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**An Investigation into Some Effects of Captivity
On the Behaviour of Gorillas and Chimpanzees
In Four British Zoos**

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Presented for the Degree of M.Phil.

By Sonya Petre Hill

Submitted to the University of Durham

Department of Anthropology

1999



26 APR 2002

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Abstract

An Investigation into Some Effects of Captivity on the Behaviour of Gorillas and Chimpanzees in Four British Zoos

Presented for the degree of M.Phil. by Sonya P. Hill, 1999

This study, conducted at four British zoos over a period of four months, investigated some of the effects of captivity on the typical daily behaviour of 14 adult chimpanzees (*Pan troglodytes*) and 9 adult western lowland gorillas (*Gorilla gorilla gorilla*), focussing primarily on the influence of zoo visitors. Instantaneous time sampling was used to collect data on focal animals regarding ape behaviour, the apes' spatial location within the enclosure, and visitor characteristics (noisiness and crowd size). Apes were grouped into one of 10 categories for analyses, based upon which zoo they were from, their sex and whether they were dominant or non-dominant (males).

Zoo animals are "on exhibit" for the whole of the zoo day, and are often unable to avoid the stares and noisiness of their human visitors should they want to. Zoo visitors, as a dynamic part of the captive environment, might be responsible for influencing the daily behaviour of the animals. This can have potential welfare implications and could also affect the zoo's success as a medium for conservation education.

Four models were proposed based on the notion that apes experience some visitor characteristics as aversive and others as enriching. It was hypothesised that large or noisy crowds of visitors would affect the behaviour and spatial location of zoo-housed apes differently from small or quiet groups of visitors. The hypotheses were supported by the data. Results indicate that apes show various responses to visitors, with certain types of behaviour being affected in some species, age and sex classes, and not in others. From the data it is not clear whether the overall effects were enriching or aversive to apes, although some tentative suggestions have been made (based on the direction of changes in behaviour) suggesting that large or noisy groups of zoo visitors are an aversive presence.

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Chapter 1 - Introduction

Statement of Purpose

This study investigates some of the effects that captivity can have on the behaviour of gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes*), focusing primarily on the influence of human zoo visitors. