 1982a; Sekulic and Chivers, 1986). The species also occupy overlapping boundary areas (Sekulic, 1982a) which are not used at same time (Altmann, 1959). Sekulic and Chivers (1986) reported that groups called when neighbouring groups were near and that inter-howl intervals were shortened as groups approached, which they suggest reinforces the role of howling in intergroup spacing. However, the authors do not include details on the location of the callers within their home range whilst calling, so it is not possible to determine the exact mechanisms of intergroup spacing.

Even within a howler species, different howl call functions have been proposed. Drubbel and Gautier (1993) suggested that Guyana red howlers differ vocally from the related species, the Venezuelan red howler, by performing calls during the night. Guyanan red howlers perform two types of loud calls; short calls which are performed during the day and long calls at night, which have different functions. The authors claim that groups defend their whole home range by sleeping at different sites located close to the home range boundary and vocalising in the early hours, vocally marking their home range and deterring neighbours from attempting to enter their home range. However, neighbouring groups were reported as not always responding to the calls of resident males and intergroup encounters were rare, making conclusions from this work highly speculative. The authors also suggest that while calls were performed throughout the day, male Guyanan howlers select a time period for calling according to optimal environmental conditions (a 'sound window'). The findings from this study do not

support the author's conclusions of howling functioning as a spacing mechanism, which involves responses to the invasion of neighbouring groups. The study provides evidence that the function of howling may be to advertise the location of resident groups, perhaps as a means of boundary defence. However, the author's do not explain the difference between home range marking and territoriality, which makes their conclusions difficult to support. In addition, if howling by *A. seniculus* functions in territorial defence, males would call in response to the calls of extra-group males, but the authors suggested that males concentrate calling to a specified sound window and that intergroup encounters did not elicit vocal responses. These findings do not support the suggested conclusions of a possible territorial function through acoustic marking; however, the observations of physical demarcation at boundary sites through defecation may indicate territorial demarcation through olfactory communication.

The use of urine and faeces in territorial defence has been reported in many primates (Irwin, Samonds, Raharison and Wright, 2004). In *Alouatta*, communal defecation has been described in a number of species; *A. seniculus* (Braza et al, 1981; Neville et al, 1988), captive *A. caraya* (Neville et al, 1988; Shoemaker, 1979), wild *A. caraya*, *A. seniculus*, *A. pigra* and *A. fusca* (see Neville et al, 1988 for review) and may be associated with territoriality. Defecation marking may aid the defence of specific home range areas, such as sleeping sites, especially when the home range itself is too large in size to defend (Gorman and Mills, 1984) and can convey information to intruders which may help to avoid conflict (Gosling, 1982). However, communal defecation has also been suggested to simply function in cleaning (Hirano, Correa and de Oliveira, 2008) and body maintenance, therefore its function is not fully understood.

In *Alouatta*, additional forms of olfactory communication are suggested to function in territoriality and sociality, such as scent marking (Hirano et al, 2008). Scent marking is suggested to be involved in territorial defence, aggression and may play a

role in conveying dominance (Neville et al, 1988). Howlers are reported to rub parts of their body such as the throat (Sekulic, 1982b; Sekulic and Eisenberg, 1983) and muzzle (Neville et al, 1988), during confrontation with conspecifics (Sekulic and Eisenberg, 1983). In *A. guariba*, a study concentrating on the context of rubbing behaviour in three howler groups found that the majority of throat/hyoid rubbing occurred during intertroop conflicts and from this, maintain that this type of rubbing is associated with agonistic encounters. From these findings, the authors state that the frequency of rubbing episodes observed was too low to draw firm conclusions (Hirano et al, 2008) but that hyoid and sternum rubbing may also have alternative functions such as body maintenance (Neville, 1972) or in a sexual context. However, as rubbing is reported to be performed alongside howling bouts (Sekulic and Eisenberg, 1983), this is the reason that throat and muzzle rubbing and also defecation are included as indicators of territorial behaviour in this thesis (Chapter 3).

### *Alouatta pigra*

The bimodal calling pattern in *A. pigra*, with a peak in the morning and more pronounced peak in the late afternoon, has been suggested as displaying territorial defence (Horwich and Gebhard, 1983), as also reported in *A. seniculus*, where calling at specified times during the day may allow identification of the caller (Drubble and Gautier, 1993). The authors reported additional evidence for territoriality, in that loud calls were performed most frequently at an actively defended border and the resident group was observed to chase a neighbouring group out of their area. However, it is unclear what area or “territorial line” the authors are referring to during defence, as the brief map of the study groups provided with this work indicates that group ranges overlap. Also in this work, only one of the study groups was observed to interact with another conspecific group and one of the study groups was geographically isolated from

all other groups; therefore the authors' greatly overestimated conclusions that howling has a territorial role are not substantiated by evidence.

### *Alouatta guariba*

There is limited research into the vocalisations of other *Alouatta* species. The calls of *A. guariba clamitans* are reported to function in territorial defence, with males actively defending their whole home range, this from observations that the majority of roaring bouts were performed along the groups' home range border (da Cunha and Jalles-Filho, 2007). However, the authors' definition of a border was vague and no information was provided on the population density of brown howler groups in the area; it is therefore difficult to assume this function. Also, the authors only studied one group of brown howler monkeys for a limited period of time; these findings are therefore clearly preliminary and more research, including experimental investigations, are required.

### *Alouatta caraya*

In the only publication investigating the function of calls of *A. caraya*, it is suggested that loud calls function to maintain intergroup spacing in a different way to those previously described for the genus, as a form of "regular advertisement of occupancy" (da Cunha and Byrne, 2006). The authors presented both observational and experimental data on one group of *A. caraya*. Observations determined no pattern in calling location and that howling was performed throughout the home range. Playback experiments, simulating conspecific group presence at border areas and invasion into the home range, showed that more howl responses were performed to calls simulating invasion of the home range, and there were fewer responses to playbacks from border areas, compared with howling rates during real intergroup encounters. Also, groups

approached the speakers whilst calling, suggesting that responses were directed towards playbacks. The authors concluded that howls function in intergroup spacing, by means of reinforcing a group's occupancy by constant advertisement, a role of howling which has not previously been described. Calling was performed from throughout the home range, females joined in calling bouts indicating that they were also defending resources which are valuable to them and home range borders were defended during playback experiments. As male subjects approached the speaker and borderline chases between neighbouring groups were observed, this form of intergroup spacing was not classed as mutual avoidance by the authors. In the study a 'response' to playback experiments was defined as a call at any time within two hours of playbacks, which may allow for unrelated howling bouts to be classed as a response to playbacks. Although this study is the first to focus on the function of howl calls of *A. caraya*, including both observational and experimental aspects to investigate howl function, it only concerns one group of *A. caraya*. In this thesis, Chapter 3 includes both observational and experimental investigations in to the function of *A. caraya* howls of multiple males, to further determine their role in this understudied species.

### **1.3.3.2. Defence of food resources**

Howl calls are not only reported to function to maintain space use; studies have also provided evidence for the defence of food resources through howling. Active defence of an area of home range "a fixed portion of an individual's or group's range in which it has priority of access to one or more critical resources over others which have priority elsewhere or at another time" is a form of territoriality (Kaufmann, 1983, p 9), therefore food-based resource defence is a suggested type of territoriality. Howler population abundance is thought to be related to food availability (Chapman et al, 1999) and listeners will almost certainly find a food resource if they approach a caller, as

howlers are known to call from the most intensely used areas in their range, such as *A. palliata* (Whitehead, 1989). In *A. seniculus* and *A. fusca*, males perform seasonal patterns of roaring which are stronger during the dry season (Sekulic 1982a; Chiarello, 1995), as intergroup encounters are higher and howling can provide an active defence of highly desired food sources, such as fig trees (Sekulic, 1982a).

### 1.3.3.3. Opponent assessment

Females are also a limiting resource for male howler monkeys; thus, transmitting information on the identification and rank of an individual may be beneficial during mate selection and defence (Sekulic, 1982b; Wich and Nunn, 2002). Research carried out by Sekulic (1982b) on *A. seniculus*, suggests that howling not only deters intergroup males from attempting to enter or invade a group, but also that opponents can be assessed through the rate and duration of their howl calls. Groups with fewer male group members howled more than groups containing a large number of males, which suggests that males with less group support invest in vocal displays to advertise their fitness and fighting ability to intergroup males, or that by all males calling, the group size of the group may appear larger than its actual size. Solitary males rarely answer the roars of neighbouring groups in order to avoid advertising their lone situation to other males; however, if a female is present, then he will respond to her roars. The author suggests that solitary males, or those in a group with a low number of males, would not benefit from investing energy into costly howl calls. However, the author does not provide any suggestions on what component or part of the howl call is being assessed by opponents (only discussing call duration) and does not include any experimental evidence for these conclusions; only four groups are studied and no details are included about the social composition of groups or ages of group members.

Subsequently, further research into the significance of howl call duration was carried out by Sekulic and Chivers (1986). The authors compared the duration of calls performed by *A. palliata* and *A. seniculus* and found longer call durations in *A. seniculus*. This finding was attributed to differences in intragroup male-male competition and female support to the caller; however, conclusions from the study were over-reaching. Inferring that call duration may be related to the presence of females in a group is a questionable assumption, as the authors did not include the number of females in the analysis. Also, the calls compared were randomly selected howls performed during the dawn chorus, and as previously suggested; the function of howl calls varies dramatically. Therefore, differences in call duration may be attributed to what stimulus they were originally responding to, which was not mentioned by the authors.

During intergroup conflict, howl calls may themselves act as an alternative to physical aggression (*A. seniculus*, Altmann, 1959, Sekulic, 1982a; *A. palliata*, Carpenter, 1934, Southwick, 1962; *A. pigra*, Cornick and Markowitz, 2002, *A. caraya*, da Cunha and Byrne, 2006). In *A. caraya*, when males encountered another group they performed howl displays and were observed to chase invading groups. Experimental evidence showed that males vocally responded to the playback of conspecifics, even with no visual cues (da Cunha and Byrne, 2006). These findings suggested that calling may function in opponent assessment without the requirement for physical encounters, but the authors do not describe how assessment occurs or what information is being assessed. Conversely, *A. guariba clamitans* are reported to engage in physical conflict during intergroup encounters, suggesting that if howling functions in intergroup spacing, howling alone does not provide a sufficient cue for group spacing or settling intergroup conflicts in this *Alouatta* species (Chiarello, 1995), but that it may allow groups to limit fighting.

Using vocalisations as an alternative to physical conflict has been reported in a number of other animals (gray wolves, *Canis lupus* [Joslin, 1967; Harrington and Mech, 1978, 1979]; kookaburra, *Dacelo novaeguineae* [Beker, 2004]; gibbons, *Hylobates* spp. [Geissmann, 2002]). Loud calls, which may be restricted in acoustic properties by the vocal tract physiology of the caller, may provide information to receivers on physical attributes (Vehrencamp, 2000), thus providing information about the caller which may help avoid conflict. Producing low cost signals which reflect the caller's vocal morphology are termed "index signals" and may be an honest signal of body size, as it is suggested that in mammals, producing lower frequency calls may be an indication of a larger body size (Morton, 1977; Fitch and Hauser, 1995). Similarly, in many wild animal species, information on an individual's body size is transmitted through their calls (toads, *Bufo bufo* [Davies and Halliday, 1978; Fitch and Reby, 2001]; Australian frog, *Uperoleia rugosa* [Robertson, 1986]; Darwin's finches, *Geospizinae* spp. [Podos, 2001]; red deer, *Cervus elaphus* [Reby and McCombe, 2003]; domestic dog, *Canis familiaris* [Riede and Fitch, 1999]). In gibbon (*Hylobates* spp) and howler (*Alouatta*) species, the loud calls produced by males are not possible until sexual maturity (Corewyn, 2003); as a result, the caller's age (most likely a signal of maturity), sex and size may be communicated through howl calls (Crockett and Eisenberg, 1984; Strier, 2000; Ey et al, 2007).

The physical adaptation of *Alouatta* to perform low frequency sounds is an enlarged hyoid bone, located in the throat (Altmann, 1959; Strier, 2000) which acts as a resonating chamber and amplifier (Carpenter, 1934; Altmann, 1959; Bernstein, 1964; Baldwin and Baldwin, 1976; Sekulic, 1983; Thorington et al, 1984; Sekulic and Chivers, 1986; Crockett and Eisenberg, 1987). The hyoid bone varies in size between each species; the largest in *A. seniculus* and *A. belzebul*, the smallest in *A. palliata* (Thorington et al, 1984; Sekulic and Chivers, 1986; see Crockett and Eisenberg, 1987)

and is sexually dimorphic, being larger in the male than the female (Crockett and Eisenberg, 1987). Such morphological variation is correlated to call production; pitch, volume, call intensity, call duration (Altmann, 1959; Hershkovitz, 1949, 1969; Sekulic and Chivers, 1986) and body mass and may lead to individual differences in vocal quality (Wich and Nunn, 2002).

Loud calls can also provide information on group composition (Crockett and Eisenberg, 1987). In *A. seniculus*, Sekulic (1982b) discusses the differences in the vocal behaviour of group males. In groups containing multiple males, the author states that simultaneous calling by more than one male can be advantageous in terms of the information communicated to neighbouring groups, with adult males often seen to howl whilst positioned side by side. Group males form alliances and may cooperatively howl, in order to avoid intergroup conflict, as single or non-breeding males in neighbouring groups are the main competitors for access to group females. It is suggested that in groups with a few subadult and adult males, if all male members perform a few bouts of loud calls, it will minimise energy expenditure.

However, it is also known that intra-group competition for females can occur in this and other species (*A. pigra*, Kitchen et al, 2004) as group males do not all have equal access to females (Sekulic, 1981). In response, in *A. seniculus*, Sekulic (1982b) suggested that the alpha-male of a group would direct his aggression towards intragroup males and not call frequently. The author states that the assessment of intra-group opponents is visual, but the evidence for this states that males did not face each other during such encounters; Sekulic classed these bouts as different to those observed during cooperative howl bouts performed towards inter-group males, as males were positioned closer to each other during howling. The author however, does indicate that group participation in calling bouts depends on intragroup relationships, an aspect which requires further investigation.

However, the fact that subordinate males do not always cooperatively howl with the alpha male of a group also suggests that howling bouts may only inform others of the minimum number of males present in the group (Kitchen, 2004). As howling has been suggested to be an energetically expensive display in relation to the low energy diet *Alouatta* consume (Milton, 1980; Garber, 1987), groups with two or more males present can produce a similar competitive display by each member producing a few loud roars. In groups containing a low number of males, daily howl rates may be higher (Sekulic, 1982b). In *A. pigra*, playback experiments have determined that listeners assess their odds when hearing a conspecific group vocalising battle and respond appropriately; howling and approaching is less likely if the odds are unfavourable (Kitchen, 2004). However, in this study the author does not report which resources males are trying to defend. Alpha males themselves do not always respond to the howls of other groups, perhaps inducing withdrawal from an area or avoiding aggressive encounters with groups with unfavourable odds (Whitehead, 1987; Kitchen, 2004). The exception would be in terms of infant presence, when alpha males howl more often and for longer durations if their group contained offspring (Kitchen, 2004).

Females of the *Alouatta* genus also perform long calls which, like those of males, are performed during intergroup encounters but also play a role in supporting group males and deterring intergroup females from gaining access to the group or their mate (Sekulic, 1982a). In a playback experiment to *A. pigra*, Kitchen (2006) tested female responses to invading males, comparing numeric odds and the presence of offspring. Females were most likely to participate in howl battles when the simulated calling group contained the same number of males as her group and were least likely to respond when numeric odds were against her group. The author suggests that females assess intergroup fighting ability and do not always call alongside group males, but will participate in howling when it can be of most use to the group. Female *A. seniculus*

have also been reported to call towards extra-group males whilst located close to their mate (Sekulic, 1983) and often displayed aggression towards extra-group females, primarily through vocalisations (Sekulic, 1982a). However, as with much of the evidence provided on the role of howling, the level at which the studies are investigating is not provided and it is not understood what information content is conveyed in calls. Research into female *Alouatta* howl calls does not discuss alternative hypotheses for howl function, such as females using howls as a warning signal to extra-group females not to approach the resident group, or as a social bonding mechanism between partners. Such ideas could be investigated by conducting playbacks of conspecific female calls and determining the responses of focal females, with behavioural and vocal responses to extra-group females suggesting that group females perform vocalisations as a defence mechanism, perhaps to defend their partner and group.

#### **1.3.3.4. Mate attraction**

In the wild, behavioural observations concerning reproduction show that most infants are born to socially dominant males (Jones, 1985; Pope, 1990, 2000; Ryan et al, 2008) to which females display a preference in mating (Jones, 1985; Jones and Van Cantfort, 2007). As it is the adult male of *Alouatta* groups which perform the majority of howling bouts (Altmann, 1959) and are the sire to most group offspring, it is suggested that howl calls hold information, whether it be an honest advertisement of male quality or simply which male is most dominant, but it is not yet known as research to date has not experimentally tested these aspects of howls. As the majority of reported howl functions in *Alouatta* are related to male-male competition, which may be further related to female choice or mate selection, it would be unusual if females were not assessing male fitness and ability through their howling.

### 1.3.3.5. Additional functions

Other functions of loud calls include maintaining group structures, where it is suggested that vocalisations maintain the dominance hierarchy in *A. caraya*. However, the author does not explain the mechanisms for this to occur (Jones, 1983), aiding females to locate reproductive partners through their calling (Whitehead, 1989) and coordinating group activities such as progression, by informing all group members so that they will respond in a similar way (Carpenter, 1934). *Alouatta* groups usually travel in single file, following distinct arboreal pathways (Sekulic, 1982a). The “incipient roar type A” vocalisation, it is suggested, functions in group coordination as it is performed at times with no external stimuli; during group progression and preceding group movements (Collias and Southwick, 1952; Altmann, 1959; Bernstein, 1963). Other roles include warning members during periods of alarm or as an aggressive display as suggested previously when discussing howling as an alternative to physical conflict (Carpenter, 1934; Sekulic, 1982a; 1983; Calegario-Marques and Bicca-Marques, 1995; Chiarello, 1995).

From the literature, it is clear that although there are many suggested functions of howling in *Alouatta* species, little is known about the function of calls by *A. caraya*. Therefore this thesis aims to investigate the behaviours performed in association with naturally occurring howl bouts and, by conducting playbacks of a range of stimuli, experimentally to test howl functions with particular interest in the territorial and mating functions of howling. In captivity, the home range of *A. caraya* are restricted to their enclosure dimensions and many groups are housed in unnatural social groupings and/ or without the exposure to the calls of conspecifics. As the consensus of howl functions relate to intergroup encounters, this thesis aims to examine further the function of howling in *A. caraya* groups housed both within regular audible access of

conspecific howls and those groups which do not have such exposure in order to provide a more detailed understanding of the role of howl calls.

This thesis will also investigate the idea of acoustic individuality in howls (Chapter 2) which has not been studied in *Alouatta* species before. Marler (1956), Thorpe (1958), Rowell and Hinde (1962) and Andrew (1963) were among the first researchers to use sonographic software to represent visually both human and animal sound patterns (Snowdon et al, 1982). From this, researchers have been able to define acoustic structures and catalogue the vocal repertoires of a variety of species, facilitating investigation into the functions of vocalisations, contexts and signal complexity (Gautier and Gautier, 1977). In response, this thesis incorporates a study into the acoustics of the howl calls of multiple male *A. caraya* in order to determine the differences within and between the calls of individuals and those calls performed in a range of differing contexts; this thesis aims to address limited knowledge into acoustic specificity in this species.

#### **1.4. Captive animal welfare**

As many primate species are under threat from extinction in the wild, *ex-situ* conservation through both European and International breeding programmes (Forthman and Ogden, 1992; for review see Glatston, 1998) is an important aspect of captive management. The goal of many captive breeding efforts is the future reintroduction of species back into their wild habitat (Snowdon, 1989; Forthman and Ogden, 1992), however, in the majority of cases this is not a viable option due to habitat destruction and human threats, resulting in many species being bred in captivity for many generations.

In captivity, the welfare of animals is a subject which has been widely studied (Broom, 1991; Morgan and Tromborg, 2007). Animal welfare refers to the physical and

psychological state of an animal and can be defined in a number of ways. These definitions incorporate three main approaches; an animal's physical state; "the state of an animal as regards its attempts to cope with its environment" (Fraser and Broom, 1990, p 437); mental state as "welfare is dependent upon what animals feel" (Duncan, 1993) and also the ability of an animal to perform its natural desires and behavioural repertoire; "nurturing and fulfilment of the animals' nature" (Rollin, 1993). In the zoo environment, managers strive to promote good welfare and strict UK legislation outlines the importance of good animal welfare. The EC Zoos Directive (1999/22/EC) and UK's Zoo Licensing Act (1981) require that animals are maintained in terms of the biological and conservation requirements for each species. The Secretary of State's Standards of Modern Zoo Practice provides guidelines for how these requirements can be achieved. Zoos have been a driving force in setting standards and improving the welfare of captive animals, which is an on-going process. Improving animal welfare requires an understanding of welfare indices and a range of welfare assessments. There are three main approaches to measuring animal welfare; based on health and reproduction, subjective 'feelings' and psychological well-being and the performance of natural behaviours (Keeling, Rushen and Duncan, 2011). Each of these indices impact on each other and so are not often used as a sole measure of welfare.

#### **1.4.1. Health and reproduction**

Animals with good welfare are deemed to be healthy and "free from pain, injury or disease" (Brambell Committee, 1965). In a zoological setting, the health of animals can be maintained through the provision of veterinary care. Poor health can limit an animal's ability to cope with the environment, influence behaviour and may lead to pain. Regular monitoring of an animal's behaviour to detect changes from normal behavioural expression can be used to determine health issues (Hosey, Pankhurst and

Melfi, 2009); however, animals expressing good health are not always experiencing good welfare and so additional measures are required to determine welfare.

In captivity, reproductive success may signify good welfare, but if an animal does not breed, it cannot be assumed to be suffering from poor welfare (Keeling et al, 2011). The birth rates of many captive populations of primates have been found to be lower than their wild counterparts; (for example; *Eulemur* species [for review see Hearn et al, 1996]; gorillas, *Gorilla gorilla gorilla* [Beck and Power, 1988]; tamarins, *Saguinus geoffroyi* [Kuhar et al, 2003] and gibbons, *Hylobates leucogenys* [Lukas et al, 2002]). Low birth rates may be influenced by the active maintenance of many captive animal populations through controlled breeding programmes. Captive breeding programmes strive to sustain breeding groups with low inbreeding and kinship values, as these factors are known to negatively impact on welfare (Hosey et al, 2009). Individuals are not provided with the choice to select a breeding partner, which may reduce the opportunity of mate selection, as individuals are transferred between breeding groups mainly due to genetic-criteria. In addition, the implementation of contraception for captive animals, including sterilisation and implants (Glatston, 1998), influences reproductive success and may have a long-term effect on fertility, which is an interesting avenue of further research.

In captivity, many species are housed in unnatural social groupings (reviewed in Forthman and Ogden, 1992). Social group composition and group size are known to have a direct impact on the reproduction of group living primate species and so may influence welfare. In common marmosets (*Callithrix jacchus*), females display increased reproductive success when housed with a higher number of males compared to pair-housed females (Koenig, 1995) and in western lowland gorillas (*Gorilla gorilla gorilla*), a lack of successful reproduction in the captive population has been linked to a lack of social experience with conspecifics at an early age (Beck and Power, 1988).

Therefore to promote reproduction, animal managers should aim to hold species in social groups as near to wild compositions as is possible.

#### **1.4.2. Psychological well-being**

The second welfare concern, referring to the experience of animals, includes the mental well-being of animals and their “freedom from fear and distress” (Brambell Committee, 1965). The idea that an animal’s emotional state and feelings may influence welfare is an important consideration (Duncan and Dawkins, 1983). Many researchers believe that animals consciously suffer pain and feelings, therefore an animal’s welfare may be determined as poor when it experiences unpleasant subjective feelings (Dawkins, 1990). An animal’s feelings may influence its ability to cope with the surrounding environment (Broom, 1991), which in captivity, may change regularly and so the ability to cope with such changes would be highly beneficial.

#### **1.4.3. Performance of natural behaviours**

The performance of natural behaviours and providing a naturalistic environment for animals to inhabit is the final index of welfare and is also outlined by the Brambell Committee (1965) as the “freedom to express normal behaviour by providing sufficient space- by providing proper facilities and company of the animals own kind” (Farm Animal Welfare Council, 2009, p 2). For captive primates, the influence of the zoo environment; including restricted enclosure space, management restrictions (Hosey, 2005) sensory stimulation and lack of control of the surrounding environment (for review see Morgan and Tromborg, 2007) can greatly affect animal behaviour. Often zoo animals cannot perform their natural behavioural repertoire (Keeling et al, 2011). In a recent review by Hosey (2005), whilst discussing the influence of restricted space on

captive primates, it was concluded that the complexity of an enclosure is more important than its size.

Zoos are now moving towards building more immersive and natural exhibits (reviewed in Miller et al, 2004), but providing naturalistic enclosures for zoo-housed species is a difficult task (Fraser, 2008). When designing an enclosure, the perceived home range of species must be taken into account, especially for species which are known to be territorial *in situ*. It has been suggested that enclosure boundaries are perceived as territorial boundaries by their inhabitants (Hediger, 1950), but the majority of recent research has been conducted on felid species (Lyons, Young and Deag, 1997) and is highly speculative. Species in which the home ranges of neighbouring groups are known to overlap (e.g. *A. caraya*; da Cunha and Byrne, 2006), are restricted in terms of space and ranging area when in captivity. Also, animals do not often come into contact with conspecific groups or experience the vocal presence of neighbouring conspecific groups, which may also influence communication networks.

Unnatural social groupings or social deprivation can be detrimental to the welfare of an animal and influence its behaviour (Forthman and Ogden, 1992). In a study on 69 zoo-housed chimpanzees (*Pan troglodytes*), it was found that socially deprived animals, raised either without their mother or conspecific group members, performed higher levels of abnormal behaviours and reduced normal behavioural patterns (Martin, 2002). Social species are often housed in pairs (Forthman and Ogden, 1992), which is often an artefact of captivity due to breeding programmes and the presence of surplus animals. In captive *A. caraya*, many groups are housed only as a pair (European Studbook), although this species lives in larger social groups in the wild. The influence of social group composition on reproduction is discussed in Chapter 4, and the influence of social grouping on vocal behaviour is investigated in Chapters 2 and 3.

Before promoting the performance of natural behaviours, researchers have suggested the need to focus on “behavioural needs”, behaviours which are important for an animal to perform, which promote good welfare (Keeling et al, 2011). Behaviours such as sexual solicitation and territoriality may be required to maintain a natural repertoire for animals and promote reproductive success, particularly for species which may one day be reintroduced back into the wild. However, behaviours such as infanticide in *Alouatta* species may not be the type of behaviour which zoos aim to encourage, as some ‘natural’ behaviours may not improve the welfare of the whole group.

#### **1.4.4. Animal welfare assessment**

The methods of animal welfare assessment depend on which definition of animal welfare is adopted. There are a number of ways that the welfare of captive animals may be monitored, both physically and psychologically. The biological functioning of an animal can be determined through immediate physiological measures such as heart rate and hormone levels (Broom, 2001), or more long-term monitoring of body condition, reproductive success, survival (Fraser, 2009) and food intake (Dallman, 2001). However, these measures are often invasive and subjective, and may not be reliable measures due to the animal’s response to its environment and the process of gaining these measures (Dawkins, 2006). Behavioural observations of animal behaviour and their responses to the environment can be a beneficial way of providing a non-invasive welfare measure, which allows for whole groups of animals to be assessed and monitored. In particular, the performance of vocalisations has been suggested as a welfare indicator as they can signal emotional states (Dawkins, 2004, Buchanan-Smith, 2010) and alongside behavioural observations can be a valuable measure of welfare.

Often, the behaviours performed by captive individuals are compared to those of wild conspecifics, most commonly aiming to determine welfare through the performance of species-typical behaviours. However, this method requires intensive knowledge of the wild behavioural repertoire of an animal and as stated earlier, suggests that natural behaviours indicate good welfare, whereas the behaviours they exhibit may be adapted to captivity, such as diet and predatory escape (Fraser, 2009). Many behaviours may not be performed due to inappropriateness of the captive environment (Shepherdson, 1998) or may not have been recorded in the wild, such as regurgitation and re-ingestion in captive gorillas (*Gorilla gorilla gorilla*) (Gould and Bres, 1986) and chimpanzees (*Pan troglodytes*) (Baker and Easley, 1996). Therefore, this type of welfare assessment requires comparison of a number of captive collections to wild-type behavioural repertoires, to fully determine the influence of captivity.

In addition to assessing positive welfare indicators, behaviours signalling poor welfare can also be monitored. Behavioural indicators of poor welfare involve mechanisms employed by animals to help them cope with their environment. Stressors can be either acute, short-term stressors which are related to behavioural and physiological responses and are adaptive in terms of helping animals to cope with their environment, or chronic, long-term stressors which result in physical and psychological changes (see Morgan and Tromberg, 2007 for review). If a stressor impairs the ability of an animal to function, the welfare of that animal is considered to be reduced (Hosey et al, 2009).

Behavioural responses to stress in primates often focus on the performance of abnormal behaviours (Buchanan-Smith, 2010), such as self-directed behaviours (SBDs) or self-injurious behaviours (SIBs). Under environmentally or socially deprived conditions, primates perform behaviours where they attack or injure their own bodies (Hosey, 2007). In Old World primate species, the behaviours categorised as SBDs

include scratching, yawning, tongue flicking, sneezing and body shaking, which are commonly related to body maintenance (Maestriperieri, Shino, Aureli and Troisi, 1992; Aureli, 1998; Castles, Whiten and Aureli, 1998; Troisi, 2002). Self-directed behaviours are also suggested to act as displacement activities, as they are performed during periods of conflict, indicating stress, frustration and an increase in anxiety (Castles et al, 1988; Maestriperieri et al, 1992; Troisi, 2002; Spruijt et al, 1992). In New World monkeys, there is little research into the performance of SDBs. In a study on eight captive white-faced capuchins (*Cebus capucinus*), elevated SDB rates (self-scratching and autogrooming) were reported when focal animals were located near to conspecifics (Manson and Perry, 2000), suggesting preliminary support for SDBs indicating anxiety in New World monkeys. SDBs have not yet been validated in *Alouatta* species, only yawning has been suggested to function as displacement behaviour (Carpenter, 1934). In Chapter 3, the performance of SDB behaviours will be described in terms of context and suggestions for their function in *Alouatta* species is discussed.

In this thesis, I use a range of animal welfare assessment methods; including short-term and long-term measures, to investigate the welfare of captive *A. caraya*. Behavioural welfare assessment is conducted in Chapter 3 by comparing the performance of SDBs during the natural performances of howl calls and during playback experiments, the reproductive success of the European population of *A. caraya* is investigated in Chapter 4, and in Chapter 5, behavioural evidence collected in Chapter 3 is compared to the responses of *A. caraya* keepers questioned about auditory playbacks and husbandry to determine welfare. Using a number of welfare measurements helps to validate findings and by sampling multiple *A. caraya* groups housed in zoological collections, allows practical recommendations for captive management of the species to be provided.

### 1.5. Howlers in captivity

The most common captive *Alouatta* species is *A. caraya*, representing 78% of internationally held howler monkeys (International Species Information System (ISIS), 2011). The captive *A. caraya* population is coordinated through both a European and International Studbook which controls the transfer of individuals between groups and dictates on the size and composition of social groups in captive collections. It is suggested that howlers rarely breed in captivity, with the only published evidence being that 48 births were recorded in 43 years at 12 Brazilian zoos (Gomes and Bicca-Marques, 2003). Although this study did not clarify the number of groups held at each zoo, this is a low birth rate as howlers are not seasonal breeders, particularly when food is constantly available, as in captivity (Shoemaker, 1979, 1982). Howler species are proposed to be difficult to maintain in the captive environment (Kinzey, 1997). *A. caraya* are suggested to be the most reproductively successful of *Alouatta* species when housed in captivity (Baker, 1987), which may be the reason why they are the most popular *Alouatta* species held in zoos.

In addition to the lack of knowledge into the vocalisations of many *Alouatta* species, there is even less known about the behaviour of *A. caraya* in captivity. Captive studies have investigated maintenance and reproductive behaviours of a group of *A. caraya* (Shoemaker, 1978, 1979; Benton, 1979) and work conducted by Neville and Gunter (1979) discusses social relations and group structures in the same two captive groups. In the wild, howler monkeys are well adapted to arboreal habitats, being typically found in the middle-upper strata of forests, sometimes on lower branches at the forest edge (Mittermeier and van Roosmalen, 1981), aided by a prehensile tail (Mittermeier et al, 1988). Being located high in the trees can make behavioural studies in the wild very difficult. By studying howlers in captivity using focal observations of

multiple groups, accurate observations and measurements of reproductive behaviour can be made.

### **1.5.1. Social grouping and reproduction in captivity**

Captive *A. caraya* group social characteristics are controlled, which not only inhibits the performance of natal emigration, a behaviour which is necessary for successful reproduction in stable groups of wild *A. caraya*, (Kowalewski et al, 1995), but can also influence male-male competition, limiting the possibility of intragroup male aggression and infanticide. Current recommendations from the European Studbook coordinator are that subadult males are removed from a group at three years of age which is when they are thought to start showing interest in the groups' breeding female and subadult females are moved at 2.5 years. Reproductive competition in *A. caraya* groups is higher between males than females (Bicca-Marques and Calegario-Marques, 1998); therefore, by reducing male-male competition within captive groups, it was assumed that this would provide a stable social group in which breeding may freely occur. However, in a study of captive *A. caraya* by Jones (1983), the adult male, subadult male and young males all copulated with group females. Although the adult male was observed to copulate fewer times than the subadult male in the group, all of his copulations were performed when the only receptive female was in peak estrus at the time. In the wild, *A. caraya* group males commonly form coalitions with other intragroup males, providing an advantage for both dominant and subordinate males for greater competitive ability over single males in the group and establishing and maintaining female possession. In *A. seniculus*, a dominant male's coalition with related males helps to increase his reproductive status (Pope, 1990). In females, although female-female competition occurs (Pope, 2000), similarly to males, wild *A. seniculus* females also form coalitions within the group, forming permanent alliances with other

females who in the group (Eisenberg, 1977). In captivity, related males and females are removed from the natal group and transferred to another group to optimise the genetic composition of offspring in a relatively small population; therefore, these social bonds are prevented from forming which may influence reproductive success.

Preliminary findings show that in the European population of *A. caraya*, reproductive rates are low (John Partridge, studbook coordinator, 2010). To elucidate the factors influencing breeding success in captivity, this thesis aims to assess the influence of a range of variables; social grouping, exposure to conspecific howling and the performance of howl calls by adult males through detailed analysis of all reproductively active individuals in the European studbook. Many *A. caraya* groups are held as a single pair (one adult male, one adult female), which is unnatural. Although housing *A. caraya* in a pair eliminates intrasexual competition, it also eliminates female mate choice and reduces intra-male competition which in turn dictates male rank and thus can influence reproductive rates. One of the studies in this thesis investigates the relationship between environmental factors and reproduction and from these findings; suggestions for the management of *A. caraya*, to increase group numbers in the future can be made.

## **1.6. Environmental enrichment**

Another concern for captive species, especially if species are to be part of a successful reintroduction programmes (Jule et al, 2008) is that as they adapt to captivity, their wild-type repertoire may be lost (Wallace, 2000; Rabin, 2003). In addition to being housed in restricted social groups, for those captive species which perform vocalisations as an important part of their communication system, may not be exposed to the calls of conspecifics, as often only one group of a species is housed in a zoological collection. Animals therefore are not exposed to the sensory stimuli that they would experience in

the wild. As one of the main aims of this thesis is to investigate the welfare of howler monkeys in captivity, the importance of this form of communication and the function of howling can be further assessed by determining the efficacy of the playback experiments as a form of environmental enrichment.

The application of environmental enrichment is one of the ways in which natural behavioural repertoires can be promoted. This husbandry technique aims to improve the biological functioning of a captive animal through modifications to its environment (Newberry, 1995). There are many working definitions of enrichment (for reviews see Line and Markowitz, 1987; Newberry, 1995; Dean, 1999; Young, 2003; Will et al, 2004) many of which include providing opportunities to perform wild-type behaviours (Carlstead and Shepherdson, 1994; Shepherdson, 1994). Enrichment can be divided into a number of types; including food-based, physical, social, sensory, cognitive (Hosey et al, 2009). For this thesis, three broad categories of enrichment are defined; food-based, manipulative and sensory (visual, olfactory and auditory), adapted from Buchanan-Smith (2010), who termed manipulative as “cognitive” enrichment. In Chapter 5, which investigates enrichment use for captive *A. caraya*, social enrichment was not deemed a separate enrichment type. The influence of conspecific presence within zoological institutions was determined by assessing auditory stimulation and was classified as a form of sensory enrichment. The category of physical enrichment was not included in Chapter 5 as the study focused on the provision and efficacy of sensory enrichments on primate species.

The captive environment is less complex, more predictable and provides less choice and control to animals than wild habitats (Carlstead, 1996). In response, the categorisation of enrichment types must address these three concepts; complexity and novelty, choice and control (Buchanan-Smith, 2010). Increasing the complexity of an animal’s enclosure may address its physical and social needs, and the addition of

enrichment may also challenge its cognitive needs, as non-complex environments may be predictable, which can lead to boredom (Buchanan-Smith, 2010). The presentation of enrichment should be goal orientated, which can be assessed in terms of welfare, therefore the efficacy of an enrichment type can be determined. When first provided, the novelty value of enrichment may be the main reason for its efficacy; however, with repeated presentation, animals may become habituated and may no longer perform the enrichment's goal behaviour (Hosey et al, 2009) and it is no longer deemed effective.

By providing an animal with a more complex environment, we are providing this animal with choice and thus control over its environment. In terms of animal welfare, providing choice may have a positive influence as the animal is given control over its environment based on its motivation and desire at any one time (Buchanan-Smith, 2010). Hutchinson (2005) outlined a number of beneficial reasons for providing choice including; "exercising the mind of a 'bored' animal", an animal's preferences may change throughout the day and that new options may be perceived as better than previously provided options. Although choice may be seen as beneficial, it can also lead to stress, with unpredictability and high levels of novelty (Chamove and Anderson, 1989). Therefore, the presentation of enrichment must be organised and monitored. The use of enrichment programmes (Dobbs and Fry, 2007) are becoming a popular method of enrichment provision. Presenting enrichments on an unpredictable schedule, or by increasing the complexity and challenge posed by the enrichment, can help to reduce habituation. Enrichments must also be species and often individual-specific, taking into account the personality and history of its recipients.

By providing goal-based enrichments, wild-type behavioural repertoires may be encouraged and the contingent link between behaviour and response achieved. As outlined by Buchanan-Smith (2010), most research on primates aims to determine enrichment preferences rather than their motivated choice of enrichment. Specific goal-

seeking behaviours which are internally motivated are termed appetitive (Hosey et al, 2009); behaviours such as finding food or performing territorial vocalisations. The behavioural response to such behaviours is goal-directed, such as actually consuming food or chasing off a competitor. By providing this contingent link we can provide animals with control over their environment as they can predict the outcome of their behaviour. If this contingency or control is lost, it may seriously influence an animal's psychological well-being (Shepherdson, 1994). As enrichment focuses on including positive features to a captive animal's life, research should investigate control over positive events such as food provision, novel items and the sensory environment (Buchanan-Smith, 2010) and provide a range of different enrichment types, to stimulate a range of behaviours.

Recent surveys highlight the application of different enrichment types in captivity, but show that there is limited use of sensory enrichments (de Azevedo et al, 2007; Hoy et al, 2010). The captive environment can be a noisy place and animals are exposed to a variety of sounds (Anthony, 1963; Konovalov, 1986). When providing auditory enrichment, the goal of playing that sound is an important consideration. For many primate species, the performance of vocalisations are an important form of communication and function in pair bonding or mate advertisement and attraction (e.g. mouse lemurs, *Microcebus murinus* [Zimmermann and Lerch, 1993]; Barbary macaques, *Macaca sylvanus* [Semple, 1998]; siamang, *Hylobates syndactylus* [Geissmann and Orgeldinger, 2000], gibbons, *Hylobates* spp. [Cowlshaw, 1996]). The playback of conspecific specific calls can help to facilitate or encourage specific behaviours. Playback of conspecific calls to captive gibbon species has shown that listeners respond to conspecific calls in an appropriate manner, suggesting a positive influence on their behavioural repertoire (Mueller's gibbons, *Hylobates muellerii* [Harraway et al. 1988; Maples et al., 1988]; agile gibbons, *Hylobates agilis* [Maples and

Harraway, 1982]; lar gibbons, *Hylobates lar* [Shepherdson et al. 1989], see Volodina and Volodin, 1999 for review).

Research into the influence of hearing conspecific neighbouring group vocalisations, located in the same institution, termed the ‘neighbor effect’ has been studied in captive chimpanzees (*Pan troglodytes*, Baker and Aureli, 1996; Videan, Fritz, Schwandt and Howell, 2005) and common marmosets (*Callithrix jacchus*, Watson and Caldwell, 2010). These studies have found that individuals perform significantly more vocal responses when exposed to higher levels of neighbour vocalisations. Both vocal and behavioural responses in these studies showed that subjects react to intergroup vocalisations, which are linked to social contagion, due to the performance of appropriate response behaviours. However, these studies also reported that ‘neighbor effect’ evoked an increase in agonistic and anxiety behaviours when vocal and noise production by the neighbouring groups were high. This suggests that exposure to conspecific calls encourages species-typical behaviours in listening groups (Baker and Aureli, 1996). As many captive-housed vocal primate species are not exposed to the calls of conspecific neighbours, there is a potential for playbacks to evoke desirable or ‘goal’ behaviours and improve the welfare of captive individuals but care must be taken to ensure they do not increase anxiety.

The influence of ‘ecologically relevant sounds’, sounds which may be heard in the wild, on animal behaviour have also been studied. Although animals may be expected to react appropriately to the sounds experienced *in situ*, in a study by Ogden, Lindburg and Maple, 1994), it was found that gorillas (*Gorilla gorilla gorilla*) responded to the playback of rainforest sounds with increased agitation and displays and did not habituate to the sounds with time. The study was carried out on a small group of gorillas; however, these preliminary findings suggest that it cannot be assumed that captive animals will benefit from exposure to a more naturalistic acoustic environment

and that introducing additional sounds into the captive environment may lead to stress (Ogden et al. 1994; reviewed by Honess and Marin, 2006).

Many of the sounds experienced in captivity and used as auditory enrichment are however, 'unnatural' and man-made. In human research, music is known to have a positive influence on psychological well-being (see Wells, 2009 for review) and in response, laboratory animal care staff play music and radios to their animals (Sherwin, 2002; Van Loo et al, 2004; Patterson-Kane and Farnworth, 2006). However, research into the application of music as a form of stimulation has presented mixed results. The influence of both radio and stereo music on captive chimpanzees (*Pan troglodytes*) has found that music had significant positive effects on behaviour; including decreased aggression and increased inactive resting and social behaviour (Howell, Roeder, Nelson, Fritz and Schwandt, 2002; Howell, Schwandt, Fritz, Roeder and Nelson, 2003). Conversely, in western lowland gorillas (*Gorilla gorilla gorilla*), playing classical music led to a decrease in conspecific-directed aggression and abnormal behaviour (Wells, Coleman and Challis, 2006). More recent studies concerning acoustic preferences of primates showed that when compared to human subjects, both cotton-top tamarins (*Saguinus oedipus*) and common marmosets (*Callithrix jacchus*) displayed a preference for slow compared to fast tempo music, but when given the choice, chose silence over hearing music (McDermott and Hauser, 2007). Although there is a requirement for further research into the influence of human-made sounds on captive primates, it is clear that these sounds are biologically meaningless. A recent study conducted by Snowdon and Teie (2010) however, investigated responses of cotton-top tamarins (*Saguinus oedipus*) to music composed specifically for the species which incorporates biological relevance. The music played contained the range of call frequencies and acoustic specificities from fear/threat and affiliative calls produced by the species and responses were compared to those performed towards human music.

The study found that tamarins were more responsive to their own music; performing increased moving, anxiety and social behaviours after hearing fear/threat-based music than affiliative-based music. The monkeys also responded to human fear/threat-based music with decreased movement. Both of these studies highlight the importance that sounds which are deemed pleasant to human listeners cannot be expected to elicit the same or similar responses in animals.

As all enrichment provided by zoos aims to be goal-based, it is difficult to understand the purpose of playing human-made sounds to animals, as there is contradictory scientific evidence of it improving welfare. One of the reasons may be to help 'mask' background noises and the sounds of visitors (Van der Weerd and Baumans, 1995; Brent and Weaver, 1996; Mallapur and Chellum, 2002; Wells et al, 2006; Wells, 2009). Unfortunately, again, the lack of scientific evidence and understanding of the information which is conveyed in sounds may be the reason that it is not a popular enrichment type in captivity (de Azevedo et al, 2007; Wells, 2009). By measuring the provision of enrichment, in particular auditory stimulation to primate species and specifically groups of *A. caraya*, this thesis explores the use of auditory enrichment for a highly vocal species. Comparisons can then be made between responses to scientific findings from playback experiments to evaluate the efficacy of enrichment and determine its use in captive husbandry.

### **1.7. Thesis aims**

This thesis reports a series of studies which investigate the vocalisations of the black and gold howler monkey (*A. caraya*) in order to determine the function of howl calls and their influence on the welfare of individuals housed in captivity. Although there has been extensive work conducted on the behaviour of howler monkeys in the wild, studies have mainly focused on three species (*A. palliata*, *A. seniculus* and *A. pigra*). This thesis aims to address the large gaps in our knowledge of the behaviour and

vocalisations of *A. caraya*; Chapter 2 concerns intensive acoustic analysis of howl calls, to be the first study to explore contextual and individual differences between the calls of multiple males and Chapter 3 aims to determine the function of howl calls in this species through both observational and experimental studies. The welfare of captive housed *A. caraya* is assessed in Chapter 4 and aims to establish the influence of both social and environmental factors on reproductive success and behaviour. The study comprising Chapter 5 aims to determine the use of environmental enrichment, in particular auditory stimulation, to provide evidence for optimal captive conditions to support the welfare of *A. caraya* groups.

## **CHAPTER 2: Individual and context-specific variations in howls of black and gold howler monkeys (*Alouatta caraya*)**

### ***Abstract***

Call individuality has been studied in a range of primate species and can be related to the vocal morphology and body size of the caller through the performance of index signals. These calls may provide cues to the body size and ultimately, fighting ability of individuals; therefore, are important in calls which may require assessment of opponents and function in intertroop competition. Within individuals, call acoustics may also vary depending on call-context, which allows for detailed research into the complexity of communication systems, and comprehensive understanding of the information conveyed in calls. We recorded the howl vocalisations performed by captive male black and gold howler monkeys (*Alouatta caraya*) and analysed the acoustic features of full howl calls to provide a detailed investigation into howl acoustics. In the wild, howl calls have a variety of functions including mechanisms of inter-troop spacing, mate defence and opponent assessment; therefore, we aimed to determine both contextual and individual differences in call characteristics. We report a vocal repertoire of 10 vocalisations, including the ‘throat pulsation’, a sound not previously described in *Alouatta* species. Findings suggest that *A. caraya* perform context-specific howls, evoked by a range of stimuli: calls of non-sympatric primate species, vehicle and machinery noise, calls of familiar conspecifics and spontaneously without any visual or acoustic trigger. We also found differences in the acoustic characteristics of calls performed by different individuals. Individuality may be explained by differences in the morphology of the hyoid bone, the resonating chamber

which amplifies sound, suggesting that howling may be an index signal, providing a low cost indication of male attributes, perhaps linked to body size.

**Keywords:** *Alouatta caraya*, context-specific, howl, vocalisation, acoustic analysis.

## 2.1. Introduction

Individual variation in the acoustics of long-distance calls (loud calls), has been reported in many primate species (Cheney and Seyfarth, 1990). Acoustic variation may be important in signalling caller identification (Thomas langur, *Prebytis thomasi*, Wich et al, 2003), sex (common marmoset (*Callithrix jacchus*), Norcross and Newman, 1993), body size (pigtail macaque, *Macaca nemestrina*, Gouzoulez and Gouzoulez, 1990) or group rank (baboons, *Papio cynocephalus ursinus*, Fischer et al, 2004), both playing a role in intertroop avoidance and mate attraction.

Within-individual variation in the calls performed in different contexts have also been studied in primate species (e.g. chimpanzees, *Pan troglodytes* [Notman and Rendall, 2005]; Barbary macaques, *Macaca sylvanus* [Fischer and Hammerschmidt, 2001; mountain gorillas, *Gorilla gorilla beringei* [Seyfarth et al. 1994]; Wied's marmosets, *Callithrix kuhlii* [Rukstalis et al. 2003]; vervet monkeys, *Chlorocebus pygerythrus*, Seyfarth et al. 1980a; common marmosets, *Callithrix jacchus* [Norcross et al. 1999]; Diana monkeys, *Cercopithecus diana* [Zuberbühler et al. 1997]) which suggests that calls are multi-functional (Wich and Nunn, 2002) and that animal vocal systems are complex.

In this paper we investigate contextual and individual variation in the loud calls of captive male *Alouatta caraya*. In the wild, *A. caraya* perform howl vocalisations in

response to naturally occurring stimuli such as inter-troop confrontations and intra-troop aggression and during extremes of weather (rain and thunder, Calegario-Marques and Bicca-Marques, 1995). The majority of howl vocalisations are performed during the dawn chorus (Da Cunha and Byrne, 2006) as found in other *Alouatta* species (*Alouatta palliata*, Altmann, 1959; Baldwin and Baldwin, 1976; Chivers, 1969; Collias and Southwick, 1952; *Alouatta seniculus*, Sekulic, 1982b). As howls are performed in a variety of situations, the functions of *Alouatta* howls are disputed and are suggested to include regulation of space use, mutual avoidance of neighbours, territorial demarcation, opponent assessment, predator avoidance, resource and mate defence (reviewed by Da Cunha and Byrne, 2006) and more recently territorial defence (Farmer, 2011, in prep). With so much variation in both contextual use of howls and the function of these calls, it seems likely that the calls themselves might communicate different information about both individuals and situations.

Howl bouts are constituted of roar vocalisations, which are comprised of a sequence of exhaled and inhaled syllables (Baldwin and Baldwin, 1976) and are sometimes described as a fusion of repeated barks (Eisenberg, 1976; Sekulic, 1982a). They involve three phases: the introduction or preface followed by a period of increased intensity and amplitude, the climax or crescendo, and end with a coda, decreasing in amplitude, which consists of progressively shorter notes (Drubble and Gautier, 1993; Whitehead, 1987, 1989; Schön Ybarra, 1986). Roar vocalisations are primarily performed by adult males, with subadult males and females of the group often joining in (Altmann, 1959; Steinmetz, 2000; Whitehead, 1995; Schön Ybarra, 1986). The majority of research has been carried out on wild populations of *A. palliata* and *A. seniculus*, studying only the roar element of the howl vocalisation (Baldwin and Baldwin, 1976; Chivers, 1969; Drubble and Gautier, 1993; Sekulic, 1982a; Thorington et al. 1984;

Whitehead, 1995; Schön Ybarra, 1986). For this study, we concentrate on complete howl vocalisations of captive *A. caraya*, which are comprised of a series of roars.

*A. caraya* is the most common howler species held in captivity, with 79% of all howler monkeys in zoos being of this species (International Species Information System, ISIS, 2011). However, there is limited research on the acoustic characteristics of the howls of this species. A study describing the acoustic characteristics of six species of *Alouatta* loud calls includes descriptions for one recording of a captive male howl (Whitehead, 1995) and a study investigating the vocalisations of one wild *A. caraya* group reported a repertoire of 11 vocalisations (Calegario-Marques and Bicca-Marques, 1995). However, this study was conducted over a short period of time (six months) and like all other papers defining the repertoire of *Alouatta* species, call descriptions and contexts were ambiguous, identifying sounds only in the conditions under which they were observed (Altmann, 1959; Baldwin and Baldwin, 1976; Carpenter, 1934). These measurements may often omit information as wild individuals are located high in the tree canopy when vocalising and some behaviours cannot clearly be seen (Schön Ybarra, 1986). Other authors have briefly discussed the calls of *A. caraya* within their papers, suggesting that the roars of *A. caraya* are similar to those of *A. seniculus* in terms of lowest frequencies (Schön Ybarra, 1986; Thorington et al. 1984; Whitehead, 1995).

The first aim of this paper is to catalogue the full repertoire of captive *A. caraya* vocalisations. Then, focusing on the howl call, we analyse the full duration of howl bouts, the first study in any *Alouatta* species, investigating all acoustic variables. We then aim to determine whether males perform acoustically different howl calls in different contexts. Finally, we aim to investigate whether the acoustic characteristics of howl calls vary between individuals, since howl vocalisations are suggested to function in mate attraction and to advertise fighting ability (Sekulic, 1982a; Kitchen et al. 2004).

As we observed males held in different social groups, we predicted that howls may also be acoustically different when performed by males housed in pairs versus family groups as howling is suggested to function in advertising a male's occupancy and as an alternative to physical conflict (Da Cunha and Byrne, 2006). Investigating context specificity of vocalisations and individual differences in call acoustics can contribute to the knowledge of animal vocal system complexity and help to address what information that is conveyed and processed by receivers. By focusing on the loud calls of *A. caraya*, this study will also provide a more comprehensive understanding of the function of howl vocalisations.

## **2.2. Methods**

### **2.2.1. Study sites and subjects**

We studied the vocal behaviour of seven captive male *A. caraya*, each housed in a separate group, held across five UK zoos. Five individuals were housed in a family group with an adult female and a range of subadults, juveniles and infants. The remaining two males were each housed as a pair, with one adult female.

### **2.2.2. Vocal recording**

We defined a howl bout as the production of a series of roar vocalisations (Schon Ybarra, 1986), lasting for a minimum duration of 60 seconds (Drubbe and Gautier, 1993). Howl vocalisations were recorded between 0800 and 1630 hours, for 16 days at each institution with an Edirol R-1 solid state recorder and Beyer Dynamic MCE 86N(C)S) directional microphone equipped with Rycote softie windshield

(sampling frequency: 44.1 kHz; 24-bit accuracy). A total of 47 howl bouts were recorded.

Table 2.1. The number of howl vocalisations analysed for each male *A. caraya*.

Individual	Number of howls analysed	Housing condition	Number of howls performed in each context				
			Spontaneous	Non-sympatric primate	Vehicle	Machinery	Conspecific howl
1	4	Family	0	0	2	1	1
2	6	Family	2	3	0	0	1
3	3	Pair	0	0	0	0	3
4	4	Family	1	0	0	2	1
5	4	Family	4	0	0	0	0
6	2	Family	0	0	1	1	0
7	5	Pair	4	0	0	0	1

### 2.2.3. Acoustic analysis

As the study was carried out in a captive setting, all recordings were inspected both audibly and visually and only files with minimum background noise and distortion were selected. A total of 28 howls were analysed. The number of calls analysed from each of the seven vocal males ranged from two to six (Table 2.2), as some individuals performed a disproportionate number of howls. Previous studies concerning howl vocalisations have only analysed one ‘roar’ or ‘climax’ component of a howl, which we define as a phrase. In this study we analysed the full duration of each howl bout performed. The criteria we set to determine a howl was that the total duration of the vocalisation was longer than 60 seconds (Drubble and Gautier, 1993) and was

comprised of a series of roar vocalisations (Eisenberg, 1976), with other types of vocalisations performed in between (Cornick and Markowitz, 2002).

We manually measured temporal variables on waveforms and frequency-related variables on spectrograms (DFT-length: 1024 points; temporal overlap: 50%; Hann window; bandwidth: 61.9 Hz; temporal resolution). A total of 13 temporal and six spectral measurements were calculated (Table 2.2; Figure 2.1). We measured frequency quartiles for a more reliable measure of frequency due to the noisy characteristics of howler calls, as recommended by Darden et al (2003). We used Raven Pro 1.4 Interactive Sound Analysis Software (Cornell Lab of Ornithology, Ithaca, NY, USA) on a Macintosh Mac Book. A phrase section of a howl bout was determined both visually and acoustically as a period of increased intensity and amplitude.

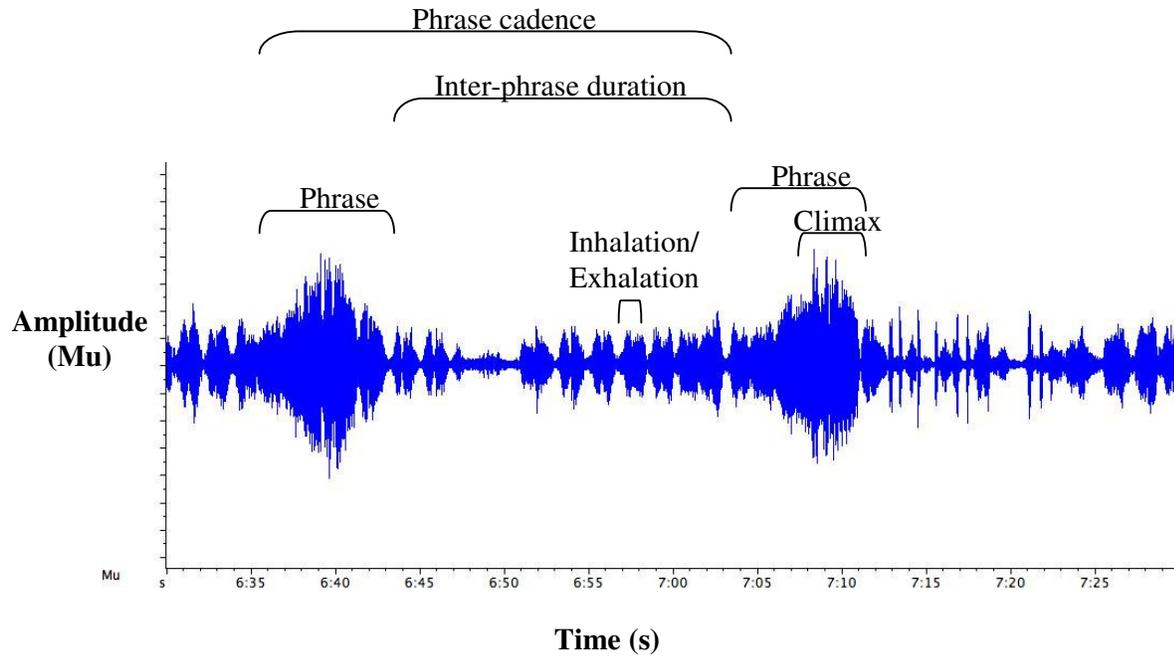


Figure 2.1. Waveform of howl vocalisation indicating acoustic measurements.

#### 2.2.4. Statistical analysis

We extracted a total of 19 acoustic measurements from the howl vocalisations. Due to our small sample size we employed the Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy for all of the original acoustic variables, to determine the appropriateness of applying a Factor Analysis to the data, by screening variables which are not strongly related to factors (Hutcheson and Sofroniou, 1999). All variables with a communality value  $< 0.60$  were dropped from the model until we reached  $KMO > 0.60$ . This method provided an overall KMO of 0.629 including nine acoustic variables (Table 2.2) with the minimum of all communalities as 0.890, the maximum as 0.976 (mean = 0.929,  $SD \pm 0.03$ ).

We conducted a Principle Components Analysis (PCA) to reduce the nine acoustic variables into a smaller set of orthogonal factors which accounted for the

variance between the acoustic measures. A varimax rotation was applied for simplification of interpretation of each variable with a single factor. We determined the number of factors to accept based on eigenvalues  $>1$ , as suggested by Kaiser (1960). We then conducted Parallel Analysis (PA) (Wilson and Cooper, 2008) on our original data, a method which computes Principle Components criteria, to determine the number of factors to retain from PCA and only factors with eigenvalues greater than the PA eigenvalues were interpreted (Franklin et al. 1995).

Table 2.2. List and description of each acoustic variable measured for acoustic analysis

(\* indicates the variables included in the PCA analysis).

<b>Acoustic variable</b>	<b>Description</b>
Howl duration (s)	Time between onset of the 1 <sup>st</sup> sound and end of the last sound
No. phrases	Mean number of phrases performed in each call
Phrase duration (s)	Mean of time between the start and end of a phrase
Inter-phrase duration (s)*	Mean time between the end of one phrase and the start of the next phrase
Phrase cadence (s)*	Mean time between the start of a phrase and the start of the next phrase
No. climaxes*	Mean number of climaxes performed in a phrase
Climax duration (s)	Mean of time between the start of a climax to the end of the climax
No. of barks	Mean number of barks between each phrase
No. of grunts*	Mean number of grunts between each phrase
I-E	Mean number of inhalation-exhalation units between each

	phrase
High roar coda	Proportion of phrases in a call which ended in a high roar coda
I duration (s)	Mean duration (time from the start of air inhalation to the end) of air inhalation in a phrase
I Q25%, Hz	Frequency at which the inhalation amplitude distribution reaches the first quartile (25%) of total distribution
I Q50%, Hz*	Frequency at which the inhalation amplitude distribution reaches the second quartile (50%) of total distribution
I Q75%, Hz*	Frequency at which the inhalation amplitude distribution reaches the third quartile (75%) of total distribution
E duration (s)*	Mean time (from the start of air exhalation to the end) of air exhalation in a phrase
E Q25%, Hz	Frequency at which the exhalation amplitude distribution reaches the first quartile (25%) of total distribution
E Q50%, Hz*	Frequency at which the exhalation amplitude distribution reaches the second quartile (50%) of total distribution
E Q75%, Hz*	Frequency at which the exhalation amplitude distribution reaches the third quartile (75%) of total distribution

We used Generalized Linear Mixed Models (GLMMs, in PASW version 18, 2010, IBM, Chicago, IL, U.S.A) with normal distribution as data were not normally distributed (Kolmogorov-Smirnov all  $P < 0.001$ ) and identity link to investigate individual, contextual and social group differences in the PCA factors. To determine individual differences the model included individual number (1-7) as the fixed factor. To measure the strength of association between individuals, effect sizes and the

associated 95% confidence intervals (CIs) were calculated using Cohen's  $d$  (Cohen, 1988). GLMMs to assess the influence of environmental contexts surrounding howling and social grouping on the PCA factors included individual number (1-7) as a random factor, and as a fixed factor; environmental context (1-5; stimuli initiating howling, Table I). For all significant results, post-hoc pairwise comparisons with Bonferroni corrections were carried and all significant results reported.

We fitted both models using a backward elimination process to find the minimum adequate model for explaining the variance of the response variable. Only significant explanatory variables and two-way interactions were retained and models with the lowest Akaike's Information Criterion (AIC) value were interpreted. All tests were two-tailed.

## 2.3. Results

### 2.3.1. Vocal repertoire

Ten vocalisations were identified (Table 2.3). A new vocal component was found to be performed during howl calls, named the 'throat pulsation', which occurred in 66.6% of howls (mean number of throat pulsations performed  $\pm$  SE, in spontaneous calls =  $2 \pm 0.62$ ; towards non-sympatric primate calls =  $\pm 0.63$ ; vehicle noise =  $0.66 \pm 0.17$ ; machinery =  $1 \pm 0.43$ ; conspecific calls =  $2.66 \pm 0.31$ ).

Howls were only performed in following contexts; spontaneously occurring, which had no visible or auditory stimulus, and initiated by four stimuli: the call of a non-sympatric primate call (both visual and auditory stimulus on occasion), the passing of a vehicle (both visual and auditory stimulus), machinery (a man-made noise such as chainsaw, strimmer or leaf blower; both visual and auditory stimulus) and conspecific howls of another *A. caraya* male. Howl duration varied from 101.32 to 976.79 ms

(mean duration =  $470.36 \pm \text{SE } 39.79$  ms) and contained between one and 11 phrases per howl (mean number of phrases =  $5.84 \pm \text{SE } 0.61$  ms) and one to 21 climaxes per howl (mean number of climaxes =  $8.99 \pm \text{SE } 0.44$  ms). 5% of howls performed contained grunts and 70% of howls contained climaxes which ended in a high roar coda.

Table 2.3. List and description of the vocal repertoire of the black howler monkey (*A. caraya*).

<b>Call type</b>	<b>Description</b>	<b>Performer</b>	<b>Situation</b>	<b>Previously noted</b>
Howl or roar	Loud, low frequency sound, fusion of slow inhalation-exhalation sounds into more intense and rapid crescendos, mouth open in funnel shape. Duration longer than 60 seconds	Adult male	Spontaneous, hearing calls of known and unknown conspecifics, hearing calls of non-sympatric primate species, machinery or vehicles passing	Type A <sub>1</sub> (Altmann, 1959, Baldwin and Baldwin, 1976), roar (Calegario-Marques and Bicca-Marques, 1995), Type 1 (Carpenter, 1934)
Incipient roar	Loud, low frequency sound, fusion of slow inhalation-exhalation sounds, mouth open in funnel shape	Adult male	Responding to mild stimuli; vehicle passing or leaf blower at a distance	Type A <sub>2</sub> (Altmann, 1959, Baldwin and Baldwin, 1976), incipient roar (Calegario-Marques and Bicca-Marques, 1995), Type 3 (Carpenter,

				1934)
High roar coda	During a roar, at the end of a crescendo a sustained note produced, higher in frequency than those usually performed	Adult male	During a roar	Type A <sub>3</sub> (Altmann, 1959, Baldwin and Baldwin, 1976)
Roar accompaniment	During a roar produced by the adult male, other group members join in	Adult female, subadult males and females in the group		Type B (Altmann, 1959), Type B <sub>1</sub> (Baldwin and Baldwin, 1976)
Male bark	Loud, low frequency sound repeated at regular intervals	Adult male		Types C <sub>1</sub> (Altmann, 1959), male bark (Calegario-Marques and Bicca-Marques, 1995), Type 9 (Carpenter, 1934)
Woof	Low frequency sound repeated	Adult male	Preceding or at the end	Type C <sub>1</sub> (Baldwin and

	at regular intervals, quieter than bark		of a roar	Baldwin, 1976)
Incipient woof	Low frequency sound repeated at regular intervals, quieter than bark, mouth closed	Adult male	At the end of a roar to towards mild stimuli	Type C <sub>2</sub> (Baldwin and Baldwin, 1976)
Scream or screech	High frequency sound, mouth open, often baring teeth	Adult female, subadults, infants	Aggression or fights, when another group member attempts to remove the infant from the mother	Type I (Baldwin and Baldwin, 1976), stress shout (Calegaro-Marques and Bicca-Marques, 1995)
Rumble	Low frequency sound repeated in rapid succession, mouth closed	All age/ sex classes	During feeding or human-interactions	Rumble (Calegaro-Marques and Bicca-Marques, 1995)

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Throat pulsation	Rapid inhalation and exhalation of air, expanding and decreasing lung volume, mouth closed, rapid movement of the whole body	Adult male	Preceding, during or after a roar	Not previously described
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### **2.3.2. Acoustic characteristics of howls**

Principle Components Analysis with Parallel Analysis determined two factors that explained 65.5% of the total variation in the data set (Table 2.4). Factor 1 explained the highest proportion of the variance and was associated with four acoustic features related to the frequency of phrases in a call, indicating that calls phrases with energy concentrated in higher frequencies had shorter exhalation durations and phrase cadences. The second factor was related to two features, showing that calls with a longer inter-phrase duration and cadence contained phrases with energy concentrated in lower frequencies and less climaxes per phrase and less grunts were performed in a howl bout.

Table 2.4. Eigenvalues, variation and factor loadings explained by the two factors generated by Principle Component Analysis.

Factor	Eigenvalue	Variation explained (%)	Associated acoustic parameters	Coefficient	Acoustic dimension
1	3.95	43.85	I Q50%	0.87	Phrase frequency
			I Q75%	0.94	
			E Q50%	0.89	
			E Q75%	0.93	
			[E duration]	-0.27	
			[Phrase cadence]	-0.02	
2	1.95	21.66	Inter-phrase duration	0.89	Phrase duration
			Phrase cadence	0.87	
			[I Q50%]	-0.34	
			[I Q75%]	-0.18	
			[E Q50%]	-0.14	
			[No. of climaxes in a phrase]	-0.54	
			[Grunt]	-0.09	

### 2.3.4. Individuality of howls

We tested whether howls were individually distinctive. The acoustic characteristics of howls were different between individuals on both PCA factors; factor 1 (GLMM:  $X^2 = 24.51$ ,  $df = 6$ ,  $P < 0.001$ ), factor 2 (GLMM:  $X^2 = 16.30$ ,  $df = 6$ ,  $P =$

0.012). Effect size calculations determined differences between individuals in both factors 1 and 2 (Table 2.5), (Figure 2.2 and 2.3).

Table 2.5. Effect size Cohen's *d* and 95% CIs for differences between individuals for factors 1 and 2. (\*\*\*) indicates 'large' effect size, \*\* = 'medium' effect size, \* = 'small' effect size).

Individual comparison	Factor 1		Factor 2	
	Cohen's <i>d</i>	95 % Confidence Interval	Cohen's <i>d</i>	95 % Confidence Interval
1+2	0.864***	0.421 to 1.307	1.615***	1.116 to 2.114
1+3	-0.962***	-1.534 to 0.389	0.255*	-0.390 to 0.900
1+4	0.744**	0.243 to 1.245	0.617**	0.053 to 1.181
1+5	2.488***	1.987 to 2.989	0.430*	-0.134 to 0.994
1+6	1.764***	1.215 to 2.313	-0.873***	-1.537 to -0.210
1+7	2.076***	1.708 to 2.445	-0.316*	-0.871 to 0.238
2+3	-2.120***	-2.539 to -1.701	-1.491***	-1.964 to -1.018
2+4	-0.129	-0.506 to -0.248	-1.163***	-1.588 to -0.737
2+5	1.942***	1.565 to 2.319	-1.384***	-1.810 to -0.959
2+6	1.096***	0.721 to 1.472	-3.046***	-3.507 to -2.585
2+7	1.191***	0.916 to 1.467	-2.144***	-2.576 to -1.711
3+4	2.030***	1.563 to 2.498	0.395*	-0.132 to 0.922
3+5	4.029***	3.562 to 4.496	0.181	-0.346 to 0.708
3+6	3.653***	3.184 to 4.122	-1.376***	-1.978 to -0.774
3+7	4.466***	4.169 to 4.764	-0.638**	-1.170 to -0.106

4+5	2.135***	1.726 to 2.544	-0.229*	-0.690 to 0.232
4+6	-0.194	-0.586 to 0.197	-1.845***	-2.306 to -1.384
4+7	1.566***	1.302 to 1.831	-1.065***	-1.538 to -0.592
5+6	-1.202***	-1.594 to -0.811	-1.714***	-2.216 to -1.213
5+7	-1.549***	-1.813 to -1.284	-0.855***	-1.382 to -0.382
6+7	0.299*	0.396 to 0.020	0.640**	0.114 to 1.167

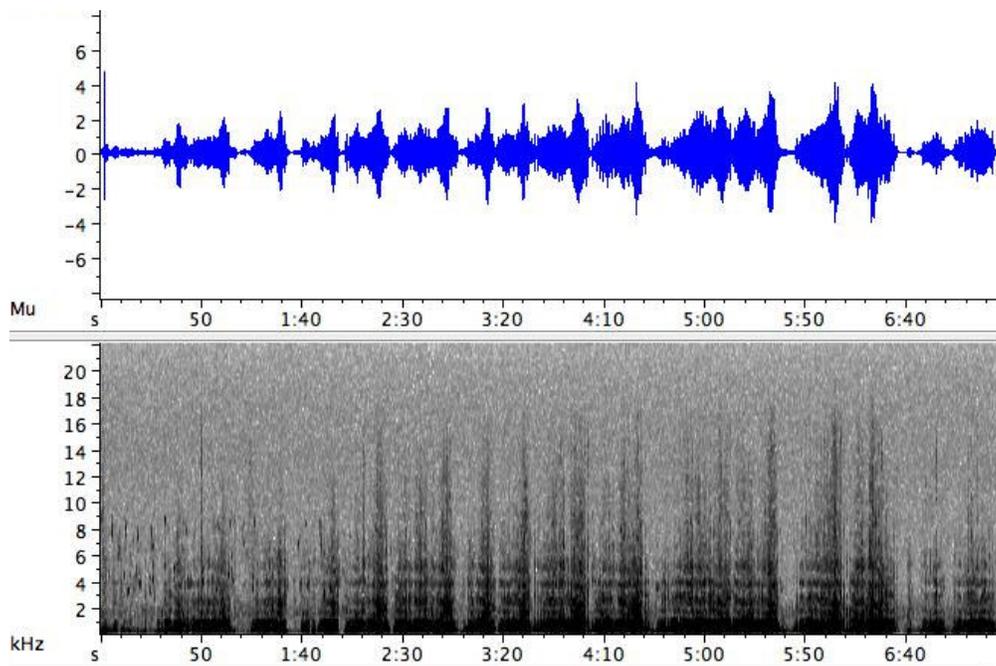


Figure 2.2. Waveform and spectrogram of a call performed by individual 1, incited by a non-sympatric primate species call.

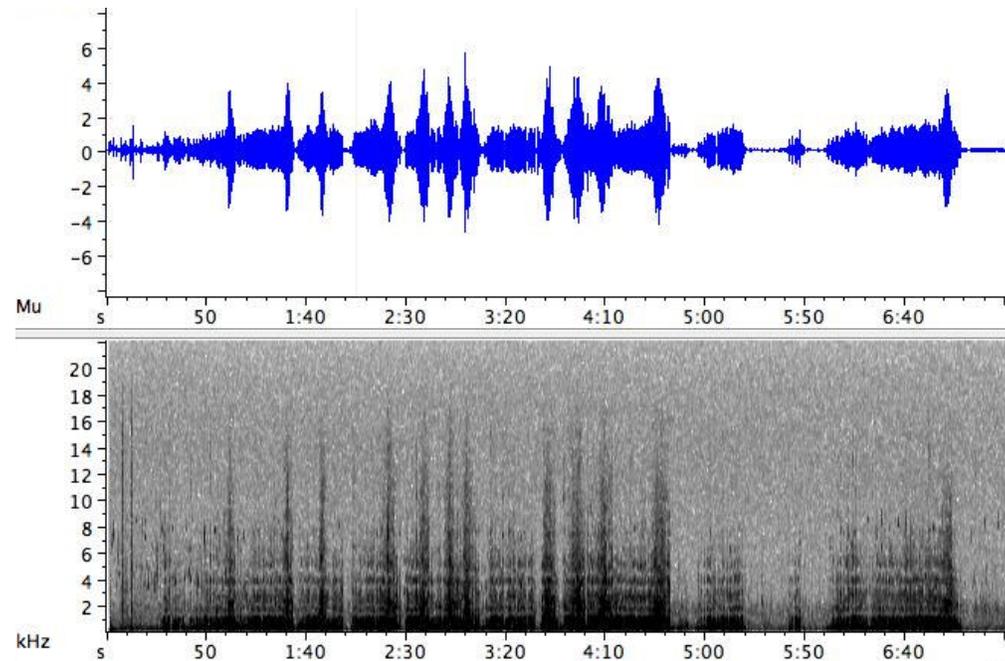


Figure 2.3. Waveform and spectrogram performed by individual 2, incited by a non-sympatric primate species call.

#### 2.3.4. Context-specificity

Acoustic characteristics of howls differed between the five contexts. Factor 1, associated with phrase frequency differed between call context (GEE:  $X^2 = 54.75$ ,  $df = 4$ ,  $P < 0.001$ ). Calls initiated by vehicle sounds contained phrases with energy concentrated in higher frequencies than spontaneously performed howls ( $P < 0.001$ ), machinery noise ( $P=0.018$ ) and those towards other species calls ( $P < 0.001$ ). Factor 2, associated with phrase duration, also differed according to call context (GEE:  $X^2 = 224.94$ ,  $df = 4$ ,  $P < 0.001$ ) with longer inter-phrase durations and cadence during spontaneous howls than those responding to other species calls ( $P < 0.001$ ) and longer

inter-phrase durations and cadence during calls initiated by vehicles and machinery than other species calls (both  $P < 0.001$ ), (Figure 2.4 to 2.6).

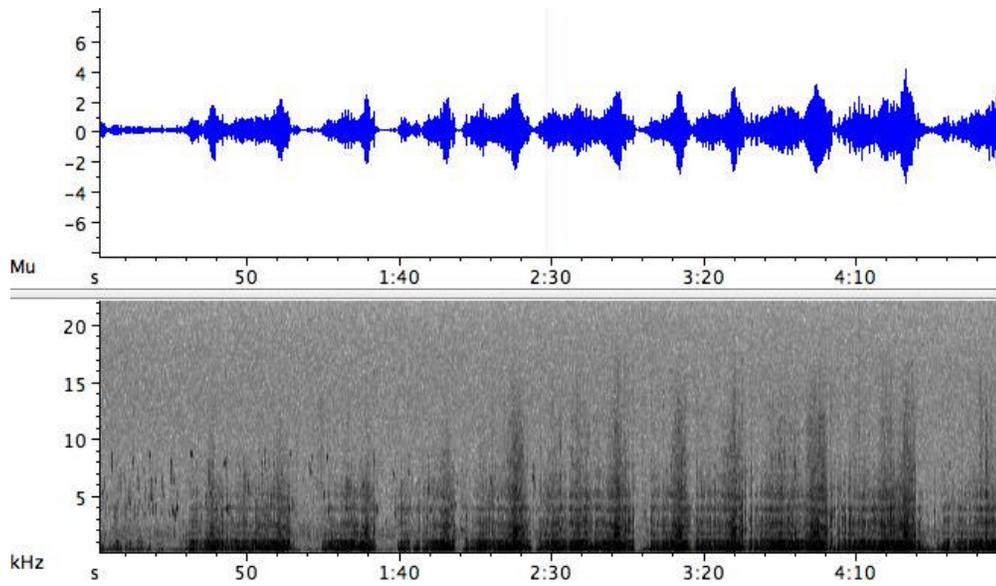


Figure 2.4 . Waveform and spectrogram of a howl incited by the call of a conspecific male.

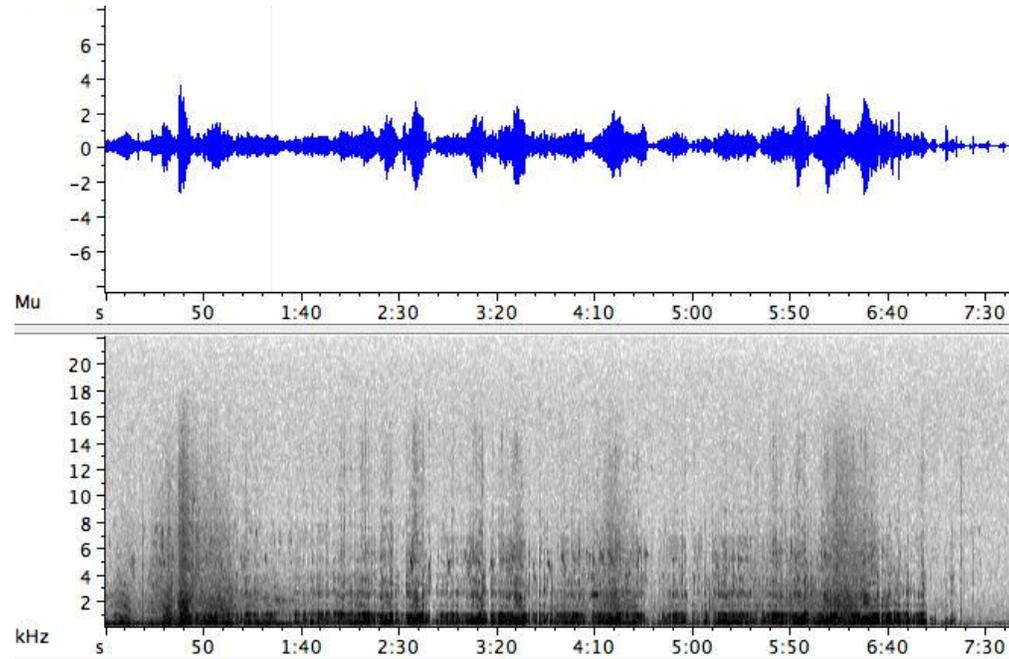


Figure 2.5. Waveform and spectrogram of a howl incited by vehicle noise.

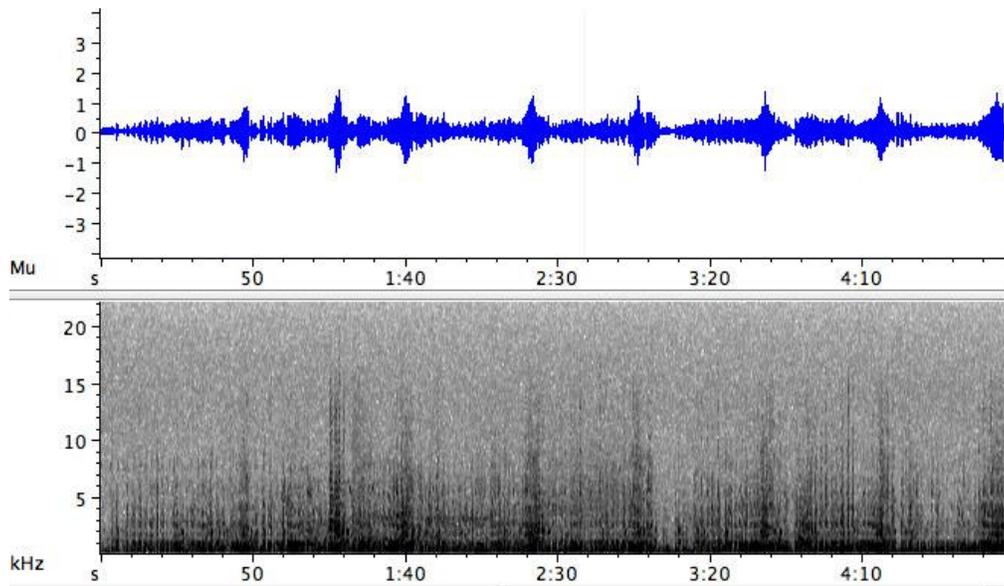


Figure 2.6. Waveform and spectrogram of a spontaneously performed howl.

## 2.4. Discussion

### 2.4.1. Vocal repertoire

Ten types of vocalisation were identified during the study, five of which had previously been described in wild *A. caraya*, 8 in *A. palliata*. In addition to the reported repertoire of *Alouatta* species, we discovered a sound which has not previously been described; which we named the ‘throat pulsation’. This sound involves the rapid inhalation and exhalation of air through the vocal tract, causing the body to shake and visible inflation of the lungs.

Our study differs from previous work by classifying a howl bout as a series of roar vocalisations which are connected with other sounds. We analysed the full duration of each howl rather than describing only the roar component (Baldwin and Baldwin, 1976; Chivers, 1969; Drubbe and Gautier, 1993; Sekulic, 1982a; Thorington et al. 1984; Whitehead, 1995; Schön Ybarra, 1986). These previous studies may provide only limited interpretation because the calls of different howler species vary significantly in frequency, structure, call duration and rates (Drubbe and Gautier, 1993; Horwich and Gebhard, 1983; Sekulic and Chivers, 1986; Whitehead, 1995) and suggest that the roar is the most important component of a howl. Our findings provide a comprehensive method for a better understanding of the vocal behaviour of howler monkeys and suggest that there are additional acoustic characteristics, such as the duration between phrases and frequency characteristics of units within a howl, that are also important.

### 2.4.2. Individual differences

Individuality in vocal signals, allowing for individual recognition has been suggested for a range of primate species (Cheney and Seyfarth, 1990). Variation in these signals may be facilitated by differences in vocal apparatus morphology, such as vocal fold length and body size, which influence the acoustic features of calls, providing low cost and reliable information about the intrinsic attributes of the caller which are termed “index signals” (Vehrencamp, 2000). In mammalian species it is suggested that producing lower frequency calls indicates a larger body size (Fitch and Hauser, 1995; Morton, 1977) which has been widely studied (Davies and Halliday, 1978, Fitch and Reby, 1997, Podos, 2001, Reby and McCombe, 2003, Riede and Fitch, 1999).

In howler monkeys, the physical development of the hyoid bone, which acts as a resonating chamber and amplifier, may be correlated to call production. Variations in hyoid bone structure and size may lead to individual differences in vocal quality, pitch, volume, call intensity and call duration (Altmann, 1959; Hershkovitz, 1949, 1969; Sekulic, 1981; Sekulic and Chivers, 1986; Wich and Nunn, 2002); therefore, howls may communicate information about the body size of the caller (Crockett and Eisenberg, 1987). Acoustic analysis of multiple *Alouatta* species has divided the genus into two groups; “*palliata*” (just the *A. palliata* species) and “non-*palliata*”, based on the duration and frequencies of roars (Whitehead, 1995). *A. palliata* roars have a lower frequency range (300-1000Hz) than “non-*palliata*” species roars (300-2000Hz) with the hyoid bone of *A. palliata* being significantly smaller in volume than “non-*palliata*” species (4.5ml, compared to an average of 47ml) (for review see Crockett and Eisenberg, 1987), suggesting possible phylogenetic constraints of vocal acoustics within the genus. However, the development of vocal folds and the larynx in

*Alouatta* species has occurred independently of body size and are together, the same size as the skull (Schön Ybarra, 1971). Therefore, vocal cord length may be a more reliable indicator of body size, as it does not show such variation in terms of body length (Fitch, 1997) and is related to producing lower frequency sounds, thus it may correlate with body size (Egnor et al, 2004). In addition, a relationship between lip rounding and threatening calls may be linked to howler behaviour. During howl bouts, the lips are flared out into a “funnel-shape” (Drubble and Gautier, 1993), which may further elongate the vocal tract and increase perceived body size of the caller (Fitch, 1997) and may provide evidence for a relationship between vocal morphology and howl frequency.

Additional variables such as the age or sex of a caller have also been suggested to correlate with body size, further highlighting the influence of body size on vocal acoustics. However, in howler monkeys, as with many New World primates, there is little variation in body size between the sexes (Ey et al, 2007) and as howlers have a reverse age-rank hierarchy, these measures may not be reliable indicators of body size and suggest that sexual selection may have a stronger influence on acoustic variation. Further research into the influence of caller age, by conducting playback experiments of different males and observing female responses, may help to elucidate the influence of this variable on acoustic characteristics.

In contrast to index signals, vocalisations which might display features according to the quality of the signaller (within the range defined by physical constraints), which are costly to produce (in terms of predator exposure and energy investment), termed “quality signals” can be performed only by high-quality callers (Clutton-Brock and Albon, 1979; Vehrencamp, 2000). The energy investment of *Alouatta* howls is speculated to be high due to the low energy diet *Alouatta* consume

(Milton, 1980) and as such, howls have been suggested to act as an honest advertisement of male quality (Sekulic, 1982a, Kitchen et al. 2004, Berglund et al. 1996). The size of the hyoid apparatus and larynx is highly exaggerated in *Alouatta* (Schön Ybarra, 1986, 1988); however, the size of the laryngeal apparatus is limited in size by the anatomy of the mandible, suggesting that not only are howls selected for the long-distance communication of howls to inter-troop males (Fitch and Hauser, 2003), but they may be more likely to be restricted by the caller's physiology. Although studies suggest that competitive males may assess body size and therefore fighting ability through howls (Chiarello, 1995; Kitchen, 2004; Sekulic, 1982a) and that by performing spontaneous howls, males may be able to regularly announce their defensive potential (Da Cunha and Byrne, 2006) to listeners, none has examined the acoustic variation of calls performed in different social situations; therefore this might be an avenue of further research.

### **2.4.3. Context-specific howls**

We found that two factors explained 65.5% of the variation in calls and that the acoustic features of howls differed depending on the context in which they were performed. The frequency of phrases accounted for the greatest variation between contexts. Roars performed spontaneously contained phrases with energy concentrated in lower frequencies than those responding to sounds which are not experienced in a wild situation (vehicle noise). The duration between phrases in a howl bout also accounted for acoustic variation between howls performed in different contexts. Spontaneous howls displayed longer inter-phrase durations and cadence than howls uttered in response to non-sympatric primate species calls. Phrases describe the

inhalation-exhalation sections between roar climaxes. Therefore longer inter-phrase durations and cadence would indicate an exaggerated build up to the climax of the howl and a longer inter-roar interval may provide a period of time for conspecifics to respond and thus callers can assess potential threats nearby. In particular, only individual 2 performed calls in response to non-sympatric primate species. However, we are aware that our sample size is small; therefore, collecting more calls from these individuals and additional calls performed by each individual in each context, is required to further investigate context-specific calls in this species.

Investigation into context specificity of vocalisations and call repertoires can help researchers to further understand the complexity of animal vocal systems and to investigate the mechanisms of how howl function is achieved. This study is unable to compare spectrograms across each context, controlling for individual variation; therefore a larger sample size is required to accurately determine individuality in howls performed in each context and to investigate whether howls vary acoustically between contexts. Through controlled experiments, we can begin to address what kind of information may have been selected for and can be processed by receivers. Playback experiments conducted on the male *A. caraya* subjects sampled in this study, found that the majority of vocal responses was towards the playback of conspecific howls, compared to those of a non-sympatric *Alouatta* species, the roars of a lemur (*Varecia rubra*) and a novel low frequency sound, a chainsaw (Farmer et al, in prep). Therefore carrying out additional playback experiments of known howl stimuli and analysis of vocal responses, may provide an insight into the potential proximate mechanisms underlying the function of howl vocalisations.

Our findings suggest that there are individual differences in the howls performed by adult male *A. caraya*, indicating a biological function allowing all

individuals to perform distinct vocal displays. We acknowledge that there might be confounding factors such as previous mating experience and body size. Measurements of body size were requested, but the institutions visited did not have such details in their veterinary records. However, even with a small sample size, this study has picked up significant differences and large effect sizes between individual calls, indicating that there are differences. Extensive studies to focus on the vocal morphology of the genus should be the ultimate goal of future investigation.

## **CHAPTER 3: An Experimental Investigation into Context Specific Variation in the Calls of the Black Howler Monkey (*Alouatta caraya*)**

### ***Abstract***

Investigating the contexts in which primate loud calls are performed and the behaviours associated with call production help to provide a comprehensive understanding of the function of these calls. The howl vocalisations performed by *Alouatta* species are suggested to play many functions within their communication system. By comparing the behaviours performed by captive adult males and females in response to naturally occurring stimuli and behaviours performed when responding to acoustic playback, we aimed to investigate context specific variation in the howl-associated behaviour of the black and gold howler monkey (*Alouatta caraya*). We then investigated three hypothesised functions of howl calls; intertroop spacing, mate defence and mate attraction and the proximate mechanisms by which these functions are achieved. Howls were naturally performed by males in response to familiar conspecific calls, other primate calls, man-made sounds and howling also occurred spontaneously, with no determinable visual or acoustic trigger. Our playback experiments tested vocal and behavioural responses towards the howls of unfamiliar conspecific groups, an allopatric *Alouatta* species (*Alouatta palliata mexicana*) howl, a red ruffed lemur (*Varecia rubra*) roar and a chainsaw sound. Our findings support the mechanism of regularly advertising occupancy of an area in the function of intertroop spacing. Our results also provide support for the role of howling in mate defence and attraction.

**Keywords:** vocalisation, howler monkey, *Alouatta caraya*, playback.

### 3.1. Introduction

Long-distance calls, also termed loud calls, are produced by a range of primate species which inhabit forest areas and require call propagation over large distances (Oliveira and Ades, 2004). These vocalisations are characteristically low frequency, which allows for long-distance transmission and minimal environmental influence (Mitani and Stuht, 1998). There are a range of functions of long-distance calls (Byrne, 1982) involving both intergroup and intragroup communication (Oliveira and Ades, 2004), however, very little is known about the type of information communicated by these calls. Howler monkeys characteristically perform loud, low frequency howl vocalisations (Whitehead, 1987, 1995). To date, few studies have experimentally investigated the function of wild *Alouatta* calls (*Alouatta caraya*, only one group; Da Cunha and Byrne, 2006, *Alouatta pigra*; Kitchen, 2004, *Alouatta seniculus*; Sekulic, 1983, *Alouatta palliata*; Whitehead, 1989). Investigations into howl function are based on variables such as the context in which howling was performed, location of the caller and howl duration which is related to opponent assessment. The proposed functions of howl calls include regulation of space use, resource defence and opponent assessment; however, the proximate mechanisms (such as mutual avoidance and mate defence) to achieve these functions are often not outlined (reviewed by Da Cunha and Byrne, 2006).

In captivity, animals are not exposed to the natural range of acoustic stimuli that influence their wild counterparts, in particular the calls of neighbouring conspecific groups. Only a handful of playback studies have been conducted on captive primates and results from these studies show that primates respond in an appropriate manner to conspecific calls (lar gibbons, *Hylobates lar* [Shepherdson et al, 1989]; Mueller's gibbons, *Hylobates muelleri* [Haraway et al, 1988; Maples et al,

1988]; agile gibbons, *Hylobates agilis*, [Maples and Haraway, 1982]). The only playback experiment conducted in *A. caraya* focused primarily on vocal and physical responses of one group of wild howlers to conspecific calls (Da Cunha and Byrne, 2006) and reported increased vocal responses to conspecific playbacks played from inside a group's boundary, mimicking group invasion. The study concluded that howling functions in the regulation of space use through regular advertisement and as an alternative to physical conflict.

There is limited research into the perception of territorial space in captive animals. Hediger (1950) was the first to suggest that captive species may perceive their enclosure as their territory; but provided no scientific evidence. Research into felid stereotypic behaviour suggests that the limits of the captive environment provide an enforced territorial boundary (Lyons, Young and Deag, 1997). More recently, Powell (2010) stated that animals may establish a territory within or encompassing the whole of their enclosure, but again provides no scientific evidence.

The definition for a territory may contain more than one criterion; including advertisement of location such as scent marking and the behavioural responses of intruders such as avoidance (Maher and Lott, 1995). Boundary marking may be performed through vocal or physical demarcation. A territorial role of howling has also been inferred in other *Alouatta* species (*A. seniculus*, Drubble and Gautier, 1993; *A. pigra*, Horwich and Gebhard, 1983; *A. guariba*, Da Cunha and Jalles-Filho, 2007), where it may help to maintain group distances (Bernstein, 1964; Drubble and Gautier, 1993). However, there is only one study including behavioural evidence for territorial marking through group defecation at boundary sites (Drubble and Gautier, 1993), a behaviour which we include in our study as a behavioural indicator of territoriality.

Male-male competition is high in wild *Alouatta* species (Crockett and Eisenberg, 1987). Vocal battles may pose the threat of male take-over as all *Alouatta* species exhibit bisexual emigration (Crockett and Eisenberg, 1987; Rumiz, 1990; Glander, 1992; Zucker and Clarke, 1998; Fedigan and Jack, 2001) and male changes may result in infanticide (*A. caraya*, Calegario-Marques and Bicca-Marques, 1996; Zunino et al. 1986). In primates, periods of conspecific conflict are often associated with anxiety, during which self-directed behaviours (SDBs) are often performed (Castles et al, 1999; Maestripieri et al, 1992; Spruijt et al, 1992; Troisi, 2002). Although the ‘vocal battles’ of wild howler monkeys (*Alouatta* species) do not involve physical contact (Altmann, 1959; Carpenter, 1934; Cornick and Markowitz, 2002; Da Cunha and Byrne, 2006), the performance of SDBs may be indicative of anxiety levels.

In this study, we investigated context specific variation in howl-associated behaviours performed by captive *A. caraya* groups, in order to further elucidate the function of howl calls. Using captive *A. caraya* allowed us to watch behaviour at a level of detail that has not been possible in previous studies on wild groups. We tested three hypothesised functions of howl calls; inter-troop spacing, mate defence and mate attraction. We also investigated the proximate mechanisms through which these functions are achieved, using both observations of the behaviours performed during naturally occurring howl vocalisations and in response to experimental playbacks. Data were collected in captivity; therefore we compared the behaviour of individuals housed in different social groupings (pairs and families) and with or without auditory access to other conspecific groups since groups who have never been exposed to conspecific calls may respond differently to groups who regularly hear conspecifics.

The three main mechanisms for inter-troop spacing that we tested were mutual avoidance, advertisement of the occupancy of an area and boundary marking or defence. If inter-troop spacing was maintained through mutual avoidance, we predicted males to orientate towards playback sounds, but not approach the speaker. If howling functions as a regular advertisement of occupancy, we predicted males to move around their enclosure more during and post-howl calls. We also predicted that males would approach and vocalise towards the playback of the howls of conspecifics and perform increased self-directed behaviours, indicating anxiety and in response towards the threat of vocal conflict with neighbouring troops. Boundary marking or defence is difficult to assess in captivity as groups have limited enclosure boundaries. However, we predicted males to approach the speaker and call towards conspecific howl playbacks, as investigative behaviours. Males and females may perform territorial behaviours such as scent marking and communal defecation, as if to repel neighbouring groups.

For the second hypothesis of howl function; mate defence, we predicted males to strongly react to playbacks, with both behavioural approach and vocal responses. To investigate the final hypothesis; mate attraction, we predicted females to approach the speaker when playing conspecific male calls, showing interest in the male calling. We also predicted that after natural howl calls and playbacks, males would perform increased social resting and grooming behaviours.

## 3.2. Methods

### 3.2.1. Subjects

Twenty four captive black howler monkeys (*A. caraya*), from 12 established groups held across eight zoological institutions in the UK were the subjects of the study. We observed the adult male and adult female of each group. It is the adult male of the group which performs howl vocalisations and we also investigated female's howl-associated behaviours, because female responsiveness may provide further evidence for the function of calls. Six groups held only a pair of adult howler monkeys (one male, one female) and six groups were comprised of a family group containing a range of group members (ranging from one male, two females and one unsexed offspring to three males and three females) (Table 3.1). In addition, six of the study groups were housed in a zoo which housed another conspecific group. These groups were categorised as having 'auditory access' to conspecific groups and regular exposure to conspecific howl calls. The adult males and females in each group were not genetically related and were considered to be the parents of all group offspring (John Partridge, studbook coordinator, 2010).

The age and experience of the offspring in groups were highly variable so they were not considered in the study. Subjects were housed in enclosures with both indoor and outdoor areas ranging from approximately 150 m<sup>2</sup> to 450m<sup>2</sup>. All howlers were fed a selection of fruit, vegetables and pellets twice daily, water was provided *ad libitum* and each enclosure contained a similar number of perches.

Table 3.1. Details of subjects and groupings.

<b>Group number</b>	<b>Zoo name</b>	<b>Subject</b>	<b>Sex</b>	<b>Age</b>	<b>Group composition</b>	<b>Social grouping</b>
1	Port Lympne	Louie	M	19	3.3	Family
	Wild Animal Park	Valerie	F	19		Family
2	Port Lympne	Snipe	M	13	3.2	Family
	Wild Animal Park	Zola	F	13		Family
3	Port Lympne	Clyde	M	20	1.1	Pair
	Wild Animal Park	Tolkein	F	9		Pair
4	Bristol Zoo	McGinty	M	7	1.1	Pair
	Gardens	Amerello	F	7		Pair
5	Exmoor Zoo	Grebe	M	10	1.1	Pair
		Wings	F	12		Pair
6	Paignton Zoo	Dunlin	M	11	1.1	Pair
	Environmental Park	Millie	F	12		Pair
7	Twycross Zoo,	Wesley	M	13	3.1	Family
	The World Primate Centre	Alex	F	12		Family
8	Twycross Zoo,	Jacob	M	15	2.3	Family
	The World Primate Centre	Amber	F	18		Family
9	Twycross Zoo,	Weederman	M	19	3.1	Family
	The World Primate Centre	Abbie	F	22		Family
10	Hamerton Zoo	Viallie	M	10	1.1	Pair
	Park	Millie	F	10		Pair
11	Banham Zoo	Amos	M	20	3.1	Family
		Jovie	F	19		Family

	Royal	Keiko	M	11	1.1	Pair
12	Zoological	Meryl	F	7		Pair
	Society of					
	Scotland,					
	Edinburgh Zoo					

### 3.2.2. Behavioural responses to naturally occurring sounds

#### 3.2.2.1. Observational procedure

For the purpose of this study, we defined a howl vocalisation bout to be a call which lasted for a minimum duration of 60 seconds (Drubbe and Gautier, 1993). Sampling occurred between 0800 and 1630 hours over 10 days per group, with all howls recorded opportunistically. The onset of a howl bout was determined during preliminary observations and was indicated when the adult male of the group would begin to increase vigilant behaviour and often travel to the highest location in the enclosure. If the start of a howl was missed, it was not included in analysis. We filmed and recorded all state and event behaviours (Table 3.2) performed during each howl and for 10 minutes after the howl had ended using continuous focal sampling. Filming was conducted using a Sony Handycam Digital Video Camera Recorder (DCR-DVD405E). The contexts in which the calls occurred was determined using the categories in Table 3.3.

Table 3.2. Behaviours recorded.

<b>Behavioural category</b>	<b>Behaviours included</b>	<b>Description</b>
Locomotion		Movement from one area to another quadrupedally, includes climbing.
Rest alone		Motionless either sitting or lying, not in contact with another individual. Eyes may be open or closed.
Social	Social rest	Motionless either sitting or lying, in contact with another individual. Eyes may be open or closed.
Groom	Autogroom	Self-inspection of coat using fingers and/or mouth.
	Allogroom	Physical contact with another individual, inspecting their coat with fingers and/or mouth.
	Play	Physical engagement with another individual includes chasing, touching, mouthing and pulling.
Self-directed	Yawn	The mouth is opened widely; the head tips back, lips are pulled back so that the teeth are exposed.
	Sneeze	Rapid expulsion of air from the nose.
	Scratch	Rhythmic movement of fingers through the coat. Performed whilst sitting or when standing on all four limbs.
	Body shake	While a sitting position the individual moves its whole body side to side in a somewhat circular motion or quickly up and down.
	Tongue flick	Tongue is stuck out of the mouth, sometimes preceded with a yawn.

Territorial	Defecation	Expellation of faeces and urine.
	Scent mark	Rubbing throat or anogenital area on enclosure substrate.

Table 3.3. Categories of stimuli which elicited a howling vocalisation.

<b>Stimulus category</b>	<b>Description</b>
Spontaneous howl	No determined trigger (visible or auditory) for the call
Familiar conspecific call	Call in response to the call of a neighbouring (known) <i>A. caraya</i> male (housed in a different group within the same zoo), immediately or within two minutes of the end of the stimulus, auditory stimulus only
Other primate call	Call in response to the call of a neighbouring primate, both visual and auditory stimulus on occasion
Vehicle response	Call in response to a passing vehicle, both visual and auditory stimulus
Machinery response	Call in response to a man-made noise such as chainsaw, strimmer or leaf blower, auditory and visual stimulus on occasion

### 3.2.2.2. Matched control data

For each call occurrence, we conducted a 10 minute matched control on the next suitable day using the same methodologies as above, to act as a baseline for behaviours. The criteria for carrying out a matched control was as follows; within the subsequent five days after the focal howl bout, under similar environmental and weather conditions, similar husbandry conditions, minimal external influences, as

close to the original howling time as possible but not to be carried out within 15 minutes of a howl performance and to be abandoned if a howl was performed during the matched control.

### **3.2.2.3. Statistics**

Of the 12 study groups, only eight of the groups performed howl vocalisations. A number of calls were omitted from our analysis due to our inability to determine their stimulant due to multiple potential stimulants. Our study includes a total of 68 calls from eight adult males (mean number of calls per individual = 8.5, range of 1 to 20 calls per male).

For the behaviours performed during howls, we calculated durations per minute of behaviours, by dividing the total duration of a behaviour by the total howl duration, expressed in seconds. This was conducted for social behaviours and locomotion, and the rate of territorial behaviours and self-directed behaviours (Table 3.2). We calculated a difference value between the durations and rates of behaviours performed post-howls and during the matched control (baseline) using the formula; difference = (post-howl behaviour)-(matched control). As a result, all positive values indicate higher durations or frequencies post-howls than during baselines, negative values indicate the opposite trend.

Data were analysed using Generalized Linear Mixed Model (GLMM) analysis in PASW 18 statistical software (PASW 2010, IBM, Chicago, IL, U.S.A). 'During howl' data were not normally distributed (Kolmogorov-Smirnov all  $P < 0.001$ ) so we applied a GLMM with inverse gaussian distribution and log link function. We conducted a GLMM with normal distribution and identity link function for all 'difference' data (comparing post howl and match control/baseline data). As factors,

we included group number (nested within social grouping, groups 1-8), sex (male versus female), social grouping (pair versus family group housed) and vocal stimuli (1-5; stimuli to which a howl response was performed, see Table 3.3).

We fitted the models using a backward elimination process to find the minimum adequate model for explaining the variance of the response variable. Only significant explanatory variables and two-way interactions were retained and models with the lowest Akaike's Information Criterion (AIC) value were interpreted. All tests are two-tailed. For all significant results, post-hoc pairwise comparisons with Bonferroni corrections were carried out and all significant results reported. If pairwise comparisons did not reveal significance (probably due to our small sample size), we further investigated the significant main effects and interactions by calculating Cohen's  $d$  effect sizes and the associated 95% confidence intervals (CIs) (Cohen, 1988). Determining effect size and associated CIs allows interpretation of non-significant results (Nakagawa and Cuthill, 2007). We do not report small effect sizes ( $d < 0.3$ ) in our results.

### **3.3. Results for responses to natural calls**

#### **3.3.1. Intertroop spacing**

Male *A. caraya* vocalised in response to a range of acoustic stimuli and also performed spontaneous howl calls. An individual's behaviour whilst howling was dependent on the stimulus that he/she had heard that elicited their howling bout (Table 3.4). Individuals locomoted more during spontaneous howls compared to those responding to known conspecifics, and this was supported by a medium effect size ( $d = 0.62$ , 95%CI -12.19 to 12.32). When comparing post howl and matched control

behaviours, we found that locomotion (GLMM:  $X^2 = 16.13$ ,  $df = 4$ ,  $P = 0.003$ ) was dependent on the stimulus evoking a howl bout (Figure 3.1). We also found an interaction between social grouping and stimuli type on locomotion durations (GLMM:  $X^2 = 6.01$ ,  $df = 2$ ,  $P = 0.050$ ) but post hoc Cohen's  $d$  tests were too small to reliably interpret. An interaction between stimulus type and sex also had a significant effect on locomotion (Table 3.4), but due to sample size limitations, effect sizes were small.

Table 3.4. GLMM results showing the main effect of stimulus on during howl behaviour.

<b>Fixed Factor</b>	<b>Dependent variable</b>	<b>Wald statistic (<math>X^2</math>)</b>	<b>df</b>	<b>P</b>	<b>Post hoc variables tested</b>	<b>Mean duration/rate</b>	<b>SE</b>
Stimulus	Locomotion	10.170	4	0.038	Spontaneous	6.98	9.199
					Conspecific	4.61	3.483
					Other primate	17.92	29.357
					Vehicle	3.15	1.286
					Machinery	4.34	5.533
	Territorial rates	10.047	1	0.002	Spontaneous	0.41	0.116
					Conspecific	0.21	0.032
					Other primate	0	0
					Vehicle	0	0
					Machinery	0	0
SDB rates	43.629	4	< 0.001	Spontaneous	2.56	5.410	
				Conspecific	2.21	3.491	
				Other primate	0	0.007	
				Vehicle	0.77	0.984	
				Machinery	0.03	0.046	
Stimulus	Locomotion	11.913	3	0.008			
x sex	SDB rates	70.562	2	< 0.001			
Sex	SDB rates	20.235	1	< 0.001	Male	0.13	0.034
					Female	0.35	0.110
Social group	SDB rates	3.637	1	0.057	Pair	0.05	0.046
					Family	0.43	0.149

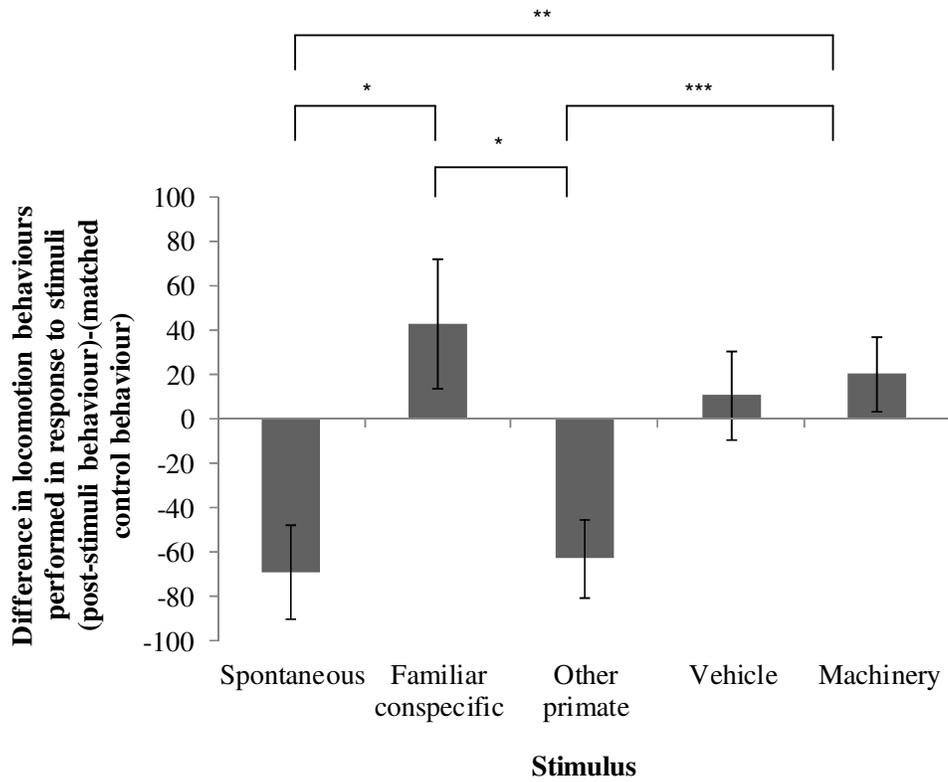


Figure 3.1. Differences in the duration of locomotion behaviour performed after howls (in response to various auditory stimuli) compared to a matched control in captive black howler monkeys. (\* $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ ).

SDB rates were performed more during spontaneous howls and howls elicited by conspecific calls but post hoc effect sizes for were all small ( $<0.3$ ), therefore are not reported. There was a significant difference in SDB rates performed between the sexes (Table 3.4), SDBs were performed at higher rates by females than males during howl bouts (pairwise comparison,  $P = 0.011$ ). There was a trend in SDB rates differing between social groups, with family groups performing higher SDB rates than those in pairs (pairwise comparisons,  $P = 0.031$ ).

Territorial behaviours were only performed during spontaneous howl calls and those provoked by known conspecifics, with a higher territorial behaviour rate during spontaneous calls than those responding to conspecific calls (pairwise comparison,  $P = 0.016$ ). After howl call performances, females performed higher rates of territorial behaviours than males (GLMM:  $X^2 = 4.18$ ,  $df = 1$ ,  $P = 0.041$ , pairwise comparison,  $P = 0.041$ ). However, overall, territorial behaviour rates were generally low.

### 3.3.2. Mate attraction

When comparing post-howl and baseline behaviours, social behaviour durations (GLMM:  $X^2 = 27.43$ ,  $df = 2$ ,  $P = 0.030$ ) were dependent on the stimulus evoking a howl bout (Figure 3.2). An interaction between social grouping and stimulus on social behaviour durations was also found (GLMM:  $X^2 = 7.05$ ,  $df = 2$ ,  $P = 0.030$ ) but post hoc Cohen's  $d$  tests were all small ( $<0.3$ ).

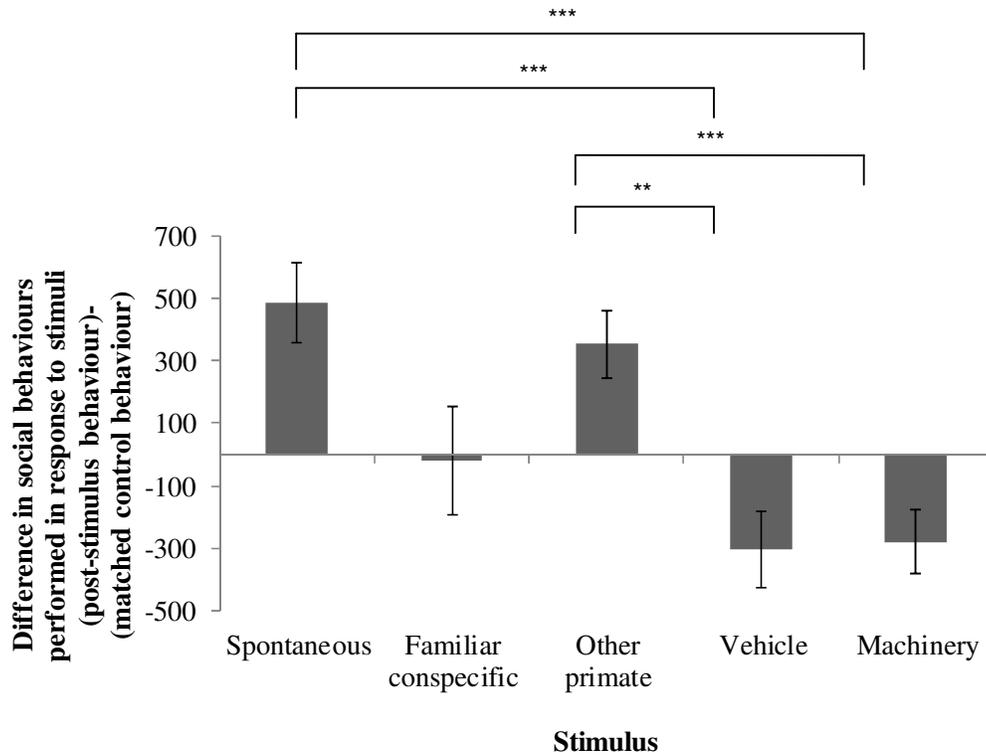


Figure 3.2. Differences in the duration of social behaviour performed after howls (in response to various auditory stimuli) compared to a matched control in captive black howler monkeys. (\* $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ ).

### 3.4. Playback experiment

#### 3.4.1. Experimental procedure

We performed playback experiments on all 12 groups. Stimuli played were the howl of an unfamiliar conspecific group, a heterospecific *Alouatta species* (*Alouatta palliata mexicana*) howl, the calls of a non-sympatric primate (red ruffed lemur, *Varecia rubra*) thought to function in troop spacing or as an alarm call (Geissmann and Mutschler, 2006) and a chainsaw sound, to represent a low-frequency sound (Figures 3.3 to 3.6) as *Alouatta* are reported to howl in response to this sound

(Bernstein, 1964; Baldwin and Baldwin, 1976; Carpenter, 1934). Unfamiliar *A. caraya* call recordings were taken at different zoological institutions to the focal group. We used 300s sections of continuous recordings of a howl call, comprised of a series of roar vocalisations (Eisenberg, 1976), performed by a range of group members. We played 60s of *A. palliata* howls, 25s of *V. rubra* and 30s of chainsaw sounds, the durations of which were determined prior to the study in accordance to naturally occurring sound durations. We recorded all stimuli, except for those of *A. palliata*, using an Edirol R-1 solid state recorder and directional microphone (Beyer Dynamic MCE 86N(C)S). Sounds were then transferred to computer with 24-bit accuracy at a sampling rate of 44.1 kHz through Raven Pro 1.4 Interactive Sound Analysis Software (Cornell Lab of Ornithology, Ithaca, NY, USA). Good quality sections of continuous recordings of each sound were selected for playback trials. We used different sections of recordings every time (McGregor et al, 1992), to avoid pseudo-replication, either from different groups or different sections of a howl from one group.

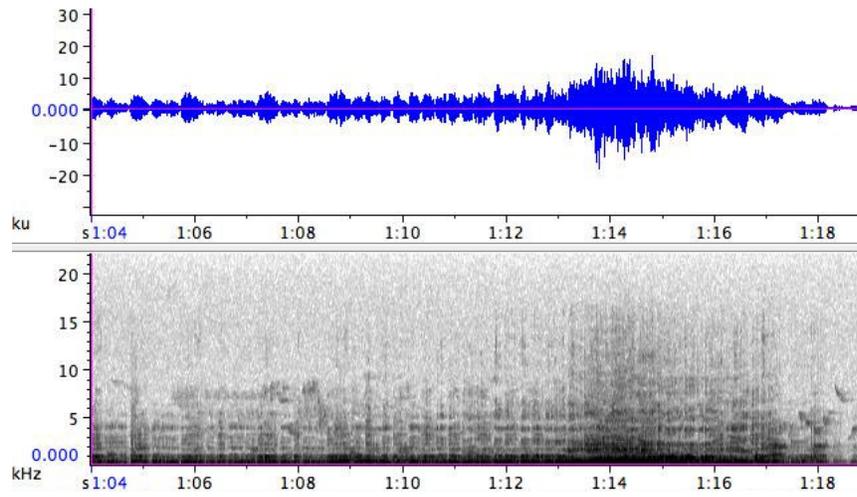


Figure 3.3. Waveform and spectrogram of an example call of *A. caraya* used during playbacks.

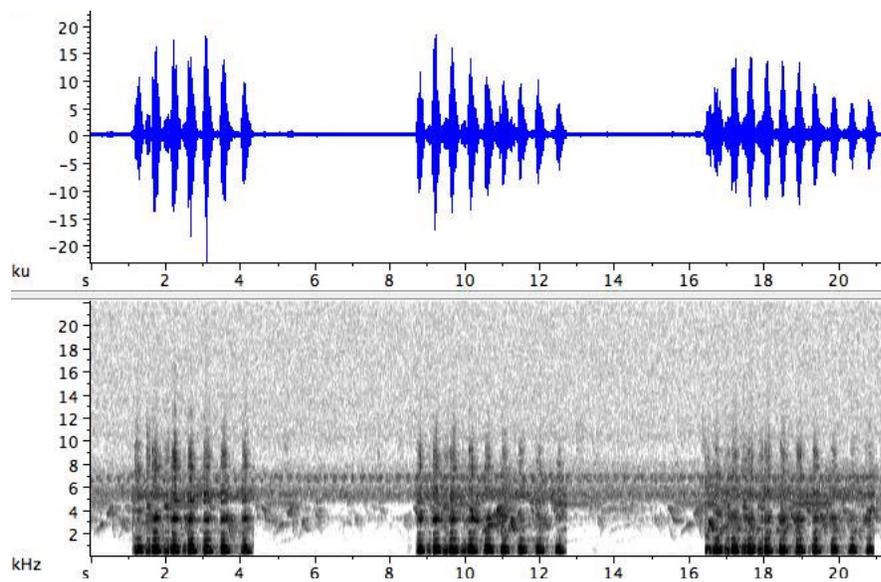


Figure 3.4. Waveform and spectrogram of an example call of *A. palliata* used during playbacks.

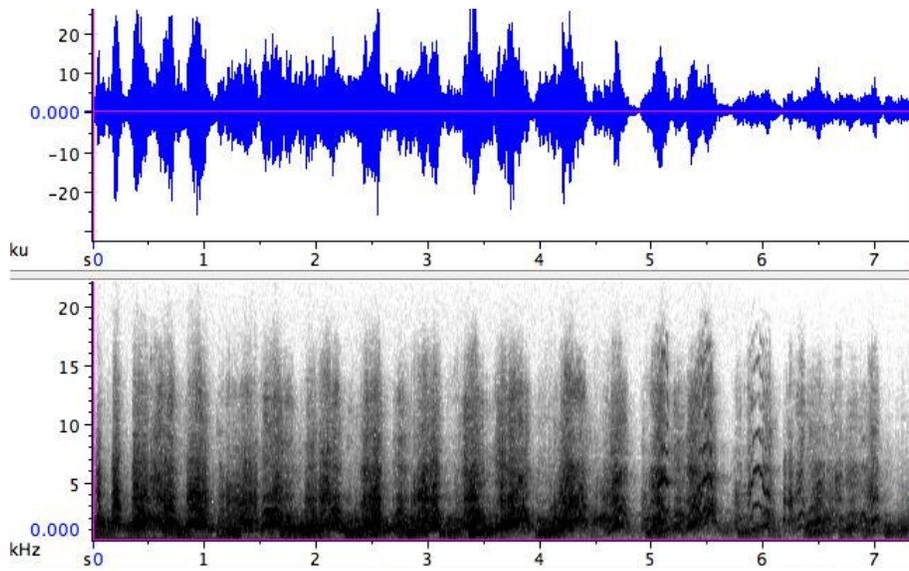


Figure 3.5. Waveform and spectrogram of an example roar of *V. rubra* used during playbacks.

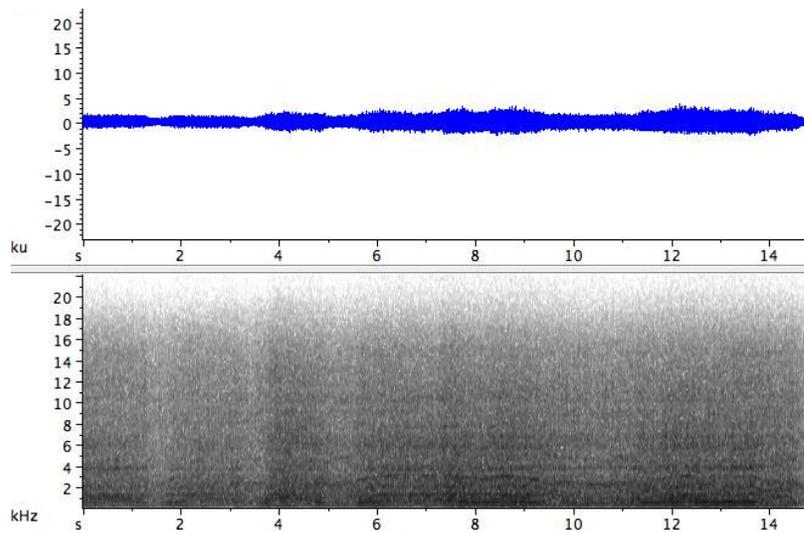


Figure 3.6. Waveform and spectrogram of an example chainsaw recording used during playbacks.

We conducted all playbacks from outside the boundary of the outdoor enclosures to minimise the effects of observer interference on responses. The location of the speaker was a 0-90° angle to the adult male at the onset of each experiment and approximately three metres from the enclosure boundary. Sounds were played through FoxPro FX5 speakers, located approximately 10-20 m away from the focal male, at an elevated level of 0.5-2m from the ground and controlled remotely. We selected playback volume beforehand to be the loudest possible without distortion. Amplitude was judged to be similar to a naturally occurring sounds and was kept as consistent as possible between trials.

We conducted playbacks over six days for each group during separate visits, with a total of 24 playbacks being conducted for each group. On a playback day, the first trial commenced between 0800 and 0840 hours. We played all four stimuli in a random order with a minimum 10 minute interval maintained between the end of one post-playback data collection session and the start of the next pre-playback session. Groups were regularly exposed to acoustic stimuli throughout the day, as captivity is a noisy environment so we were not concerned by overexposure. Criteria for the onset of playback experiments were that at least 20 minutes had elapsed since subjects had been allowed access to their outdoor enclosure to allow subjects to settle outside and that no calls had been performed by the focal male in the preceding 15 minutes for subsequent playback experiments that day. We recorded all behaviours performed by the focal subjects using continuous focal sampling as above for 10 minutes prior to each playback, for the duration of the playback and for 10 minutes post-playback trials, again using a video camera. We also determined the immediate response of the adult males and females to playbacks as in Table 3.5.

Table 3.5. Immediate responses to playbacks.

<b>Response name</b>	<b>Response description</b>
Orientate towards speaker	The subject lifted its head and looked towards the location of the speaker (within a 45 <sup>0</sup> angle of the speaker location)
Approach speaker	The subject travelled towards the direction of the speaker, all four feet had to move along the substrate (within a 45 <sup>0</sup> angle of the speaker location)
Vocal response	The subject performed a vocalisation (howl or bark) during the playback or within five seconds of the playback ending

The latency (in seconds) for the focal male to perform a vocal response from the start of the playback (if a response was performed) and type of vocalisation performed in response to a playback experiment (howl or bark, definitions by Carpenter, 1934; Altmann, 1959; Da Cunha and Byrne, 2006) were also recorded.

### 3.4.2. Statistics

To compare immediate behavioural responses to playback stimuli, we used GLMMs for binary logistic responses and included the same factors as above, including day (1-6) in the model. We calculated durations per minute of the behaviours performed during a playback experiment, using the same behavioural categories as above. To compare behaviours performed post-playback and baseline (pre-playback) we used the formula; ‘difference’ = (post-playback behaviour)-(pre-

playback behaviour) and results were interpreted as above. Data were not normally distributed (Kolmogorov-Smirnov all  $P < 0.001$ ) so we conducted GLMMs with an inverse Gaussian distribution and identity link were used to analyse behaviours performed 'during' playbacks, GLMMs with normal distribution and identity link function for all 'difference' data (comparing post playback and matched control data). The same variables as above were included in the analyses, with the additional factor of auditory access (the presence of another group of conspecifics in the zoo versus no other conspecific groups). We did not include playback order or repetition as factors in the model as order was randomly assigned and preliminary analysis showed no meaningful effects of repetition day. Post-hoc tests were carried out as above.

### 3.5. Results of playback experiment responses

Table 3.6. Total positive immediate behavioural responses to all playback conditions.

<b>Behavioural response</b>	<b>Stimulus</b>	<b>Male % positive responses (total 72 trials)</b>	<b>Female % positive responses (total 72 trials)</b>
Orientate towards speaker	<i>A. caraya</i>	91.6 (66)	80.6 (58)
	<i>A. palliata</i>	81.9 (59)	61.1 (44)
	Lemur	55.5 (40)	36.1 (26)
	Chainsaw	38.8 (28)	18.1 (13)
Approach speaker	<i>A. caraya</i>	58.3 (42)	36.1 (26)
	<i>A. palliata</i>	30.5 (22)	18.1 (13)
	Lemur	6.94 (5)	6.9 (5)
	Chainsaw	2.77 (2)	4.2 (3)
Vocal response	<i>A. caraya</i>	56.9 (41)	13.8 (10)
	<i>A. palliata</i>	13.8 (10)	0 (0)
	Lemur	2.77 (2)	0 (0)
	Chainsaw	1.38 (1)	0 (0)

#### 3.5.1. Inter-troop spacing

Stimulus type played affected immediate behavioural responses (Table 3.6), males orientated towards the speaker (GLMM:  $X^2=317.567$ ,  $df = 3$ ,  $P<0.001$ ) more to conspecific playbacks than when they heard the other types of sounds. Repetition day had a significant effect on male orientation towards the speaker (GLMM:  $X^2 = 28.45$ ,  $df = 5$ ,

$P < 0.001$ ), with responses decreasing with subsequent repeats (percentage (total) 1<sup>st</sup> repetition = 47.2% (34), 2<sup>nd</sup> = 45.8% (33), 3<sup>rd</sup> = 45.8% (33), 4<sup>th</sup> = 50% (36), 5<sup>th</sup> = 43% (31), 6<sup>th</sup> = 36.11% (26).

Males vocally responded (GLMM:  $X^2=96.365$ ,  $df=3$ ,  $P<0.001$ ) more to conspecific playbacks than when they heard the other types of sounds. Conspecific call playbacks elicited calling in previously non-vocal groups. In all previously calling males, vocal rates were lower on playback days, but this result was not statistically significant. Auditory access to other groups of conspecifics significantly affected male approaches to the speaker (GLMM:  $X^2 = 6.748$ ,  $df = 1$ ,  $P = 0.014$ ). Males with auditory access to other conspecific groups approached the speaker more than those without (percentage (total) 62.5% (45) and 36.11% (26) respectively).

During playbacks, stimulus type had a significant effect on social behaviours (GLMM:  $X^2 = 9621.22$ ,  $df = 2$ ,  $P < 0.001$ ). There is a significant interaction between auditory access and sex on locomotion durations, with more locomotion performed by males with auditory access to conspecifics than females with auditory access (pairwise comparisons,  $P = 0.001$ ) and less in males with no auditory access than females (pairwise comparisons,  $P < 0.001$ ). During playbacks, stimulus had a significant effect on behaviours locomotion, solitary resting and SDB rates (Table 3.7), but Cohen's  $d$  results were small, probably due to the limited sample size.

Table 3.7. GLMM results showing the main effect of stimulus on during playback behaviour.

<b>Fixed Factor</b>	<b>Dependent variable</b>	<b>Wald statistic (<math>X^2</math>)</b>	<b>df</b>	<b>P</b>
Stimulus	Social	30.96	3	< 0.001
	Locomotion	9621.22	2	< 0.001
	Solitary resting	11.04	3	0.011
	SDB rates	23.50	2	< 0.001
Stimulus x auditory access	Social	10.56	3	0.014
Auditory access x sex	Locomotion	122.27	2	< 0.001

When comparing behaviours performed after playbacks and matched controls, an interaction between sound type and auditory access had a significant effect on locomotion (GLMM:  $X^2 = 13.69$ ,  $df = 6$ ,  $P = 0.033$ ), but effect sizes were small.

### 3.5.2. Mate defence

Male responses to playbacks by approaching the speaker was significantly influenced by stimulus (GLMM:  $X^2 = 76.024$ ,  $df=3$ ,  $P<0.001$ ). More responses to conspecific playbacks were performed compared to the other stimulus types (Table 3.6).

### 3.5.3. Mate attraction

Females orientated towards (GLMM:  $X^2 = 58.98$ ,  $df = 3$ ,  $P < 0.001$ ) and approached the speaker (GLMM:  $X^2 = 30.14$ ,  $df = 3$ ,  $P < 0.001$ ) more when conspecific calls were played. During playbacks, stimulus had a significant effect on

social behaviours (GLMM:  $X^2 = 30.96$ ,  $df = 3$ ,  $P < 0.001$ ), with less social behaviours performed during *A. caraya* call playbacks than the other three sounds (pairwise comparisons,  $P = 0.001$ , Figure 3.7). The presence of other howler monkeys in the zoo (classed as auditory access) and stimulus had an effect on social behaviours performed (GLMM:  $X^2 = 10.56$ ,  $df = 3$ ,  $P = 0.014$ ). More social behaviours were performed by those with auditory access during conspecific call playbacks, indicated by a large effect size ( $d = 0.71$ , 95%CI -4.99 to 3.58).

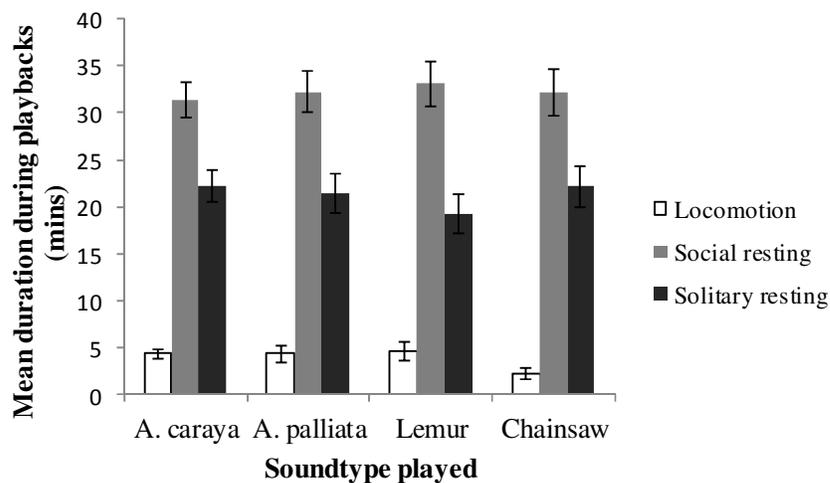


Figure 3.7. Differences in the duration (seconds) of behaviour performed during playbacks (in response to various auditory stimuli) in captive black howler monkeys.

### 3.6. Discussion

The function of howling in inter-troop spacing was investigated by assessing three proximate mechanisms. Our first hypothesis of troop spacing through mutual avoidance can immediately be rejected as males and females approached the speaker during playbacks of conspecific male howls. Although approaching neighbouring groups during intense vocal battles is known to increase the tendency for groups to move apart in *A. palliata* (Southwick, 1962; Chivers, 1969), if all group members, as

we observed, approach the neighbouring group, this does not support mutual avoidance. We are presuming that animals perceive their captive enclosure as their territory and by approaching the simulated location of a neighbouring conspecific male suggests that groups are simply intolerant of each other and are not actually avoiding each other.

The observed locomotion patterns of groups both during and after howl bouts and heightened responses to conspecific playbacks, strongly support the hypothesis of the regular advertisement of occupancy as the mechanism of inter-troop spacing in captive *A. caraya*. By moving around an enclosure during howling, howlers may further advertise their location (Da Cunha and Byrne, 2006) and thus warn off neighbouring groups. Individuals locomoted more during spontaneous howls compared to familiar conspecific calls. Conversely, after howling, individuals locomoted less after spontaneous howls, and more after howling when stimulated by conspecific calls. Howls which are performed with no stimuli (spontaneous) may not require the caller to patrol their territory or boundary after a howl. Spontaneous calls may play a role in discouraging neighbouring groups and solitary individuals from moving their way during the day (*A. seniculus*, Sekulic, 1982a), or as suggested in wild *A. caraya*, regularly advertise a groups' location (Da Cunha and Byrne 2006).

Playback experiments, simulating the calls of unfamiliar conspecific howls, elicited more vocal and behavioural responses than other primate and man-made sounds. During playbacks, males who had auditory access to conspecific calls moved around their enclosure more than females. Howls are primarily performed by adult males, with subadult males and females of the group sometimes participating in calling bouts (Altmann, 1959; Schön Ybarra, 1986; Whitehead, 1995; Steinmetz, 2000). Therefore males may be moving around their enclosure more than females, as

they are the first to respond to the threat of neighbouring groups. We also found that groups with auditory access responded more to playbacks and males with auditory access locomoted more after conspecific playbacks than those without auditory access. Howling is suggested to play a role in *Alouatta* male-male competition (*A. pigra*, Kitchen, 2004; *A. seniculus*, Sekulic, 1982a, 1982b). Although we cannot infer a causal link between auditory access and howl-associated behaviours, we suggest that males which are regularly exposed to the calls of conspecifics may be more responsive to the simulated presence of unfamiliar conspecifics. However, males with no auditory access would also be expected to respond, as they are also exposed to a threat which they are not expecting. The playback of unfamiliar conspecific male calls may pose the threat of invasion of a new male to all *A. caraya* groups, irrespective of social group composition. Further playback experiments investigating the numeric odds of the listener, as conducted by Kitchen (2006), would help to further elucidate the influence of social group characteristics on vocal responses in *A. caraya*.

Of particular interest are the howl-associated behaviours performed by female *A. caraya*. Higher rates of SDBs were performed by adult females than males during naturally occurring howls, providing evidence that females are anxious around howling events. We also found that SDB rates were lower during the playback of conspecific calls compared to playbacks of *A. palliata*. If SDBs are indicative of anxiety, it would be expected that rates would be higher when exposed to conspecific calls, rather than a non-sympatric *Alouatta* species. Perhaps the calls of *A. palliata* are perceived as threatening as they are not recognised as there are no captive *A. palliata* held in European zoos; therefore, our study subjects will not have previously heard this species' calls. After howl bouts, females perform more territorial behaviours than males. It is suggested that female howler monkeys support group males during

howling bouts, by deterring intertroop females from gaining access into the troop or to their mate (Sekulic, 1982a). Further research into the influence of different male callers on female behaviour, through additional playback experiments both in captivity and the wild, may help to elucidate male assessment mechanisms and the role of females in group calling.

The final mechanism of intertroop spacing hypothesised was boundary marking or defence. Our findings support the role of physical territorial demarcation, as territorial behaviours were only performed during spontaneous howls and those howls performed naturally, in response to the calls of familiar conspecifics. Our playback experiments did not elicit territorial behaviours; however, during playback experiments, males approached the speaker more during unfamiliar conspecific call playbacks, which may be an investigatory or agonistic behaviour. If we apply these ideas, our findings do support this hypothesis, but as captive animals are restricted to their enclosure, we are assuming that animals perceived their cage boundaries as their territory limits. Therefore, by conducting future studies, playing back the calls of familiar and unfamiliar conspecific male howls, we may help to elucidate whether conspecific playbacks are equivalent to natural calls, and further clarify responses to natural and simulated male presence in terms of territoriality.

For the function of mate defence we hypothesised that males will strongly react to playbacks, both approaching and vocally responding to playbacks, which our results confirm. Female participation in vocal responses to conspecific call playbacks might further support this hypothesis. Female *A. seniculus* call towards extra-group males whilst located close to their mate (Sekulic, 1983). By howling during intergroup encounters, females may help to support group males and deter intergroup females from gaining access to their mate or group (Sekulic, 1982a). Playback

experiments have shown that *A. pigra* females participate in calling bouts if numeric odds are even, but less if odds are against her group (Kitchen, 2006), a time when groups would most require support. However, the social composition of our study groups may weaken support for this hypothesis. The European population of *A. caraya* is managed through a captive breeding programme. The movement of animals between groups is based on maintaining genetic stability of the population; therefore, social group composition does not always reflect that of wild groups.

Although results support the predictions of mate attraction; females responded more to the playback of conspecific calls than non conspecifics and we found an increase in social interactions after spontaneously performed howls. Conversely, during playback experiments simulating the presence of unfamiliar conspecifics, we found that social behaviours were performed to a lesser degree. This result does not support the hypothesis of mate attraction as it would be expected that hearing an intergroup conspecific male howl would encourage the performance of social and soliciting behaviours. The presence of other howler monkey groups in the zoo also influenced the performance of social behaviours; groups with auditory access to conspecifics were more social during the playbacks of unfamiliar conspecific calls than groups without regular exposure to howls. Again, without implying a causal link between auditory access and social behaviours, our results suggests that regular exposure to neighbouring male howls may heighten social responses to unfamiliar males. However, it would be expected that those with no auditory access would also respond, perhaps being more threatened by the presence of conspecific males. The idea that howling has a function of mate attraction has been suggested in wild *A. seniculus* (Altmann, 1959; Sekulic, 1982b) and findings in other *Alouatta* species suggest that females may use male calls to assess mate potential (*A. fusca*; Chiarello,

1995; *A. pigra*; Kitchen, 2004), but this has not been documented in *A. caraya*. In *A. pigra*, females are more attracted to the dominant male in a group who starts howling bouts (Van Belle and Estrada, 2008; Kowalewski and Garber, 2010). However, as we did not observe high frequencies of sexual behaviour, as previous howler monkey studies have reported (Altmann, 1959; Shoemaker, 1979), further investigation into the role of howling in promoting social bonding in *Alouatta* species would be beneficial.

Our results strongly support the function of *A. caraya* howling in intertroop spacing, by means of regular advertisement of occupancy and also provide preliminary support for mate defence and attraction. We suggest that further research into the howls of *A. caraya* and other *Alouatta* species is required to elucidate the function of howl calls. By comparing behaviours conducted both in captivity and the wild may help to further determine the influence of social and environmental factors on howling.

**CHAPTER 4: The relationship between reproductive success, vocalisations and social housing in captive howler monkeys (*Alouatta caraya*)**

*Abstract*

Over the last 12 years the European captive population of black and gold howler monkeys, *Alouatta caraya*, has increased at a slow rate and many groups have not produced offspring. This study aims to determine the influence of social organisation of captive groups and both performing and hearing howl vocalisations on reproductive success. Data were extracted from the European Studbook to calculate three variables of female reproductive success per capita, for each year of their reproductively active life (from three years of age). Reproductive success for females was measured as the occurrence of a birth each year, the total number of births per year and the number of successful births per year (offspring surviving to one year of age). Male data were analysed separately, using behavioural observations in addition to studbook data, to determine the effect of daily howling rates on reproductive success (mean number of offspring surviving to one year of age). We found that more offspring were born to and survived (both  $P < 0.001$ ) from females held in family groups than those in pairs. Male howler monkeys held in family groups had a higher mean number of offspring born per individual than those held in a pair ( $P < 0.001$ ) and males which performed a higher howl rate also had increased reproductive success. We also found that for females, regularly hearing the howls of familiar conspecifics was related to an increase in reproductive success ( $P = 0.003$ ). This study provides the first evidence of a link between howling and reproductive success in A.

*caraya* and provides suggestions for the management of captive black howlers to increase the current captive population.

**Keywords:** *Alouatta*, *Alouatta caraya*, howl, reproduction, captivity, zoo.

#### 4.1. Introduction

In the wild, many species are threatened with extinction, thus captive breeding programmes are an important aspect of ex situ conservation. Captive breeding is supported particularly by zoological institutions and the majority of species are managed through European and International breeding programmes (for review see Glatston, 1998). Maintaining captive populations is not only important in terms of species preservation, but also for potential reintroduction into the wild (Snowdon, 1989). However, due to habitat destruction and deforestation, the natural habitats of many species are now under threat and the opportunity for reintroduction is declining. As a result, many species are being maintained in captivity for many generations.

In some species the birth rates of captive populations are lower than in situ; as found in *Eulemur* species (for review see Hearn et al, 1996); gorillas, *Gorilla gorilla gorilla* [Beck and Power, 1988]; tamarins, *Sanguinus geoffroyi*, [Kuhar et al, 2003]; gibbons, *Hylobates leucogenys* [Lukas et al, 2002] and small felids (Mellen, 1991). Howler monkeys are known for their inability to adjust to captivity due to specialised nutritional requirements and stress (Benton, 1976) and rarely breed under captive conditions (Crockett, 1998; Gomes and Bicca-Marques, 2003). In order to maintain endangered populations in captivity, it is important to assess the factors which affect reproductive success and what actions can be taken to encourage breeding.

There is a growing body of literature on the effects of captivity on reproduction (for review see Carlstead et al, 1999). Two important factors related to increasing captive breeding are social grouping and the performance of natural, wild-type behaviours. The group composition of captive species plays an important role in facilitating reproduction and providing socialisation opportunities (for review see Forthman and Ogden, 1992). Social housing needs are species specific; housing small felids in groups larger than a pair leads to reduced reproduction (Mellen, 1991) whereas the presence of more than one female conspecific in black lemurs (*Eulemur macaco*) increases reproductive rates (Hearn et al, 1996). The loss of wild-type behaviours can be observed as a species adapts or adjusts to life in captivity (Rabin, 2003; Wallace, 2000). One of the main goals of captive animal management is the promotion of natural behaviours and the prevention of abnormal behaviours (for review see Hearn et al, 1996) in order to facilitate successful reintroduction programmes (Jule et al, 2008). In management terms, some of the most important behaviours to maintain are those associated with sexual reproduction such as courtship and mating.

Of the 14 species of howler monkey (genus *Alouatta*) recognised by the IUCN Red List, two are endangered, two vulnerable and 10 classified as least concern. Within the European zoo population, the most commonly held species is the black and gold howler monkey, *Alouatta caraya*, which is classified as least concern, defined as a widespread and abundant taxa in the wild. Our study focused on *A. caraya* because all zoo institutions aim to breed the individuals in their collection and *Alouatta* species are difficult to breed in captivity. *A. caraya* are not an endangered species, which makes them a good 'example' species to examine the factors which

might help encourage captive breeding which can then be applied to more threatened species.

In order to assess the influence of social grouping on breeding in this species, the social composition of natural groups must be determined. Wild *A. caraya* group size is the largest of all howler species (Aguilar et al, 2009), ranging from two to 19 individuals (for review see Moura, 2007). Groups in the wild are mixed-gender, containing multiple males (Aguilar et al, 2009; Juarez and Fernández-Duque, 2005), one to seven adult females (Thorington et al, 1984) and several younger members (Rumiz, 1990). Reproducing groups contain up to three adult males, one to four adult females and a number of subadults and infants (Calegario-Marques and Bicca-Marques, 1993a; Peker et al, 2009). In the wild, most infants are born to socially dominant males (Jones, 1985; Pope, 2000; Ryan et al, 2008) to which females display a preference in mating (Jones, 1985; Jones and Van Cantfort, 2007). Males which do not achieve high rank generally do not reproduce (Jones, 1980, but see Van Belle and Estrada, 2008 for an exception). Wild female howlers are known to be promiscuous, mating with both group and extra-group males (Jones, 1985; Jones and Van Cantfort, 2007) and all group females are stated to reproduce equally (Crockett and Eisenberg, 1987). In captivity, it is only the socially dominant female which bears offspring; lower ranking females do not conceive young or even appear to undergo oestrous cycles (Shoemaker, 1979). Of the captively housed *A. caraya* in Europe, 38% (n=9) are housed in a pair and 62% (n=15) held in family groups ranging from three to six members (ISIS, International Species Information System, 2010). Since it seems that pairs rarely naturally occur in the wild, we examined whether breeding success was reduced for howler monkeys held in pairs versus family groups.

As well as a natural social grouping, the performance of wild-type behaviours may also function to facilitate/be related to successful reproduction. The genus *Alouatta* are characterised by the production of loud, low frequency howl vocalisations (Whitehead, 1987, 1995). The functions of howl calls include regulation of space use, mutual avoidance of neighbours, territorial demarcation, opponent assessment, predator avoidance and resource and mate defence (see review by Da Cunha and Byrne, 2006). Howling plays a role in male-male competition through transmitting information on an individual's characteristics and fighting ability (Crockett and Eisenberg, 1987). It is also used for attracting females directly (Sekulic, 1982a, b), and as a result may be an important aspect of mate choice (Farmer, unpublished results).

This study aims to investigate the following experimental hypotheses 1) the influence of social grouping, 2) the performance of howl vocalisations, and 3) hearing the calls of familiar conspecifics (classed as auditory access) on the reproductive success of captive howler monkeys. In this study we expect that reproductive success will be higher in those housed in family groups, those with a higher howl rate and groups which regularly hear conspecific howls, since these conditions are closest to those experienced by wild howler monkeys.

## **4.2. Methods**

### **4.2.1. Subjects**

Data were taken from the black and gold howler monkey (*A. caraya*) European Studbook (ESB) which was current up to 31<sup>st</sup> December 2009, using SPARKS (Single Population Analysis and Records Keeping System) software. The

studbook contains information on all zoo-housed individuals in EAZA (European Association of Zoos and Aquaria) member collections dating back to 1994. Information on individuals before this date (from 1987) was gained by the studbook keeper from zoo records. Data on all individuals of reproductive age in the studbook; 30 females and 28 males were extracted to look at the influence of hearing other groups of howlers on reproductive success. In addition, from the studbook we extracted data for 12 females and 12 males housed with these females which had previously been studied by the first author, to examine the relationships between grouping (pair vs family) and howl production by the males on reproductive success.

#### **4.2.2. Data set**

We defined the first possible age of reproduction as three years in both females (Thorington et al, 1984) and males (Shoemaker, personal communication, in Jones, 1983). Three reproductive variables were used as measures of female reproductive success and were calculated per capita for each year of a female's reproductively active life, from three years of age to the end of 2009; 1) the occurrence of a birth each year (yes or no); 2) the total number of births per year and 3) the number of successful births per year (the number of offspring born surviving to one year of age). The studbook coordinator determined that only the adult male of each group sired offspring, from findings that in the wild, most infants are born to socially dominant males (Jones, 1985; Pope, 1990, 2000; Ryan et al, 2008). Male reproductive success was defined as the mean number of successful offspring born. Successful offspring were defined as those surviving to one year, the age at which an infant howler is weaned (Rumiz, 1990). Since only one female in each group gave birth during the period, we could discard the possibility that greater reproductive

success by dominant males housed in family groups is simply due to the presence of a larger number of females with which to breed.

### 4.2.3. Data analysis

#### 4.2.3.1. Social grouping effects

We included data collected on both adult males and adult females during visits to 12 established groups of *A. caraya* held at eight UK zoological institutions (Table 4.1). The social grouping for each of the 12 groups were classified as a pair, where one adult male and one adult female were housed together, or a family group comprised of three to six individuals, with multiple male (1-3) and female (1-3) group members.

Table 4.1. Information on focal group social composition, auditory access and howl rates per dominant male.

<b>Group number</b>	<b>Date visited</b>	<b>Social composition (male.female)</b>	<b>Auditory access</b>	<b>Mean daily howl rate</b>
1	March 2006	3.3	Yes	1.2
2	March 2006	3.2	Yes	0.8
3	October 2006	1.1	Yes	0.2
4	November 2006	1.1	No	0
5	June 2007	1.1	No	0
6	July 2007	1.1	No	0.3
7	October 2007	3.1	Yes	0.1
8	October 2007	2.3	Yes	0.3

9	May 2008	3.1	No	2.1
10	March 2009	1.1	No	0
11	April 2009	3.1	No	0
12	September 2009	1.2	Yes	0.8

#### 4.2.3.2 Howl vocalisation effects

For the 12 males studied, the rate of howling performed by each individual was calculated (Table 4.1). It is usually one adult male of the group who performs howl vocalisations therefore the influence of daily howling rate was only analysed for male reproductive data. At each group the researcher opportunistically recorded the occurrence of every howl vocalisation performed by standing at the enclosure between 08:00h and 16:30 h over 16 days, from which we calculated the mean rate of howls per day for each adult male. In this study we define a howl vocalisation to be a call which lasted for a minimum of 60 seconds (Drubble and Gautier, 1993). For each of the 12 males, we then used studbook data to calculate their mean reproductive success over the years since they were visited.

#### 4.2.3.3. The influence of conspecific howls

The influence of hearing the calls of familiar conspecifics was analysed for all 30 females and 28 males. Individuals were classed as either having auditory access (able to hear conspecific calls) or not, when no other howler monkey groups were housed at the zoo. A previous study shows that 100% of groups housed with another conspecific group in the zoo howl themselves (Farmer, unpublished results). Therefore, for individuals who were housed in zoos with more than one group of conspecifics, it was expected that they would be exposed to howling bouts.

#### 4.2.4. Statistical analysis

We analysed female and male data separately. To analyse social grouping effects on the subset of 12 groups previously studied, we carried out a GLMM analysis in PASW statistical software (PASW version 18, 2010, IBM, Chicago, IL, U.S.A) with a normal distribution identity link model and included social grouping (pair or family) as a fixed factor. The influence of howling rates on the reproductive success of males was analysed using a GLMM with inverse gaussian distribution and factors as above, including the fixed factor of howl rate (mean rate of howling per day).

To assess the influence of conspecific howler groups housed in the zoo on the occurrence of births per year for females we used Generalized Estimating Equations (GEE) analysis with a binomial logit model. As fixed factors we included individual number as a repeated measures subject variable (nested within auditory access), auditory access (the presence of another conspecific group in the zoo) and age as a covariate (from 3 years to age at the end of 2009). To analyse female and male reproductive success we carried out a Generalized Estimating Equations (GEE) analysis using a normal distribution identity link model and the same factors as the previous analysis.

We fitted the models using a backward elimination process to find the minimum adequate model for explaining the variance of the response variable. Only significant explanatory variables and two-way interactions were retained and models with the lowest Akaike's Information Criterion (AIC) value were interpreted. All tests are two-tailed. For all significant results ( $P < 0.05$ ), post-hoc pairwise comparisons with Bonferroni corrections were carried out and all relevant results are reported.

### 4.3. Results

#### 4.3.1. Descriptive statistics on the historical studbook data of *Alouatta caraya*

The youngest female to give birth was 25 months (however births at less than 3 years of age were not included in analysis), the oldest was 168 months old, with a mean age at first birth of 75 months. In males, the youngest birth was recorded as 17 months, the oldest at 168 months. The oldest female survived to 20 years, the oldest male to 23 years of age. Litter sizes for all recorded births were of one offspring. The gestation period is approximately 187 days (Rowe, 1996; Shoemaker, 1979). No seasonal pattern of births was found (Figure 4.1).

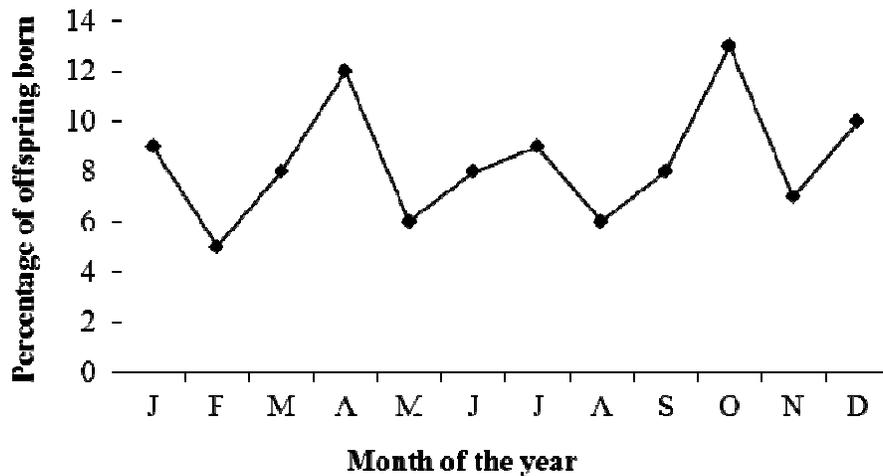


Figure 4.1. Seasonality of births from *A. caraya* studbook between 1994 and 2009, (n=130).

#### 4.3.2. Social grouping effects

The social grouping of females had a significant relationship with the number of offspring born ( $X^2_1 = 16.45$ ,  $P < 0.001$ ) and number of surviving offspring ( $X^2_1 = 15.69$ ,  $P < 0.001$ ). More offspring were born to mothers held in a family group than those held in pairs (family mean  $\pm$ SE:  $0.82 \pm 0.072$ , pair mean  $\pm$ SE:  $0.25 \pm 0.120$ ) and more offspring survived from family housed mothers than those held in pairs (family mean  $\pm$ SE:  $0.62 \pm 0.075$ , pair mean  $\pm$ SE:  $0.18 \pm 0.025$ , pairwise comparisons were both significant,  $P < 0.001$ ). In males, social grouping had a significant relationship with the mean number of successful offspring produced ( $X^2_1 = 17.94$ ,  $P < 0.01$ ) with more successful offspring born to males held in family groups than pairs (family mean  $\pm$ SE:  $0.20 \pm 0.083$ , pair mean  $\pm$ SE:  $0.72 \pm 0.092$ , pairwise comparison  $P < 0.001$ ).

#### 4.3.3. Howl rate influence

Mean daily howl rate of males had a significant positive relationship with the mean number of successful offspring (i.e. surviving to 1 year of age) born ( $X^2_6 = 24.615$ ,  $P < 0.001$ ) with more successful offspring born to males with a higher howl rate (Figure 4.2).

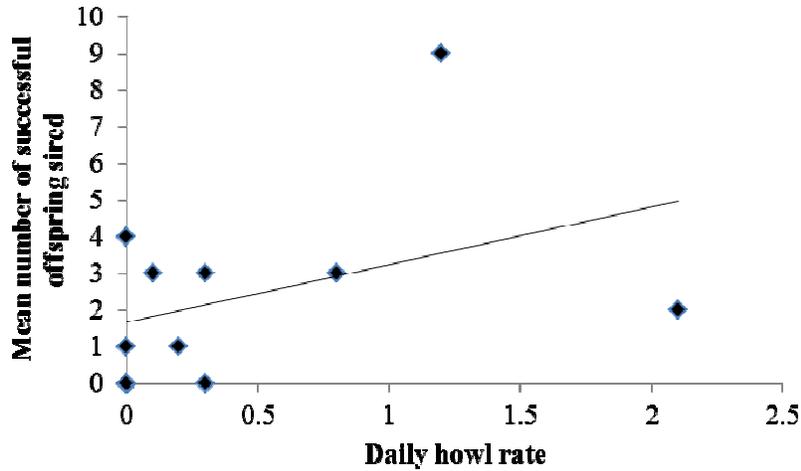


Figure 4.2. Mean number of successful offspring (i.e. surviving to 1 year of age) of captive male black howler monkeys in relation to their daily howl rate (n=12).

#### 4.3.4 Influence of conspecific howls

We found that auditory access to the calls of familiar conspecifics was significantly related to the occurrence of births each year ( $X^2_1 = 7.729$ ,  $P = 0.005$ ), with more births by females with auditory access (mean 0.65) than without (mean 0.4). There was a positive, significant relationship between auditory access and the number of successful births each year ( $X^2_1 = 8.852$ ,  $P = 0.003$ ), with more successful births by females with auditory access (with access mean  $\pm$ SE:  $0.78 \pm 0.077$ , without access mean  $\pm$ SE:  $0.45 \pm 0.080$ , pairwise comparisons  $P = 0.003$ ). There was no effect of auditory access on the mean number of surviving offspring ( $X^2_1 = 1.55$ ,  $P = 0.213$ ).

#### 4.4. Discussion

In accordance with previous studies, we found no seasonality in births in the captive population (Shoemaker, 1979, 1982). In the wild, a pattern of birth seasonality in *A. caraya* is argued, with evidence for both a lack of seasonal births (Kowalewski and Zunino, 2004; Zunino et al, 1996) and for seasonal patterns (Calegari-Marques and Bicca-Marques, 1993). Births depend on food availability and ecological differences in habitat (Kowalewski and Zunino, 2004), with conception occurring during a peak in food availability and a concentration of births in the dry season, depending on the type of habitat. With no such limitations in the captive environment, there is no specific time of the year to focus on facilitating *A. caraya* reproduction.

##### 4.4.1. Social grouping

We found that both males and females in family groups, containing multiple males and females, have higher reproductive success than those held as a pair. Wild *A. caraya* group sizes vary dramatically (for review see Moura, 2007) and there is conflicting evidence from wild studies on the influence of group composition on reproductive success. In *A. seniculus*, reproductive success is significantly correlated with the number of breeding females in a group where females produce more offspring if they recruit their daughters to form coalitions and to cooperatively defend food sites (Pope, 2000). However, in *A. palliata*, the presence of other females in a group negatively affects reproduction (Ryan et al, 2008) as infanticide rates increase with a higher number of group females (Janson and Goldsmith, 1995; Ostro et al, 2001).

Wild subadult or young male and female *A. caraya* are known to emigrate from their natal group (Rumiz, 1990), more so subadult females (Calegaro-Marquez and Bicca-Marquez, 1996). These emigrants can remain solitary until they join other small groups, or often young males will invade neighbouring howler groups which can result in infanticide (Rumiz, 1990). Natal emigration is necessary for successful reproduction in stable, wild groups of *A. caraya* (Kowalewski et al, 1995), however in captivity, studbook coordinators control the emigration and immigration of individuals between groups. Studbook recommendations for *A. caraya* are that subadult females are removed from the natal group at 2.5 years of age and males at three years (although this can vary in practice depending on individual and group circumstances). Such management involves removing males when they show signs of interest in the groups' breeding female thus reducing the opportunities for male-male competition, so providing a stable group in which breeding may freely occur.

There is no record of single pairs of howlers breeding in the wild, but 38% of captive groups of *A. caraya* held in European institutions are housed as pairs (ISIS, 2010). This suggests that either howlers do not join to form pairs in the wild, or that a pairing is not the optimum social grouping for breeding. Our evidence supports this since we found higher reproductive success in group-held individuals.

#### **4.4.2. Influence of howl vocalisations**

Our results show a link between the daily rate of howl vocalisations performed by males and their reproductive success, with higher mean offspring survival rates enjoyed by more regularly howling adult males. In the wild, one of the roles of howling is in mate choice, where females are more attracted to dominant group males which start a howling bout (Van Belle and Estrada, 2008; Kowalewski and Garber,

2010). Males performing a higher daily howl rate would have an increased chance of breeding and thus, reproductive success, and this may be occurring in captivity.

However, in captivity, the studbook determines that it is only the dominant adult male of each group which sires offspring and it is this male which initiates howling bouts. Captive females may not have the choice of potential breeding partners as in wild groups, which may also influence reproductive success.

Howling also functions in female defence and attraction in howler species (Altmann, 1959; Sekulic, 1982b; Crockett and Eisenberg, 1987), especially if infants are present (Kitchen, 2004). Adult male howler monkeys do not actively participate in parental care (see review Treves, 2001), but may help indirectly via howling bouts to defend the group against, and ousting, invading males (Kitchen et al, 2004; Sekulic, 1982b). In the wild, male howlers are more likely to vocally respond to a neighbouring group if their group contains infants (Kitchen, 2004). Females also call alongside their mate to strengthen the pair bond and encourage defensive behaviour in order to protect group infants (Sekulic, 1983) as infanticide is a common occurrence in *Alouatta* species (Agoramoorthy and Rudran, 1995). In captivity, although there is no physical threat of extra-group male conflict, howling rate may aid offspring protection and lead to higher reproductive success through displaying fitness and also maintaining social relations (Wang and Milton, 2003).

#### **4.4.3. Auditory access to conspecifics**

We predicted that reproductive success would be higher in groups that are regularly exposed to the howls of familiar conspecifics. Our findings show that females held in groups with auditory access to conspecific howls produce higher numbers of offspring and have higher reproductive success than those in groups

which are the only *A. caraya* housed at an institution. In relation to breeding, howls are performed during extra-group male contests (Sekulic, 1982b; Sekulic and Chivers, 1986) as an aggressive display (Mittermeier, 1973) and an alternative to physical conflict (Da Cunha and Byrne, 2006). If regularly exposed to the howl calls of conspecifics, males may be advertising their fitness through howling performance, displaying to females that they are more able to defend a group or mate (Kitchen et al, 2004; Sekulic, 1982b).

Being exposed to conspecific vocalisations regularly, as are those captive groups with auditory access, may be a more natural auditory environment and promote natural behaviours. It is known that male *A. caraya* call spontaneously and that most howl bouts are performed in response to seeing or hearing a conspecific group (Calegari-Marques and Bicca-Marques, 1995; Farmer, unpublished results; Thorington et al, 1984). In wild *A. caraya*, males vocally responded more to playbacks simulating conspecific invasions compared to normal howling patterns (Da Cunha and Byrne, 2006). In captivity, groups of *A. caraya* responded more behaviourally and physically to unfamiliar conspecific call playbacks than other primate calls and these responses did not habituate over time (Farmer, unpublished results).

Our findings have highlighted links between the performance of howling and the influence of hearing the calls of other conspecific groups housed in the zoo on reproductive success. We cannot determine a causal direction of these relationships, however, as we know that there is a positive relationship between howling rate and reproductive success, encouraging the performance of howl vocalisations is recommended to try and increase breeding in captivity. Groups who regularly hear the calls of conspecifics are found to howl more themselves, therefore simulating the

presence of other vocal groups may elicit a calling response from focal groups. Studies conducted on gibbon species (*Hylobates* spp.) have found that when playing the calls of conspecifics to captive individuals, listeners vocally responded, suggesting a positive influence on their behavioural repertoire (see Volodina and Volodin, 1999 for review). In addition, research concerning the influence of hearing the vocalisations of neighbouring conspecific groups which are housed in the same institution, termed the ‘neighbor effect’, have found that individuals perform significantly more vocal responses when exposed to higher levels of neighbour vocalisations (chimpanzees, *P. troglodytes* [Baker and Aureli, 1996; Videan, Fritz, Schwandt and Howell, 2005] and common marmosets, *C. jacchus* [Watson and Caldwell, 2010]). This study has highlighted a relationship between exposure to conspecific howl calls and reproductive success, and although there is no evidence it is a causal link, simulating the presence of neighbouring groups may be beneficial.

For groups which are the only howlers held in a zoo, simulating conspecific presence can be achieved by either introducing another group of conspecifics into the zoo or using acoustic playbacks of conspecific calls daily (Farmer, unpublished results), to mimic the presence of nearby *A. caraya*. Playbacks may encourage the performance of wild-type behaviours and provide a contingent link between behaviour and response. By the researcher ending the playback of conspecific calls when the listener begins to howl, males who respond can perceive to ‘win’ a vocal contest. This method would provide animals with perceived control over their environment, allowing them to predict the outcome of their behaviour, ultimately improving their captive welfare.

We have also found a relationship between social group type and reproductive success. Again the causal direction cannot be determined but we suggest

that manipulating group size may also promote increased breeding in captivity. We recommend that captive individuals are held in group sizes larger than one adult male and one adult female. However this may be difficult to achieve in practice due to potential aggression when introducing new individuals to established pairs e.g. introducing unrelated individuals leads to aggression in captive spider monkeys (Davis et al, 2009). In all *Alouatta* species, both sexes disperse from their natal group in the wild (Crockett and Eisenberg, 1987). In *A. caraya*, new groups are formed when mates are available and habitat conditions are optimal (Rumiz, 1990). In the wild, the immigration of *Alouatta* females into an existing breeding group is rare (Sekulic, 1982c). Males are prevented from joining an established group by resident males (Sekulic, 1982c; Crockett and Pope, 1988) and wild female *A. seniculus* are known to display aggression towards extra-group females and intra-group females which are not their daughters (Pope, 1990). The current typical husbandry practice is to pair an unrelated male and female together when they reach dispersal age. Potentially, more animals could be put together at this stage to form entirely new groups rather than pairs and avoid the need to introduce new individuals to established pairs.

The effects of a larger group could also be achieved by housing additional groups of *A. caraya* in close proximity to existing pairs, to mimic a larger group size. Providing visual contact with neighbouring groups may elicit both behavioural and vocal responses to their presence. In addition, olfactory contact with conspecifics may further help to simulate natural conspecific encounters. *Alouatta* species perform communal defecation within their home range which may play a function in the inter-group communication of aggression and dominance (see Neville et al, 1988). As

captive enclosures are limited by physical boundaries, this may help groups to perceive the maintenance of their territory.

#### 4.5. Conclusions

Reproductive success in captive *A. caraya* is related to the presence of family group members, howl bout performances and hearing conspecific howls. Findings show that when *A. caraya* are housed in a way that is comparable to wild environmental situations, where groups are composed of multiple male and female members and howlers are exposed to the calls of neighbouring groups regularly, reproductive success is higher. Howling, the behaviour which characterises the *Alouatta* genus, may be a good indicator of welfare, with animals held under optimal conditions both howling and breeding more. Therefore, even though this study does not allow us to make a causal link between howling and breeding, since they are clearly related, stimulating howling behaviour of males is recommended, even if to only increase their welfare.

**CHAPTER 5: Auditory enrichment: efficacy, keeper opinion and its future in husbandry practices for zoo-housed primates, particularly howler monkeys (*Alouatta caraya*)**

*Abstract*

The provision of environmental enrichment is a common husbandry technique in captivity; however, the use of auditory stimulation as enrichment is limited and little understood. We developed a questionnaire to investigate the presentation of environmental enrichment, particularly auditory enrichment, for captive primates to determine the types of sounds used and opinions of animal care staff on the efficacy of this form of enrichment. Our study then investigated the use of auditory enrichment for a highly vocal primate species, the black and gold howler monkey, *Alouatta caraya*, which is characterised by the production of loud howl calls. Responses to questions about *A. caraya* were compared to findings from previously conducted playback experiments, to determine attitudes towards the use of auditory enrichment in improving the welfare of this species. We sent our questionnaire to all European zoos holding *A. caraya* and obtained responses from 77% of institutions. We found that all primate species, including howler monkeys, are provided with environmental enrichment, with food-based items being the most common form used, sensory enrichments were only presented by half of respondents. Music and radio were the most popular sounds played. For howler monkeys, sensory devices are the least provided form of enrichment and were rated as the enrichment type that groups were the least responsive to. In reference to the playbacks conducted, keepers were unenthusiastic about the use of auditory stimulation for improving captive welfare in

*A. caraya*; however, they stated that they would use this form of enrichment in the future. These results compliment previous findings outlining the limited use of sensory enrichment and the requirement for additional research and assessment of the application of this form of enrichment.

**Keywords:** environmental enrichment, sensory stimulation, playback, captive, howler monkeys, *Alouatta*.

### 5.1. Introduction

In the captive environment animals are exposed to a wide range of sounds (Anthony, 1963; Konavalov, 1986), few of which would be heard in the wild and are seemingly unnatural (Kerridge, 2005; for review see Newberry, 1995). Many species are sensitive to sound frequencies beyond human range (Brown and Pye, 1975; Sales et al, 1988; Stoskopf and Gibbons, 1994) and as these sounds are rarely monitored or controlled (Milligan et al, 1993), acoustic conditions may disrupt communication between individuals. The captive management of species can lead to individuals being housed in socially unnatural groups; solitary, without the opportunity to communicate with conspecifics (Shepherdson et al, 1989), or with no extra-group stimulation to perform their full vocal repertoire. In primates, the production of vocalisations is an important aspect of their communication system as calls are produced in many contexts (e.g. alarm calling: vervet monkeys, *Chlorocebus pygerythrus* [Cheney and Seyfarth, 1988; Macedonia and Evans, 1993]; diana monkeys, *Cercopithecus diana diana* [Zuberbühler, 2000]; Campbell's monkeys, *Cercopithecus campbelli*, [Zuberbühler, 2001]; tufted capuchin monkeys, *Cebus apella nigritus* [Wheeler, 2008] and mate selection to indicate mate quality: Barbary macaques, *Macaca*

*sylvanus* [Semple, 1998]; Delgado, 2006 for review). To provide the opportunity to perform ‘natural’ behaviours such as calling, animal care staff may provide environmental enrichment as part of their husbandry routine.

Environmental enrichment is a well-studied topic and has many definitions (for review see Young, 2003). In this paper we provided a description of enrichment as “any steps taken to provide more than the basic housing and husbandry requirements, with the aim of keeping animals occupied, preventing abnormal behaviours and encouraging the performance of wild-type behaviours”. The provision of enrichment should be goal-orientated, focusing on encouraging the performance of biologically relevant behaviours. Providing an animal with a more complex enclosure and ultimately choice, can have a positive influence on captive animal welfare (Buchanan-Smith, 2010). To date, the majority of research conducted on enrichment concerns food-based devices (de Azevedo et al, 2007), with little application of sensory enrichment, which focuses on stimulating an animal’s senses. A particular lack of provision (Hoy et al, 2010) and limited research into the efficacy of auditory devices seems to be due to inadequate understanding of the information conveyed in sounds (de Azevedo et al, 2007; Wells, 2009).

Our study concerns the use of auditory enrichment which includes the simulation of a ‘naturalistic’ environment (conspecific calls and ecologically relevant sounds) and the playback of ecologically ‘non-relevant’ sounds such as music. Research into both of these types of auditory stimulation have returned mixed results (for review see Wells, 2009). When providing naturalistic acoustic stimuli, by considering the behavioural needs of an animal we can encourage the performance of wild-type behavioural repertoires (Keeling et al, 2011). In primate species, the playback of conspecific calls has been found to encourage the performance of natural

vocal and physical behavioural responses (Mueller's gibbons, *Hylobates muelleri* [Haraway et al, 1988; Maples et al, 1988]; lar gibbons, *Hylobates lar* [Shepherdson et al, 1989]). Being exposed to the calls of conspecifics has been found to elicit higher vocal rates in listening groups, termed the 'neighbor effect', and evoke an increase in species-typical behaviours (chimpanzee, *P. troglodytes*, Baker and Aureli, 1996; Videan, Fritz, Schwandt and Howell, 2005; common marmoset, *C. jacchus*, Watson and Caldwell, 2010). Therefore, by encouraging the performance of natural behaviours, considered to enhance captive animal welfare (Buchanan-Smith, 2010), the provision of biologically meaningful sounds may be an enriching acoustic stimulus for captive animals. However, many of the sounds experienced by captive animals are unnatural, such as music and radio. The negative responses of captive animals to music have been reported in reviews of both zoo and laboratory enrichment (Patterson-Kane, 2006; Wells, 2009), and although both cotton-top tamarins (*Saguinus oedipus*) and common marmosets (*Callithrix jacchus*) appear to prefer for slow compared to fast tempo music, when given the choice, chose silence over hearing music (McDermott and Hauser, 2007). These findings suggest that although music is known to have a beneficial influence on human behaviour (for review see Wells, 2009), we cannot assume that animals perceive music as an enriching stimuli.

Providing an acoustically stimulating environment can be a beneficial addition to captive husbandry; however, the addition of sounds in an animal's acoustic environment can lead to stress (reviewed by Honess and Marin, 2006; Ogden et al, 1994; Patterson-Kane, 2006). One benefit of planned auditory stimulation is that the sounds played can 'mask' unavoidable noise such as machinery or visitor sounds (Brent and Weaver, 1996; Mallapur and Chellum, 2002; Van der Weerd and

Baumans, 1995; Wells et al, 2006; see Wells, 2009) and may help to reduce stressful effects of background noise (Wells, 2009). These findings highlight the requirement for the provision of goal-based auditory enrichment and the constant monitoring of responses towards enrichment.

In this study we survey the use of auditory enrichment for captive primates and determine the types of sounds used and their perceived efficacy by animal care staff. To further address the use of auditory enrichment in captive primates, our survey then focuses on enrichment practices, in particular auditory stimulation, for a highly vocal species, the black and gold howler monkey (*Alouatta caraya*). Similarly to gibbons, the loud calls of *Alouatta* species have multiple functions (see Da Cunha and Byrne, 2006 for review) and play a major role in communication in the genus. However, previous findings have shown that many captive groups do not howl (Farmer, unpublished results). Through the application of auditory playbacks of conspecific calls, howling and associated behaviours can be encouraged (Farmer et al, 2011, in prep); therefore, this study surveys the use of auditory enrichment for this species at all European zoos which hold *A. caraya* to determine current practices. Keeper opinions on the use of playbacks as enrichment for *A. caraya* were then compared to observational evidence gained during experimental playbacks, to evaluate implications for the future use of auditory enrichment.

## **5.2. Methods**

### **5.2.1. Questionnaire**

We sent a questionnaire to all European zoos holding *A. caraya* ( $n = 22$ ). The questionnaire was divided into four sections with a total of 15 questions. We asked

questions about enrichment practices for all primates held at the zoo and specific questions focussing on enrichment practices for *A. caraya* groups. The majority of questions asked was ‘closed’, requiring “yes” or “no” responses so that respondents could quickly provide answers from a set of given responses. Where personal opinions of respondents were surveyed we included ‘scale-response’ questions (Frazer and Lawley, 2000) (Appendix III). We requested that a minimum of three howler monkey keepers at each zoo fill out the questionnaire. Before sending the questionnaire, it was approved by the British and Irish Association of Zoos and Aquariums (BIAZA) Research Group and letters of support from both the European Studbook Keeper for *A. caraya* and the European Association of Zoos and Aquaria (EAZA) Cebid Taxon Advisory Group (TAG) were gained (Appendices IV to VI).

### **5.2.2. Experimental playback at zoos**

Eight of the zoos surveyed contained 12 groups of howler monkeys which had previously been visited by the first author whilst carrying out behavioural studies and playback experiments on *A. caraya*. Therefore, we gained evidence on actual howling frequencies over a 16 day period, which could be compared to keeper ratings in the survey. For these zoos visited, an additional section was included in the questionnaire concerning the playback experiments conducted. Playback experiments were carried out to investigate behavioural and vocal responses of adult males and females to the calls of unfamiliar conspecifics, the howls of an allopatric howler monkey species (*Alouatta palliata mexicana*), a non-sympatric primate species (red ruffed lemur, *Varecia rubra*) and a chainsaw sound (for methodologies see Farmer et al, 2011, in prep). From this, we were able to experimentally test responses to each auditory

stimuli and determine the immediate responses of the adult male monkey in each group (orientate toward the speaker, approach the speaker and vocalise) to assess playback efficacy. Evidence-based knowledge could then be compared to the opinions of the keepers at these zoos.

### **5.2.3. Statistics**

Responses were investigated using descriptive statistics (Plowman, 2008). We asked each of the zoos to complete a minimum of three questionnaires but only five of the zoos sent more than one completed questionnaire. For those which did send two or three completed forms, we conducted Intra Class Correlations (ICC) (Shrout and Fleiss, 1979), to measure inter-rater reliability between keepers. We then carried out a two-way mixed model, specifying absolute agreement computation. ICC allowed us to determine whether the answers provided were statistically reliable to include as individual responses or whether we should accept an average rating for all responders at a zoo.

## **5.3. Results**

### **5.3.1. Questionnaire responses**

We received replies from 77% of zoos ( $n=17$ ), providing responses from keepers on 19 groups of howler monkeys. Responses from seven of the eight zoos visited during playback experiments were received which provided playback-related answers for 11 groups. Answers about the effectiveness and future use of playbacks were provided by four of those zoos.

Five zoos provided multiple questionnaire responses, from which the mean ICC for single measure reliability was 0.63; therefore, we had to accept that different keepers provided varying answers to our questionnaire. The average agreement between keepers was then calculated to measure reliability, results for which were more reliable, with a mean of 0.73 which indicates strong agreement. As a result, our results discuss the average of keeper responses for each categorical question.

### **5.3.2. Primate enrichment practices**

When asked if environmental enrichment (EE) was provided to the primate species housed in the zoo, 100% (n=17) of respondents confirmed that they practise EE as part of their husbandry routine. 73% of primates are provided with enrichment daily, 13% were provided enrichment weekly or monthly, and two zoos did not provide answers. The types of enrichment used were indicated and more than one type could be chosen by responders. Food-based enrichments were provided by all zoos (100%), the next common enrichment type were manipulative devices (87%). In terms of sensory enrichments, olfactory and auditory enrichments were provided by 60% of respondents, visual enrichment by 47% of respondents.

### **5.3.3. Primate auditory enrichment**

The majority of auditory enrichment sounds played for primate species was music and radio. ‘Other’ sounds used were the sound of splashing water (see Figure 5.1).

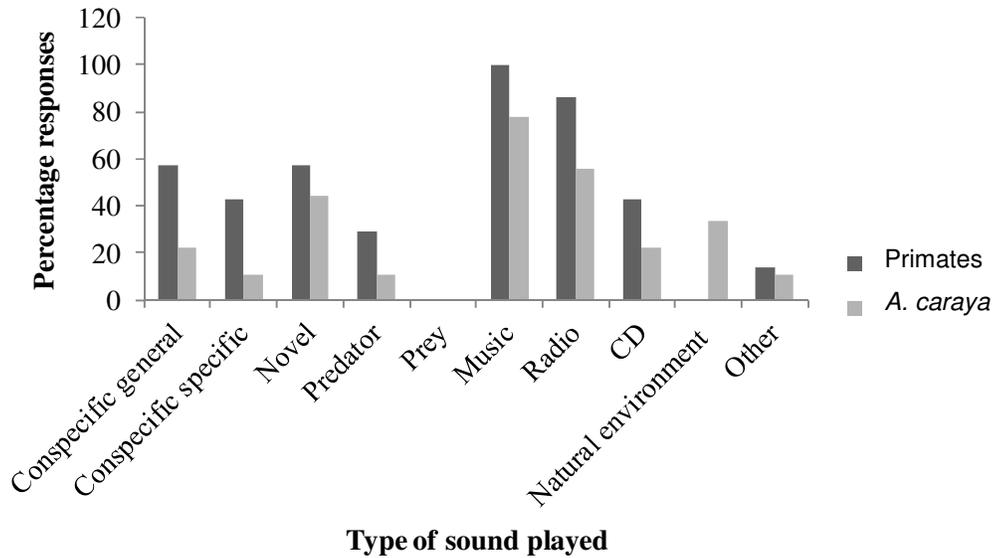


Figure 5.1. Percent of zoos providing different types of auditory enrichment for captive primates and howler monkeys (*A. caraya*) ( $n=8$ ).

According to keepers, the responses of primates to the sounds of conspecific general, novel, predator, music, radio sounds and CDs were 100% positive, i.e. encouraged the performance of natural behaviours or ‘goal’ behaviours such as affiliative behaviours towards group members or a vocal response. One of two keepers playing conspecific specific sounds, such as alarm calls, reported negative responses by the receiving animals.

#### 5.3.4. Howler monkey enrichment practises

All howler monkey keepers reported that their animals perform howl vocalisations. The frequency of howling was suggested to vary according to season and environmental factors; the majority of howler groups were reported to perform

howl vocalisations daily. In comparison to data gathered previously, in six of 11 cases, keepers reported higher rates of calling than those observed in our previous study, in four case keepers underestimated howling rates (Figure 5.2).

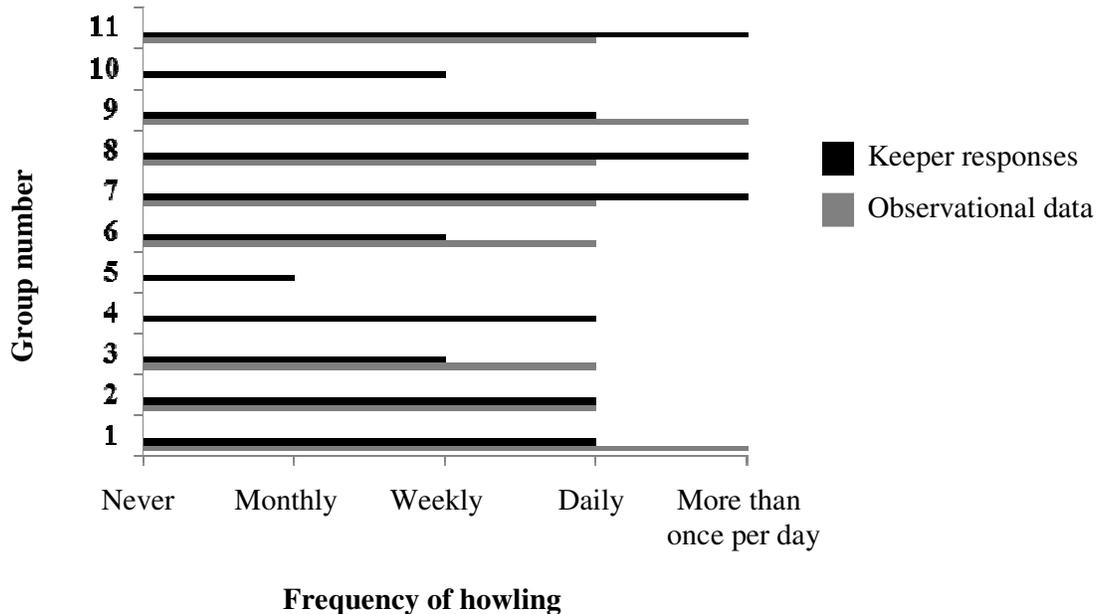


Figure 5.2. Frequency of howling by adult male *A. caraya* ( $n=11$ ).

The environmental factors which evoked howling in *A. caraya* were listed and more than one factor could be selected by responders. The most common stimulants reported to initiate howling bouts were vehicles ( $n = 12$ ) and machinery noise ( $n = 11$ ). Keepers and husbandry sounds were both reported to evoke howling (both  $n = 8$ ), as well as other primate species ( $n = 7$ ) and conspecific howling ( $n = 6$ ). Extremes of weather were the least frequent initiator of howling ( $n = 3$ ) and other sounds including background noises, construction work, horses and in the event of being let out of their indoor enclosure were also reported as stimulants.

All howler monkey keepers provided environmental enrichment to their animals. This enrichment was provided on variable schedules. The majority of

howlers were provided with enrichment once per day (47%,  $n = 9$ ), 37% ( $n = 7$ ) of howler groups were enriched weekly, a few were provided enrichment monthly (11%,  $n = 2$ ) and only one group was provisioned enrichment more than once per day (5%,  $n = 1$ ). Food-based enrichments were provided for all howler groups (100%,  $n = 19$ ), the next popular being manipulative devices (68%,  $n = 13$ ). Sensory enrichments were less provisioned; visual enrichment to only 32% ( $n = 13$ ) of groups, olfactory and auditory enrichment both to only 47% ( $n = 9$ ) of howler groups. Novel enrichment devices were provided to 26% ( $n = 5$ ) and ‘other’ enrichments to 16% ( $n = 3$ ) of howler monkey groups.

Howlers were rated to respond mostly to food-based enrichments and least to auditory enrichment. Most responses were towards food-based devices (Figure 5.3).

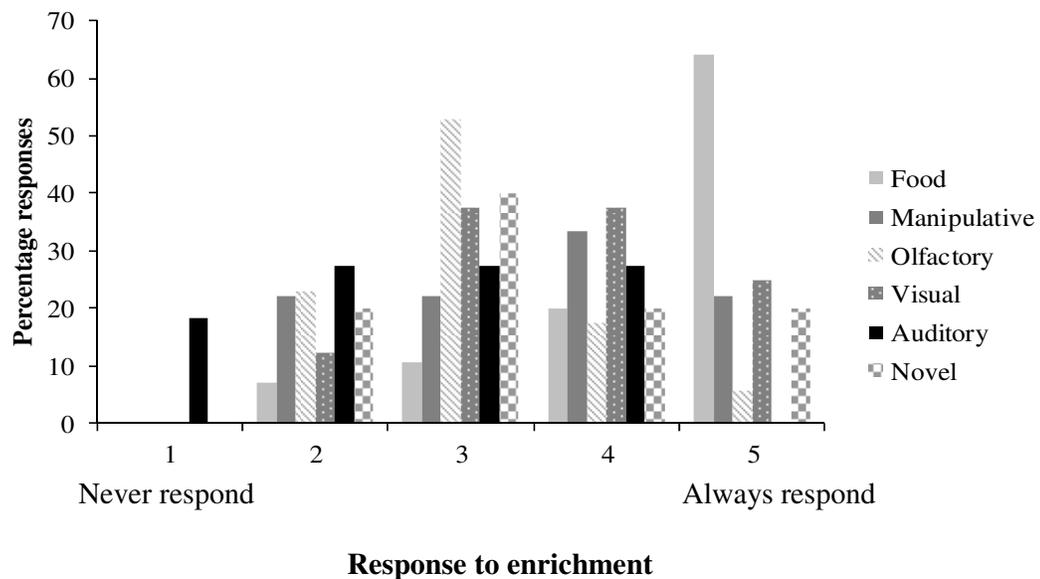


Figure 5.3. Keeper rating of *A. caraya* responses to different enrichment types ( $n=9$ ).

The most common sounds used as auditory enrichment for howlers were music and the radio. The ‘other’ sound reported was the banging of a bucket on the floor (Figure 5.1). All of keepers rated the auditory enrichment they used as having a positive response by the receiving howler monkeys. No negative responses towards auditory enrichment were reported.

### 5.3.5. Playback experiment at visited zoos

Of the zoos visited, keeper responses on the rate of actual howling and the rate of howling after the playback experiments had been performed were generally in agreement (Figure 5.1). When asked if keepers felt that playbacks encouraged howling, 50% ( $n = 2$ ) responded that playbacks were “effective” and 50% ( $n = 2$ ) of keeper responses were neutral. When asked if playbacks encouraged the performance of social behaviours, 50% ( $n = 2$ ) rated neutral, 25% ( $n = 1$ ) rated playbacks as having low efficacy and 25% ( $n = 1$ ) of responders rated playbacks as “not effective”. When asked if playbacks were perceived as improving the welfare of howler monkeys in their care, 75% ( $n = 3$ ) of responses were neutral, and 25% ( $n = 1$ ) rated playbacks as “not effective”.

Behavioural evidence from playback experiments showed immediate responses, both physically and vocally, to the playbacks of a range of sounds, but particularly to the playback of unfamiliar conspecific howls (Figure 5.4). This study also found that playbacks evoked howling in previously non-vocal groups (Farmer et al, 2011, in prep).

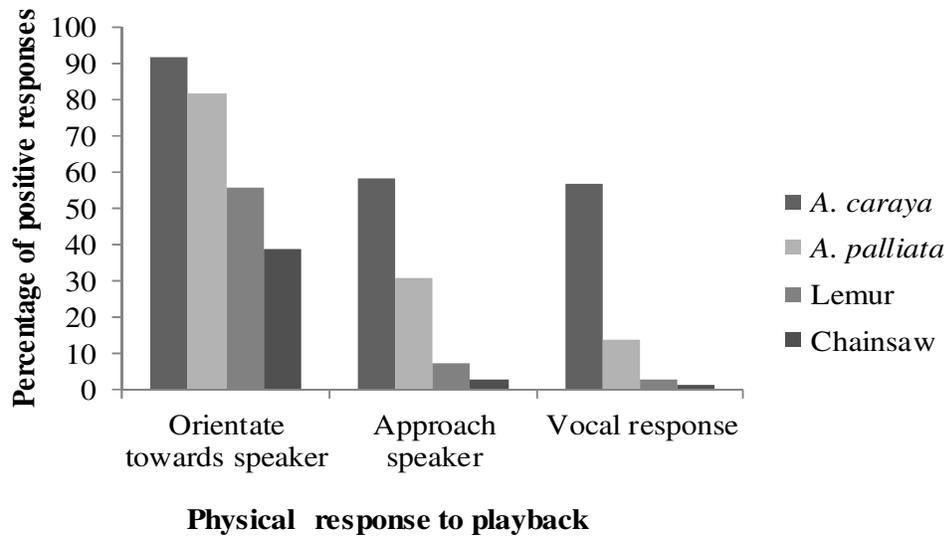


Figure 5.4. Physical responses of adult male *A. caraya* to playback experiments (data from Farmer et al, 2011, in prep) ( $n=12$ ).

Finally, when asked if the keepers would use playbacks as enrichment for their howling monkeys in the future, 25% ( $n = 1$ ) answered that they “would use playbacks”, 25% ( $n = 1$ ) “might use playbacks” and 50% ( $n = 2$ ) of responses were neutral.

## 5.4. Discussion

### 5.4.1. Primate enrichment practices

All of the zoos surveyed provided environmental enrichment for the primate species in their collection and, as often found in zoo husbandry, the most common type of enrichment presented was food-based (de Azevedo et al, 2007), followed closely by manipulative enrichments. Sensory enrichments were provided by approximately half of the zoos. These findings are similar to those found in a recent

survey of enrichment practices for captive mammals (Hoy et al, 2010) where keepers identified food-based enrichments as the most important, and visual and auditory enrichment as the least important type of enrichment provided.

Our study focused on the use of auditory enrichment, therefore the remaining questions on primate husbandry concentrated on this topic. We found that the majority of zoos which provided auditory enrichment played music as a stimulant, which has been found to be beneficial to many species in decreasing aggression and has a calming influence on behaviour (for review see Wells, 2009). The radio was also a commonly used sound; however, it is not clear whether the radio stations chosen included music (and of which genre), narrative or both. Many keepers use music and radios as a cheap way to provide auditory stimulation (Patterson-Kane and Farnworth, 2006), a form of enrichment which also benefits the keepers themselves (Sherwin, 2002; Van Loo et al, 2004) as the radio can be played whilst cleaning enclosures. As outlined by de Avezedo et al (2007), further investigation must be carried out into what aspect of the music or sound played is improving welfare, as sounds are complex (Newberry, 1995) and it is not fully understood what information is conveyed.

We found that the use of conspecific and ‘naturalistic’ sounds to simulate the acoustic conditions of wild habitats, were used by around half of zoos and that the majority of the responses by primates to auditory stimulation promoted positive behaviours (encouraging the performance of natural or ‘goal’ behaviours). The playback of ‘conspecific specific sounds’ such as alarm calls, were suggested to result in the performance of negative behaviours; classed as abnormal or undesirable behaviours. It may be expected that natural sounds would be more enriching to animals than unnatural sounds, but it has been argued that ‘natural’ sounds may hold

no meaning to animals housed in captivity and that listeners may not be able to interpret these sounds (Newberry, 1995). As sounds are complex signals, it is difficult for investigators to distinguish what component of the sound the animal is responding to (de Azevedo et al, 2007); therefore, playing sounds such as those produced by conspecifics and predator calls, may lead to stress, as animals' may not know how to respond appropriately (Guildford and Dawkins, 1991; Wells, 2009).

#### **5.4.2. Howler monkey enrichment practices**

Of the zoos previously visited, keepers reported that all of the howler monkey groups in their care performed howl vocalisations, with the majority howling once per day. When compared to behavioural observations, we found that although our findings were generally in agreement with keepers, many overestimated the frequency of howling bouts performed by males, which may be attributed to keepers not genuinely knowing how often howler groups call as they do not work near to the howler enclosures during their daily routine. Other possible explanations are that respondents are not able to remember the relevant information or are withholding the truth (Nisbett and Wilson, 1977), which may be stimulated by 'social desirability bias', where questionnaire respondents exaggerate or lie in their answers to please the researcher (Arnold and Feldman, 1981; Crowne and Marlowe, 1964; Taylor, 1961; Thomas and Kilman, 1975). As this questionnaire was distributed after the first author's visit to the zoos, keepers may be reporting howl frequencies in order to show their howler group in a good light, as howling is part of the natural behavioural repertoire of howler monkeys and was the focus of the research visit.

Keepers specified a range of environmental factors which evoked howling, including vehicle and machinery noise, conspecific howling and extremes of weather.

In the wild, *Alouatta* species are known to howl in a range of contexts including conspecific confrontations (Baldwin and Baldwin, 1976; Calegario-Marques and Bicca-Marques, 1995; Carpenter, 1934; Chiarello, 1995; Chivers, 1969; Da Cunha and Jalles-Filho, 2007; Thorington et al, 1984) and extremes of weather (rain, wind and thunderstorms [Baldwin and Baldwin, 1976; Bernstein, 1964; Calegario-Marques and Bicca-Marques, 1995; Carpenter, 1934; Chivers, 1969; Horwich and Gebhard, 1983]). Rarely in the wild would howler monkeys experience vehicles or machinery noise, the main reported stimulants of howling bouts in the captive European population of *A. caraya*. This is interesting in terms of the function of howl vocalisations; as these stimuli would not be expected to elicit the mechanisms to achieve howl functions. Perhaps howlers are performing howls in response to man-made stimuli simply as a threat display to low frequency stimuli. Further, involving playback experiments and acoustic analysis of the man-made sounds evoking a howl response would help to determine the purpose of responding vocally to these sounds.

In terms of environmental enrichment practices for howler monkeys, all groups received enrichment; however, the schedule in which they receive enrichment was infrequent, with less than half of groups being provided with enrichment daily, and only one group receiving enrichment more than once per day. This may be due to the diurnal inactivity of howler monkeys. Even in the wild, during the day howlers spend approximately 24% of their time feeding; 10-24% travelling and 60% of the time resting (Silver et al, 1998; Altmann, 1959). Or simply, that the howlers in this study do not noticeably respond to enrichments, unless they are food-based. As was found for primate species overall, all howler groups were provided with food-based enrichments which they were classified as most responsive to and the next popular type of device provided involved manipulative enrichment. Sensory-based

enrichments were provided to less than half of howler monkey groups and groups were rated to be least responsive to this enrichment type.

As we have already suggested, the efficacy of sensory enrichment is difficult to fully measure (de Azevedo et al, 2007) and as keepers often do not have the time within their routine to observe the animals and many do not formally evaluate enrichment or know what the 'goal' or desired behaviours are, this may limit assessment (Hoy et al, 2010). The most popular types of sounds used as auditory enrichment were music and radio, with conspecific sounds being used for less than one quarter of howler groups, similar findings to that of primate auditory enrichment in general. Music and radio are often played for a prolonged period of time, whilst keepers are working, which may lead to habituation to this type of stimulus. Unlike enrichment devices containing food, for which efficacy can easily be measured by keepers through observing the volume of food which has been consumed at the end of the day, auditory enrichment may not promote long-term positive effects on behaviour as many responses may be immediate and short in duration. Keepers may not see an animal's response to auditory stimulation, or know what goal behaviours this enrichment type should evoke and therefore they do not rate this type of enrichment as being effective. Or a lack of responses may simply be due to the types of sounds currently being used which are not evoking a behavioural response by howlers. If this is the case, the sound types used as stimulation may be a more important factor in the provision of this enrichment type, which again depends on the goal of provision, and implores further research into the use of auditory enrichment.

### 5.4.3. Playback experiments at visited zoos

We found that keepers were unenthusiastic about the use of auditory stimulation, with only half of responders rating playbacks as effective at evoking a vocal response in howler groups, the remaining answers were neutral. Findings from study observations showed that playbacks evoked vocal and behavioural responses by all male *A. caraya*, and that conspecific call playbacks encouraged howling in previously non-vocal groups (Farmer et al, 2011, in prep), thus it was concluded that playbacks were an effective form of enrichment. However, the goal of the study was to evoke acute immediate behavioural responses to playbacks, assessed within a short period of time after playbacks were conducted. Without introducing keepers to the goals of auditory enrichment or training them to observe for behavioural changes, it may have been difficult for keepers to assess playback efficacy, especially as responses may not have been obvious later in the day or they may not be present to observe immediate responses. Also, since we asked keepers to recall the effects of our playback experiment conducted approximately a year previously, their responses may have been affected by memory decline over time. Respondents may no longer recall the event in question, or simply do not think about their responses and just follow a set pattern, answering either neutral or negatively, a theme labelled as following ‘response sets’ (Cronbach, 1946).

Respondents deemed playbacks to have a neutral effect, or no effect on improving the welfare of *A. caraya*. However, despite relatively negative opinions on the effectiveness of auditory enrichment, half of the keepers said that they would use playbacks in the future. This finding may reflect demand characteristics (Orne, 1962), where those completing questionnaires respond with the answers that they think the researcher would want to hear, i.e. the researcher spent time conducting playback

experiments and therefore agreeing to implement this type of enrichment in the future may please the researcher. Although keeper opinions on the future of auditory enrichment for their collection may seem positive, the disconnect between actual efficacy and perceived efficacy is something that should be examined in the future, particularly as keepers are the key initiators of enrichment.

From our findings, we can provide detailed recommendations for the provision of auditory enrichment for captive *A. caraya*. As the provision of enrichment should be goal-orientated, we recommend that the calls of conspecific *A. caraya* groups be used as stimuli to encourage species-typical behaviour responses, one of the main goals of enrichment (Carlstead and Shepherdson, 1994; Shepherdson, 1994). As wild *A. caraya* are known to call at dawn (da Cunha and Byrne, 2006) and we have observed that they also call throughout the day (Farmer, unpublished results), we suggest that stimuli are played on a randomised schedule, including days when no sounds are played. Providing enrichment on a randomised schedule helps to maintain novelty and reduce habituation. In terms of the stimuli, the duration howl calls performed by *A. caraya* very significantly (Farmer et al, 2011, in prep); therefore, we recommend that the duration of howls played be of various lengths. In addition, we suggest that the same stimuli or section of a call is not played in succession, perhaps maintaining a four week gap between exposure to further maintain novelty.

## 5.5. Conclusions

Our findings show that for captive primates sensory enrichment is the least utilised form of enrichment and is suggested to be the least successful and important enrichment type (also see de Azevedo et al., 2007; Hoy et al., 2010). Although evidence on the efficacy of auditory enrichment is limited, we know that depending

on the goals of enrichment it can be a valuable addition to captive husbandry practices. Our study is the first to concentrate on enrichment practices solely for primate species and confirms that auditory enrichment is not regularly used. We also provide an insight into the efficacy of auditory enrichment in howler monkeys. For captive *A. caraya*, we promote the implementation of conspecific playbacks as a form of auditory enrichment as behavioural responses have been studied and we can confirm that this sound type does not promote adverse behavioural responses or stress. Through introducing playback experiments and demonstrating their ease of application, keepers may be more inclined to provide sensory stimulation in the future, but without reassessment and further studies into this area of enrichment, it may be difficult to determine its value, which is crucial to justify maintaining or increasing its use as a regularly provided form of environmental enrichment. It is possible that the perceptions of keepers in this study reflect reality, such that auditory enrichment produces the least behavioural change when compared to other forms of enrichment, or it may be that the timescale of these changes is much shorter, and therefore more easily missed. Future studies are required to investigate these possibilities.

## CHAPTER 6: Discussion

### 6.1. Functions of howls in *A. caraya*

The results of this thesis provide both observational and experimental evidence for multiple functions of the howl calls performed by male *A. caraya*. Previous research has suggested that in this species, the main role of howling functions to maintain intergroup spacing through regularly advertising the location of a caller (Da Cunha and Byrne, 2006). But this study is limited in sample size and there is a lack of intensive observations of howl-associated behaviours. From the evidence that I have collected, I provide additional support for this hypothesis and present additional roles for howling vocalisations.

In chapter 3 I provide evidence for a potential function of intergroup spacing in *A. caraya*, by means of regular advertisement of occupancy. By moving around their enclosure more during howling, males may further advertise their location (Da Cunha and Byrne, 2006) to neighbouring conspecific groups. However, we have to assume that in captivity, animals perceive their enclosure as their territory, as suggested by Lyons, Young and Deag (1997). In the captive environment, enclosures limit the home ranges or territories of groups, although they never experience group invasions, the threat of intertroop males may be exaggerated. As territorial behaviours were only performed during spontaneously occurring howls and during howls responding to the calls of known conspecifics, I suggest that this provides further evidence of intergroup spacing. Territorial behaviours are suggested to help maintain group distances in wild *Alouatta* groups (Southwick 1962; Bernstein 1964; Chivers 1969; Baldwin and Baldwin 1976; Drubbe and Gautier 1993), thus performing territorial behaviours during howl bouts may help groups to further defend

their location. The behaviours performed by female *A. caraya* also support the role of constant advertisement. Females performed more SDBs during howling, suggesting that they are anxious during howl bouts. Females also performed more territorial behaviours after howl bouts, which may deter intergroup females from entering the group (Sekulic, 1982a), and further supports the hypothesis of advertising the group's occupancy.

The role of howling in mate defence was also supported from findings in chapter 3. Males behaviourally and vocally responded more to the playback of unfamiliar conspecific males and females also contributed to howling bouts during playback experiments of unfamiliar conspecific males. Females have been suggested to support group males during howling bouts, by deterring intertroop females from gaining access into their group or mate (Sekulic, 1982a) and are known to participate in calling bouts if numeric odds are even, but less if odds are against her group (*A. pigra*, Kitchen, 2006).

The findings presented in chapters 2 and 3 suggest that the howls performed by adult males may convey information about the caller to neighbouring troops, a form of index signal (Vehrencamp, 2000). The acoustic individuality of howl calls may be attributable to differences in hyoid bone morphology, which may restrict the vocal production of howls and thus, be an honest advertisement of a caller's attributes, such as body size. Previous research has suggested that hyoid bone differences may be related to differences in individual call quality (Which and Nunn, 2002), but no clear suggestions of a link between call acoustics and male fitness or quality in *Alouatta* species have previously been proposed. In a previous study on captive *A. caraya*, Jones (1983) suggested that male rank is a function of body size and as I found that dominant group males initiated howling bouts, my study provides

supporting evidence that calling may transmit information on body size, which has previously been reported in a range of species including birds (Darwin's finches, *Geospizinae* spp. Podos, 2001), amphibians (toads, *Bufo bufo*, Davies and Halliday, 1978; Fitch and Reby, 2001; frogs, *Uperoleia rugosa*, Robertson, 1986) and mammals (red deer, *Cervus elaphus*, Reby and McCombe, 2003; domestic dog, *Canis familiaris*, Riede and Fitch, 1999).

Behavioural evidence in chapter 3 also suggests that howls may function to aid in mate defence. Research on *A. seniculus* suggests that howling functions in both deterring intergroup males from attempted invasion and that those opponents can be assessed through their howl calls (Sekulic, 1982b). This may be particularly important in terms of access to mates, with females being a limited resource for male howler monkeys (Sekulic, 1982b). During playbacks, females responded more to the stimuli of unfamiliar conspecific males than the howl of an allopatric *Alouatta* species, non-sympatric primate call and a chainsaw sound. Responses may be due to females being attracted to the caller as females are known to be more attracted to males which initiate howling bouts (Van Belle and Estrada, 2008; Kowalewski and Garber, 2010).

The findings presented in chapters 3 and 4 support the role of howling in male assessment and attraction by female *A. caraya*. In chapter 3, I showed that more social behaviours (social resting, grooming and playing) were performed after spontaneously performed howls, and this provides supporting evidence for a role in mate attraction. Spontaneously performed howls may allow for males to advertise their fitness to both neighbouring groups and intra-troop individuals as female howlers are known to be more attracted to the dominant male in their group which starts howling bouts (Van Belle and Estrada 2008; Kowalewski and Garber 2010). More social behaviours were also performed by groups with regularly auditory access

to conspecifics, when responding to the playback of conspecific calls. This finding supports the role of howling in social bonding, as high levels of male-male competition is in *Alouatta* species and males may not only try to deter extra-group males from the resident group, but also to maintain social bonds with group females as they are known to be promiscuous (Crockett and Eisenberg, 1987; Jones, 1985; Jones and Van Canfort, 2007).

Finally, after investigating reproductive trends in the European captive population, I found a link between howling rate and reproductive success. Males with higher howling rates sired a higher mean number of surviving offspring. Evidence not only that there may be a relationship between howling and reproduction, but further evidence that howling may be an indicator of male quality or overall body size, which links back to the influence of hyoid bone morphology and individuality of calls.

## **6.2. Influence of captivity on behaviour**

In terms of captive influences on *A. caraya* behaviour, my results have highlighted that the social grouping of howler monkeys may influence both vocalisations and reproduction. In chapter 2, I showed that the acoustics of howls performed by males housed in pairs and family groups differ, with paired males performing lower frequency calls. This finding may be linked back to the functions of mate defence and attraction and perhaps paired males produce lower frequency calls to indicate higher quality and fitness compared to other males.

One of the major limitations of captivity is that the movements of individuals between groups is controlled externally and thus, even if pair-housed males sound more attractive or are perceived as physically threatening, they are not able to attract additional females or contest with intergroup males. Conversely, I found that family

housed females have a higher reproductive success than paired females. Paired howler monkeys are not a commonly reported social grouping in the wild, therefore the restriction in captivity from being able to emigrate from the natal group, a commonly observed behaviour in wild *A. caraya* (Calegaro-Marquez and Bicca-Marquez, 1996), and choose a reproductive partner may influence captive breeding.

The results of my thesis also suggest an influence of auditory exposure to the howl calls of conspecifics on behaviour. In chapter 3, my results provide an insight into the influence of auditory access on howling-associated behaviours. Males housed in groups with auditory access to conspecifics physically responded more than those with no auditory access to the playbacks of conspecific calls and performed more social behaviours after spontaneously performed howls compared to baseline behaviours. These findings again support the roles of howling in mate defence and attraction and are further confirmed by higher offspring production and reproductive success in females housed in groups which had auditory access to the calls of conspecifics. Resident males may be stimulated to howl more often by conspecific groups within the same zoo. In chapter 3 I found that males with auditory access responded more to the playback of conspecific calls, therefore they have heightened responses to conspecific male presence. In the wild, female howler monkeys are more attracted to males which initiate howling bouts (*A. pigra* [Van Belle and Estrada, 2008]; *A. caraya* [Kowalewski and Garber, 2010]), which is reflected in my findings of captive groups, as it is the dominant adult male of the group who performs howl vocalisations and this male is the only recorded sire of group offspring.

This thesis also aimed to assess the welfare of captive *A. caraya* groups. In terms of optimal social grouping, my findings indicate that housing this howler species in family groups is linked to higher reproductive success, resembling the

intragroup competition and social contact experienced in wild groups. Hearing the howl calls of conspecifics, whether naturally or simulated through playbacks, elicited elevated behavioural and vocal responses similar to those found in the wild where howlers regularly experience the howls of neighbouring groups. My study investigating experimental playbacks, chapter 3, provides evidence that playbacks are successful in stimulating howling and that howlers perceive conspecific calls as an interesting event. These findings are however, not reflected in the opinions of keeping staff at the zoos I visited to conduct playbacks and my findings in chapter 5 confirm that auditory enrichment is the least used and valued type of enrichment, as also found by de Azevedo et al. (2007) and Hoy et al. (2010). I believe that the unenthusiastic views of keepers on the playbacks I conducted are due to keepers and indeed general researchers not fully understanding how to measure and quantify the efficacy of auditory enrichment. Also, inadequate understanding of what information is conveyed through playbacks (de Azevedo et al, 2007; Wells, 2009) may inhibit its use. This is a major limitation in encouraging the use of auditory enrichment for such a highly vocal primate species.

From the findings of this thesis, I can provide detailed recommendations for the provision of playbacks for captive *A. caraya*, which include all three concepts of enrichment; complexity, choice and control (Buchanan-Smith, 2010). I have conducted a range of animal welfare assessment methods to investigate the welfare of captive *A. caraya*. The behavioural responses of wild *A. caraya* to playbacks, and howl-associated behaviours have not previously been described in as much detail as in this thesis. One of the main concerns of captive welfare is the performance of abnormal or self-directed behaviours in primate species. In chapter 3, I found that although SDBs were performed during howl bouts, with higher rates in females than

males, the playbacks of *A. caraya* calls did not elicit similar rates of SDBs. These findings suggest that playbacks do not encourage the performance of anxiety behaviours, related to reduced welfare and so recommend the inclusion of conspecific calls as a regular form of sensory enrichment.

As the provision of environmental enrichment should be goal-orientated, results have highlighted that the playback of conspecific male calls evoke the most appropriate (behavioural and vocal) responses in *A. caraya*. Therefore, I recommend that the howls of unfamiliar conspecific males be used as acoustic stimuli, providing a naturalistic stimulus and to promote species-typical behaviours. In the wild, *A. caraya* call during the dawn chorus (da Cunha and Byrne, 2006) and I observed that they also call during the day, both spontaneously and in response to a range of stimuli. In captivity, housing and husbandry limitations, such as being locked inside an enclosure at dawn may influence an animal's perception of the onset of dawn, thus affecting the timing of their howl call production. In response, I suggest that playbacks are conducted at random times throughout the day, as in the wild, groups would encounter neighbouring groups whilst moving around their habitat. Playing calls on a randomised schedule, including rest days when no sounds are played, will also help to simulate a more naturalistic environment. Including non-playback days may also help to maintain the novelty of playbacks and reduce habituation. As outlined in the introduction, little is known about the duration of wild *A. caraya* howl bouts. I found that durations varied between 101.32 and 976.79 ms (mean duration =  $470.36 \pm SE$  39.79 ms), therefore I recommend that the duration of howls played be of differing lengths.

Providing goal-based enrichments which encourage the performance of wild-type behaviours can provide a contingent link between behaviour and response

(Buchanan-Smith, 2010). In *A. pigra*, playback experiments conducted by Kitchen (2004), found that when listening to the calls of conspecifics, males assess the numeric odds of the neighbouring group and are less likely to respond if the odds are unfavourable. I suggest providing collections with a range of calls performed by both solo males and groups of *A. caraya* for use during playbacks. Keepers could manipulate the numeric odds of the simulated neighbouring group. By playing calls performed by males housed in a known social group composition, keepers could stop playbacks when numeric odds are favourable to the focal group and if they vocally respond, providing them with perceived control over their environment. By ending the playback as soon as the focal animal begins to vocally respond allows the animal to perceive that it has ‘won’ the contest with the neighbouring male and has successfully defended his territory or group. By withdrawing the speaker when the focal male responds, keepers can simulate that the caller has retreated, and that the focal male has maintained spacing between his group and the invading neighbouring group. These methods may help to promote animals’ well-being, by providing natural auditory stimuli, thus improving their welfare.

### **6.3. Limitations**

Whilst my findings are novel and of potential importance for informing husbandry policy in future, there are some limitations to my studies that should be taken into account when considering the impact and general applicability of my conclusions. In chapter 2 I suggest that individual differences in howl acoustics may be related to hyoid bone morphology. Although I gained body weights for four of the 12 males studied, such measurements are taken opportunistically by veterinary staff at each zoo and due to the times they were taken were deemed inaccurate even for

preliminary investigation. It would be helpful to get body weights for all of the males in my study in order to determine whether howl acoustics are indeed systematically related to body size, and therefore hyoid bone morphology.

An often cited limitation of multi-institutional data collection is that institution effects may lead to differences between groups. These effects may include differences in husbandry techniques, housing and social group composition. However, by observing a wide range of groups from the majority of zoos holding *A. caraya*, I controlled statistically for this factor in my data analysis and found that institution effects were not so large as to mask the effects of other variables.

In the studbook analysis in chapter 4, the sire of each group is presumed to be the adult male member of the group, however, as breeding is rarely observed in both wild and captive howler monkeys (Crockett, 1998; Gomes and Bicca-Marques, 2003), and as females are suggested to be promiscuous (Jones, 1985; Jones and Van Canfort, 2007), this may not be the case. However, many studbooks involving species of a similar social composition work to the same guidelines so my interpretation of results is consistent with other studbook practices. Future genetic analysis of group members may help to determine whether current studbook data are accurate and evaluate extra pair copulations in captive howler monkeys which may also influence the age at which individuals are transferred between groups.

As this thesis focuses on the howling behaviour of *A. caraya*, and this species is known to perform howl vocalisations at dawn (Da Cunha and Byrne, 2006), there is a chance that I missed the calls which were performed before 7.45am. However, this seems unlikely since at many of the zoos, keepers who lived on site confirmed that the groups did not call until I arrived as they were locked inside their indoor enclosure until 8am, despite this, it may be the case that any performances before my arrival

may influence the howl rate data which is included in chapters 4 and 5. In addition, it may be the husbandry regime itself which is responsible for unnatural howling behaviour. Individuals may not be able to determine the onset of dawn, and those which were housed in a zoo with more than one group of howler monkey were not exposed to the calls of conspecifics early in the morning, as experienced in the wild.

#### **6.4. Application of findings and future work**

My results provide detailed evidence for a range of functions of the howl calls of *A. caraya* from intergroup spacing to mate defence and selection. Based on these findings I suggest that the performance of howling is an important aspect of howler behaviour and that efforts to encourage the performance of howl bouts should be made, not only to maintain or improve the welfare of captive individuals but also potentially encourage breeding in the current population. This can be accomplished through the application of auditory enrichment, in particular the playback of conspecific male calls.

As discussed earlier, providing a contingency between behaviour and response can greatly improve an animal's welfare. By playing the calls of conspecific *A. caraya* using a method that reacts to the vocal responses of the focal male, may not only improve the welfare of the animal, but may also influence reproductive success in captive pairs of *A. caraya*. If enrichment providers allow the focal male to perceive that he has won a vocal contest by stopping the playback as soon as he starts to howl in response, it can be speculated that this may be appropriate in encouraging pairs to breed, as females are known to be more attracted to dominant group males which start howling bouts (Van Belle and Estrada, 2008; Kowalewski and Garber, 2010). Primate species which are exposed to the calls of conspecifics housed in the same institution,

termed the 'neighbor effect', perform significantly more vocalisations (Baker and Aureli, 1996; Videan et al, 2005; Watson and Caldwell, 2010). By evoking a vocal response through conspecific playbacks, males may advertise to group females that they are more able to defend a group or mate (Sekulic, 1982b; Kitchen et al, 2004) and thus may promote the performance of social behaviours and ultimately breeding.

However, my studies have indicated that encouraging the animal care staff which maintain howler husbandry to incorporate auditory enrichment into enrichment programmes or daily routines may be a difficult hurdle to overcome. After conducting research at each institution I provided the *A. caraya* keepers with a CD of the conspecific howl calls that I had used during playback experiments. These sounds could then be easily used in the morning, played through on a CD player, whilst the groups were locked outside while keepers cleaned their indoor enclosure.

As previously mentioned, one of the limitations of captive management is the controlled movement of individuals between groups, which when compared to natural natal emigration in *Alouatta* species, may be a limiting factor in captive breeding and welfare. Research into the social organisation of spider monkeys (*Ateles* spp.) recommends that individuals be transferred according to wild movements; female dispersal and male philopatry to reduce incidents of aggression (Davis et al., 2006). In *A. caraya*, we know that natal emigration occurs in both genders and thus, I suggest that captive howlers should also be managed in an active manner.

One area of interest for future work is to investigate the relationship between hyoid bone size and body size in male howlers. Extensive research has been carried out on a range of species into the advertising of caller body size through acoustics cues, however little work has been carried out on vocal production and body size in primates (rhesus macaque, *Macaca mulatta*, Fitch, 1997; black and white colobus

monkey, *Colobus guereza*, Harris et al, 2006). It would therefore be interesting to examine this relationship in *A. caraya*, by attempting to confirm whether it is an honest signal of male size. To further investigate the role of howling in mate attraction and selection, experimental playbacks of the calls of different sized males and observations of both male and female responses could be conducted. Differences in male behavioural responses to playbacks may help to establish whether opponent assessed is achieved through vocal cues. From female responses, researchers will be able to assess the role of howling in mate choice and thus help to determine whether females show a preference for specific males based on morphological variation and vocal behaviour.

My results provide an insight into the acoustic characteristics of male *A. caraya* howl vocalisations and from my findings I can assert that there is context-specificity and individuality in calls, however, with a larger sample size of howls, future research exploring individual differences and context specificity in more detail will give us a better idea of the nature of howler communication and thus underpin relationships with environmental and social factors.

In conclusion, this thesis has shown that the howls of *A. caraya* play a role in a range of functions including territoriality, mate defence and attraction. I discovered a relationship between howling and reproductive success and although my results emphasise the efficacy of auditory enrichment, current keeper practise does not value or thoroughly understand the application of this enrichment type. I recommend that *A. caraya* in captivity are housed in groups containing more than one adult male and one adult female. I also advocate the use of conspecific call playback, with concomitant welfare assessment to ensure it is having the desired positive effect, as a valuable addition to howler monkey husbandry. Both of these factors provide a more

naturalistic environment for captive individuals. This thesis contributes to our knowledge of howler monkey behaviour and our understanding of the effects of captivity on a vocal primate species, which will be valuable for the captive breeding and welfare of the species and has application for species with critical conservation status.

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**APPENDIX I: Behaviours recorded**

<b>Behavioural category</b>	<b>Behaviours included</b>	<b>Description</b>
Locomotion		Movement from one area to another quadrupedally, includes climbing.
Rest alone		Motionless either sitting or lying, not in contact with another individual. Eyes may be open or closed.
Groom-self		Self-inspection of coat using fingers and/or mouth.
Social	Social rest	Motionless either sitting or lying, in contact with another individual. Eyes may be open or closed.
	Play	Physical engagement with another individual, includes chasing, touching, mouthing and pulling.
	Allogroom	Physical contact with another individual, inspecting their coat with fingers and/or mouth.
Self-directed	Yawn	The mouth is opened widely, the head tips back, lips are pulled back so that the teeth are exposed.
	Sneeze	Rapid expulsion of air from the nose.

*Appendix I: Behaviours recorded*

	Scratch	Rhythmic movement of fingers through the coat. Performed whilst sitting or when standing on all four limbs.
	Body shake	While a sitting position the individual moves its whole body side to side in a somewhat circular motion or quickly up and down.
	Tongue flick	Tongue is stuck out of the mouth, sometimes proceeded with a yawn.
Territorial	Defecation	Expellation of faeces and urine.
	Scent mark	Rubbing throat or anogenital area on enclosure substrate.
Feed/forage		Feeding from available food source, either within enclosure or provisioned by keepers

## During natural howls

Main effect or interaction	Behaviour	Pairing	Cohen's <i>d</i>	95 % Confidence Interval
Stimulus	Locomotion	Spontaneous > familiar conspecific	0.62	-12.19 to 12.32
		Other primate > familiar conspecific	0.24	-24.01 to 23.53
		Other primate > vehicle	0.28	-20.99 to 21.56
SDB rates	Locomotion	Familiar conspecific > other primate	0.25	-3.49 to 3.99
		Familiar conspecific > machinery	0.24	-3.89 to 4.17
		Vehicle > other primate	0.27	-1.41 to 6.85
		Vehicle > machinery	0.35	-0.39 to 0.31
		Machinery > other primate	0.26	-0.92 to 1.44
Stimulus x sex	Locomotion	Familiar conspecific, female > male	0.33	-5.48 to 4.83
		Other primate, female < male	0.23	-46.73 to 47.19
		Machinery, female > male	0.37	-3.08 to 2.34

**Post-howl and matched control (baseline)**

<b>Main effect or interaction</b>	<b>Behaviour</b>	<b>Pairing</b>	<b>Cohen's <i>d</i></b>	<b>95 % Confidence Interval</b>
Stimulus x social group	Locomotion	Spontaneous, family > pair	1.44	-22.30 to 25.18
		Familiar conspecific, family > pair	0.45	-40.38 to 39.48
		Other primate, family < pair	1.18	-41.61 to 43.97
		Vehicle, family < pair	0.34	-39.30 to 48.19
		Machinery, family < pair	0.94	-26.11 to 24.24
	Social	Spontaneous, family > pair	1.84	-44.19 to 140.52
		Familiar conspecific, family < pair	0.25	-239.23 to 239.74
		Other primate, family > pair	1.51	-258.07 to 255.05
		Vehicle, family < pair	0.30	-237.39 to 237.99
		Machinery, family < pair	0.55	-144.43 to 145.53

**During playbacks**

<b>Main effect or interaction</b>	<b>Behaviour</b>	<b>Pairing</b>	<b>Cohen's <i>d</i></b>	<b>95 % Confidence Interval</b>
Sound type	Solitary resting	Conspecific < <i>A. palliata</i>	0.25	-6.32 to 45.83
		Conspecific < lemur	0.21	-7.77 to 7.34
		Conspecific < chainsaw	0.28	-9.45 to 8.89
	SDB rates	Conspecific < <i>A. palliata</i>	0.21	-0.46 to 0.05
		Conspecific < lemur	0.20	-6.63 to 6.23
Sound type x auditory access	Social	<i>A. palliata</i> , auditory access < no auditory access	0.32	-8.71 to 9.34
		Lemur, auditory access < no auditory access	0.26	-10.71 to 11.24

**Post-playback and matched control (baseline)**

<b>Main effect or interaction</b>	<b>Behaviour</b>	<b>Pair</b>	<b>Cohen's <i>d</i></b>	<b>95 % Confidence Interval</b>
Auditory access	Locomotion	Conspecific, auditory access > no auditory access	0.42	-10.82 to 11.65
		Lemur, auditory access > no auditory access	0.35	-10.89 to 11.57
		Chainsaw, auditory access < no auditory access	0.44	-11.67 to 10.79

## APPENDIX III: Questionnaire

### A survey of the use of auditory stimulation as a form of environmental enrichment

(All of the data provided will be treated as STRICTLY CONFIDENTIAL)

**Background:** The use of, and responses of animals to, auditory enrichment in the zoo environment is rarely documented, however it is a recognised form of enrichment used in many zoos internationally. This survey aims to investigate:

1. The extent of use of auditory enrichment relative to other enrichment types across a range of species
2. What types of sounds are used for auditory enrichment
3. Typical responses of a range of species to auditory enrichment
4. Detailed responses of howler monkeys to auditory enrichment (section not included if you do not hold howler monkeys).

Outcomes of this study will aid our understanding of the effects of using auditory stimulation as a form of enrichment and provide valuable information for husbandry and welfare issues.

**Please return to:** Holly Farmer, Field Conservation and Research Department,  
Paignton Zoo Environmental Park, Totnes Road, Paignton, Devon, TQ4 7EU, UK  
**Email:** holly.farmer@paigntonzoo.org.uk

**Please return by: 30<sup>th</sup> November 2010 (if possible).**

***Thank you!***

I would like to thank you for participating in this study, which has been designed to require minimum effort to save staff members valuable time.

**Definitions for the purposes of this survey;**

- **Environmental enrichment:** any steps taken to provide more than the basic housing and husbandry requirements, with the aim of keeping animals occupied, preventing abnormal behaviours and encouraging the performance of wild-type behaviours.
- **Food-based enrichment:** devices or techniques which can be used by an animal to obtain food e.g. forage pole or puzzle box; excluding scatter feeding or presenting food in a bowl.
- **Manipulative enrichment:** devices or objects which are manipulated by an animal but do not result in a food reward e.g. rubber Kongs or cardboard boxes.
- **Sensory- visual:** objects or techniques which provide visual stimulation (e.g. sun-catchers, light shows)
- **Sensory-olfactory:** objects or techniques which provide smells or scents for stimulation (e.g. blood, herbs).
- **Sensory-auditory:** providing sounds for stimulation (e.g. conspecific calls or music)
- **Conspecific:** an animal of the same species.

**Section 1: General Enrichment Regime**

**Do you provide environmental enrichment for your animals?**

(Please circle appropriate answer) **Yes**

**No** (please go to section 3)

**1.a. Enrichment frequency**

Please tick all boxes that apply to describe how often you typically provide enrichment to your collection. Please cross out taxa which you do not hold.

Provision schedule	Primates	Ungulates	Marsupials & monotremes	Pinnipeds	Elephants	Bats	Rodents	Carnivores	Birds	Reptiles	Fish	Amphibians
Daily												
Weekly												
Monthly												
Occasionally												
Never												

**1.b. Enrichment types used**

Please tick all boxes that apply to describe which enrichment types you provide for your collection. Again, please cross out taxa which you do not hold.

Type of auditory stimulation	Primates	Ungulates	Marsupials & monotremes	Pinnipeds	Elephants	Bats	Rodents	Carnivores	Birds	Reptiles	Fish	Amphibians
Food based												
Manipulative												
Sensory-visual												
Sensory-olfactory												
Sensory-auditory												
Other/novel												

Please give details of 'other/novel' enrichments if used

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**Section 2: Auditory enrichment**

**2.a. Auditory enrichment sounds used**

If you ticked yes to using auditory enrichment, please tick the following which apply. Please cross out taxa which you do not hold.

Type of auditory stimulation	Primates	Ungulates	Marsupials & monotremes	Pinnipeds	Elephants	Bats	Rodents	Carnivores	Birds	Reptiles	Fish	Amphibians
Conspecific general												
Conspecific specific e.g. alarm call												
Other novel species call												
Predator sound												
Prey sound												
Music												
Talk radio												
CD												
Other/novel												

If you have ticked CD, please provide the name of the CD

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Please give details of ‘other/novel’ enrichments if used

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**2.b. Responses to auditory enrichment**

Please fill out the following table to describe the behavioural responses of your animals to auditory enrichment. Please respond with your overall view after repeat presentations of the sounds.

**Positive (+ve) responses;** natural behaviours or behaviours you aim to encourage e.g. groom/affiliative behaviours towards group members, call back.

**Negative (-ve) responses;** behaviours that you may class as abnormal or those which would prevent you from using playbacks in the future e.g. self-harm, aggression, lunging towards speaker

Please tick all boxes that in your opinion describe your animal’s responses to auditory stimulation. Please cross out taxa which you do not hold.

Type of auditory stimulation		Primates	Ungulates	Marsupials/motremes	Pinnipeds	Elephants	Bats	Rodents	Carnivores	Birds	Reptiles	Fish	Amphibians
Conspecific general	+ve												
	-ve												
Conspecific specific e.g. alarm call	+ve												
	-ve												
Other novel species call	+ve												
	-ve												
Predator sound	+ve												
	-ve												
Prey sound	+ve												
	-ve												
Music	+ve												
	-ve												
Talk radio	+ve												
	-ve												
CD	+ve												
	-ve												
Other/novel	+ve												
	-ve												

**2.c. Have there been any instances when you would classify an animal’s response to be so negative that that specific sound was not used as enrichment again?**

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### Section 3: Howler monkey specific information

This survey is being conducted as part of a PhD study into the behaviour and vocalisations of captive black and gold howler monkeys (*Alouatta caraya*) and use of playbacks in stimulating call responses. The following section of the survey therefore is specifically on howler monkey enrichment.

According to ISIS you currently hold the following howler monkeys, if this is not correct, please correct the following table.

Number of adult males	Number of adult females	Number of juveniles

#### 3.a Group housing

If the animals you hold are housed in separate groups please give details in the table below;

Group number	Number of adult males	Number of adult females	Number of juveniles	Distance to nearest other howler monkey enclosure if more than one group at zoo (approximately, in metres)
1				
2				
3				

#### 3.b. Vocal activity

**Do your howler monkeys vocalise?**

(Please circle appropriate answer) **Yes**

**No** (please go to section 4)

**3.c If they do, how often do your howler monkey groups vocalise?** (Please tick the appropriate answers)

Group number	Never	Monthly	Weekly	Once per day	More than once per day
1					
2					
3					

**3.d. Which of the following environmental factors do you think influence howling?**

(Please circle any that apply)

Other howler monkeys calling / other primate species calling / husbandry regime / presence of keepers / motor vehicles passing enclosure / strimming, grass cutting or chain sawing / extremes of weather (heavy rain and strong wind)  
 Other, please specify

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**Section 4: Howler monkey environmental enrichment**

**4.a. Do you provide environmental enrichment for your howler monkeys?**

(Please circle appropriate answer) **Yes**

**No** (please go to section 5)

**4.b. Enrichment regime**

Please tick all boxes that apply to describe how often you provide enrichment for your howler monkeys.

Group number	Never	Monthly	Weekly	Once per day	More than once per day
1					
2					
3					

**4.c. Enrichment types used**

Please tick all boxes that apply to describe which enrichment types you provide for your howler monkeys (using the same enrichment type definitions on the front page). (Please tick the appropriate answers)

Type of enrichment	Group 1	Group 2	Group 3
Food			
Manipulative			
Olfactory			
Visual			
Auditory			
Novel			
Other			

Please give details of 'other' sounds if used

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**4.d. Enrichment responses**

If a type of enrichment is provided, how do the animals respond? (Please tick the appropriate answers)

Type of enrichment	Never respond ←————→ Always respond				
	1	2	3	4	5
Food					
Manipulative					
Olfactory					
Visual					
Auditory					
Novel					
Other					

Please give details of 'other' sounds if used

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**4.e. Auditory enrichment sounds used**

If you ticked yes to using auditory enrichment, please tick the following which apply.

Sound type	Group 1	Group 2	Group 3
Conspecific general			
Conspecific specific e.g. alarm call			
Other novel species call			
Predator sound			
Prey sound			
Natural environment e.g. rainforest sounds			
Talk radio			
Music			
CD			
Other			

Please give details of 'other' sounds if used

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**4.f. Responses to auditory enrichment**

Please fill out the following table to describe the behavioural responses of your animal's to auditory enrichment. Please respond with your overall view after repeat presentations of the sounds.

Sound type		Group 1	Group 2	Group 3
Conspecific general	+ve			
	-ve			
Conspecific specific e.g. alarm call	+ve			
	-ve			
Other novel species call	+ve			
	-ve			
Predator sound	+ve			
	-ve			
Prey sound	+ve			
	-ve			
Music	+ve			
	-ve			
Talk radio	+ve			
	-ve			
CD	+ve			
	-ve			

**4.g. Have there been any instances when you would classify a howler monkeys response to be so negative that that specific sound was not used as enrichment again?**

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### Section 5: Playback

During my research visit to your zoo in date year, I carried out 6 days of playback experiments to stimulate your howler monkeys to vocalise.

#### 5.a. Since my visit, how often do your howler monkey group(s) vocalise?

Group number corresponds to the group information that you provided in Section 3a.

(Please tick the appropriate answers)

Group number	Never	Monthly	Weekly	Once per day	More than once per day
1					
2					
3					

#### 5.b. Effectiveness of playbacks

How would you rate the effectiveness of the playbacks I conducted?

(Please tick the appropriate answers)

Measure of effectiveness	Group number	Not effective ←————→ Very effective				
		1	2	3	4	5
Encourage howling	1					
	2					
	3					
Encourage social behaviours	1					
	2					
	3					
Improve welfare	1					
	2					
	3					

#### 5.c. Future use of playbacks

How do you feel about continuing to use playbacks as enrichment for your howler monkeys

(Please tick the appropriate answers)

Group number	Would not use playbacks ←————→ Would use playbacks				
	1	2	3	4	5
1					
2					
3					

**Please return to:** Holly Farmer, Field Conservation and Research Department,  
Paignton Zoo Environmental Park, Totnes Road, Paignton, Devon, TQ4 7EU, UK  
**Email:** holly.farmer@paigntonzoo.org.uk

**Please return by: 30<sup>th</sup> November 2010 (if possible)**

## APPENDIX IV: BIAZA Letter of Support



### BIAZA Research Group (BRG)

#### Letter of Support for Zoo-based Research Projects

The BIAZA Research Group, which operates under the auspices of BIAZA's Conservation and Animal Management Committee, supports basic and applied research of conservation relevance both *in situ* and *ex situ*.

This study by **Holly Farmer from the University of Exeter and the Whitley Wildlife Conservation Trust, Paignton Zoo Environmental Park** has been given the following level of approval by the Research Group:

1. the methodology presented by this applicant will, in the opinion of BRG, be able to provide data that can answer the research question set by the applicant.
2. the outcomes of this project are likely to be relevant and useful to zoos and aquariums.

In the interest of scientific training and, where applicable, the furthering of science, the BIAZA research group encourages members to take part.

In providing this letter of support, the BIAZA office will have given **Holly Farmer** the appropriate contacts from within the BIAZA membership.

Yours faithfully,

A handwritten signature in black ink, appearing to read "Amy Plowman". The signature is fluid and cursive, with a large initial "A" and "P".

Amy Plowman  
Chair, BIAZA Research Group

## APPENDIX V: Studbook Letter of Support



Creating a sustainable future  
for wildlife and people

23<sup>rd</sup> August 2010

To whom it may concern

**Black and Gold Howler Monkey *Alouatta caraya***  
**Research Questionnaire from Holly Farmer**

As the European Studbook Keeper for *Alouatta caraya*, I am pleased to support this research questionnaire prepared by Holly Farmer, who is an Assistant Research Officer at the Whitley Wildlife Conservation Trust, Paignton, Devon, UK.

**John Partridge**  
**Senior Curator of Animals**  
**European Studbook Keeper for the Black and Gold Howler Monkey**  
**Bristol Zoo Gardens**  
**Bristol BS8 3HA**  
**United Kingdom**

## APPENDIX VI: TAG Letter of Support



14<sup>th</sup> September 2010,

### **Re: Investigations into the howling vocalizations of the black and gold howler monkey**

The effect of captivity on the vocalizations of our species has become an increasingly important area of research in recent years. Assessing the vocalization capabilities and the functions of vocalizations of our animals will allow us to understand the effects of such communication on pair bonding and psychological fitness, and thereby assess the welfare of our animals more thoroughly. To this end EAZA Cebid TAG would like to encourage all institutions holding howler monkeys to participate in the research questionnaire accompanying this letter.

The EAZA Cebid TAG recognizes the value of this research and supports the researcher (Holly Farmer). We would encourage all zoos to participate with this necessary research.

A handwritten signature in brown ink that reads "Kirsten Pullen".

Dr. Kirsten Pullen  
Co-chair EAZA Cebid TAG  
Zoo Research Officer

Totnes Road, Paignton, Devon TQ4 7EU, UK  
Telephone (Reception) 01803 697500 (Direct Line) 01803 697513  
Fax 01803 523457 Email [trustsecretary@wwct.org.uk](mailto:trustsecretary@wwct.org.uk)

## APPENDIX VII: Ethics Approval from University of Exeter



Psychology Research Ethics  
Committee

Psychology, College of Life  
& Environmental Sciences

Washington Singer Laboratories  
Perry Road  
Exeter  
EX4 4QG

Telephone +44 (0)1392 264626  
Fax +44 (0)1392 264623  
Email Marilyn.evans@exeter.ac.uk

**To: Holly Farmer**  
**From: Cris Burgess**  
**CC: Lisa Leaver**  
**Re: Application 2005/108 Ethics Committee**  
**Date: January 30<sup>th</sup>, 2006**

The School of Psychology Ethics Committee has now discussed your application, **2005/108 – The function of howling in the Black-and-Gold Howler Monkey (*Alouatta caraya*)**. The project has been approved in principle for the duration of your study.

The agreement of the Committee is subject to your compliance with the British Psychological Society Code of Conduct and the University of Exeter procedures for data protection (<http://www.ex.ac.uk/admin/academic/datapro/>). In any correspondence with the Ethics Committee about this application, please quote the reference number above.

I wish you every success with your research.

A handwritten signature in black ink, appearing to read "Cris Burgess", with a horizontal line underneath.

Cris Burgess

## **APPENDIX VIII: Transcript of professional activities**

### **Awards**

2011 Best Research Project Commendation for PhD project.

### **Peer-reviewed research articles**

Farmer, H.L., Plowman, A. B. & Leaver, L. A. 2011. Role of vocalisations and social housing in breeding in captive howler monkeys (*Alouatta caraya*). Applied Animal Behaviour Science, doi:10.1016/j.applanim.2011.07.005

### **Published work**

Farmer, H. 2010. Research report from the Aquarium Working Group (AWG) and National Aquarium Workshop (NAW). Zoo Research News BIAZA Research Group Newsletter 11.1.

Farmer, H. & Melfi, V.A. 2010. Songs of Experience. Zooquaria 71: 21.

Worsfold, H. & Farmer, H. 2010. The provision of environmental enrichment for African penguins to increase water-based behaviours without changes to the current feeding regime. Zoo Research News BIAZA Research Group Newsletter 11.2.

Taylor, S. & Farmer, H. 2010. Environmental enrichment and its effects on South American fur seal (*Arctocephalus australis*) behaviour. Zoo Research News BIAZA Research Group Newsletter 11.3, supplement.

Bailey, T., Pullen, P.K., Farmer, H. & Bowkett, A.E. 2009. Does inbreeding affect reproductive behaviour in a captive colony of Inca terns *Larosterna inca*? Zoo Research News BIAZA.

Farmer, H. 2008. Animal Cameo- Black and gold howler monkey- *Alouatta caraya*. Feedback, The ASAB Education Newsletter 41.

Farmer, H., Dayrell, E. & Pullen, P.K. 2006. Encouraging enclosure use for red river hogs using scatter feeding. Shape of Enrichment 15: 11-13.

#### **Conference presentations**

Farmer, H., Plowman, A., Green, K. & Taylor, L. 2010. Should Zoo Food be Chopped? ABWAK Symposium, Port Lympne Wild Animal Park, UK.

Farmer, H. 2010. Research needs and needs of researchers: how can we join them up? National Aquarium Workshop (NAW), Bristol, UK.

Farmer, H. Leaver, H. & Plowman, A. B. 2010. Captive black howler monkeys (*Alouatta caraya*) respond behaviourally and vocally to conspecific calls in playback experiments. ASAB Spring Meeting, Exeter, UK.

Farmer, H. Leaver, L. & Plowman, A.B. 2009. The application of auditory playback to stimulate the performance of natural vocalisations in captive howler monkeys (*Alouatta caraya*). 22<sup>nd</sup> International Bioacoustics Congress, Lisbon, Portugal.

Farmer, H., Leaver, L. A. & Plowman, A. B. 2008. Comparisons Of Behavioural Patterns And Vocalisations In Pair Housed And Family Housed Captive Howler Monkeys (*Alouatta caraya*). International Primatological Society XXII Congress, Edinburgh, UK.

Farmer, H., Leaver, L. A. & Plowman, A. B. 2008. Comparisons Of Behavioural Patterns And Vocalisations In Pair Housed And Family Housed Captive Howler Monkeys (*Alouatta caraya*). IPS Pre-congress satellite workshop: Vocal Communication in Birds and Mammals, St. Andrews, UK.

Farmer, H. 2008. Is it music to their ears? 2<sup>nd</sup> British and Irish REEC, Bristol Zoo Gardens, UK.

Farmer, H. 2007. What's in a howl? Comparing the vocal behaviour of captive howler monkeys. EAZA Research Conference, Poznan, Poland.

Farmer, H. 2007. What's in a howl? Comparing the vocal behaviour of captive howler monkeys. University of Exeter Postgraduate Conference, UK.

Farmer, H. 2007. What's in a howl? Comparing the vocal behaviour of captive howler monkeys. ASAB Summer Meeting, UK.

Farmer, H. & Melfi, V. A. 2007. Is it music to their ears? International Conference on Environmental Enrichment, Vienna.

Farmer, H. 2005. Preliminary investigations into howling vocalisations and associated behavioural patterns in captive black and gold howler monkeys (*Alouatta caraya*). ASAB Winter Meeting, ZSL, UK.

Farmer, H. & Pullen, K.P. 2004. Preliminary observations on the function of howling vocalisations in the black howler monkey (*Alouatta caraya*). XX International Primatology Congress, Turin, Italy.

### **Conference proceedings**

Farmer, H. & Baker, K. 2010. A Keepers Guide to Evaluating Enrichment. Proceedings of the 3rd Regional Environmental Enrichment Conference, REEC, May 10-12<sup>th</sup>, Marwell Wildlife, UK.

Farmer, H., Madden, J., Leaver, L. & Plowman, A.B. 2009. You're talking my language: howler monkeys respond to conspecifics. 9<sup>th</sup> International Conference on Environmental Enrichment. Riviera Centre Torquay, UK.

Farmer, H., Melfi, V. & Leaver, L. A. 2008. Is it music to their ears? Proceedings of the 2nd Regional Environmental Enrichment Conference, REEC, Paignton Zoo Environmental Park, UK.

Doran, L., Farmer, H., Dobbs, T., Fry, A., Manning, L., Jegou, N., Chapman, J. & Melfi, V.A. 2006. A synergistic enrichment programme for Sulawesi macaques (*Macaca nigra*) at Paignton Zoo Environmental Park. Proceedings of the EAZA Conference, September 2005, Bristol Zoo Gardens. EAZA Executive Office, Amsterdam. pp 336-339.

- Farmer, H. 2006. Enrichment, a Natural Evolution. Proceedings of the 1<sup>st</sup> Regional Environmental Enrichment Conference. REEC, Paignton Zoo Environmental Park, UK.
- Harden, C. & Farmer, H. 2006. Interspecies interactions and enclosure use of the Avocets, (*Recurvirostra avosetta*) and the Stilts, (*Himantopus mexicanus*) in the Wader's Estuary at Living Coasts, Torquay. Proceedings of the 8<sup>th</sup> Annual Symposium on Zoo Research. BIAZA/Colchester Zoo, UK.
- Farmer, H. & Pullen, P.K. 2005. Preliminary investigations into howling vocalisations and associated behavioural patterns in captive black and gold howler monkeys (*Alouatta caraya*). In: Hiddinga, B. (ed.). Proceedings of the EAZA Conference 2004, Kolmarden. EAZA Executive Office, Amsterdam. ISBN 90-77879-01-3. pp 269-273.

### **Workshops**

- Farmer, H. 2010. How to evaluate enrichment Part 1. 3rd British and Irish REEC, Marwell Wildlife, UK.
- Farmer, H. & Baker, K. 2010. A Keepers Guide to Evaluating Enrichment. Proceedings of the 3rd Regional Environmental Enrichment Conference, REEC, Marwell Wildlife, UK.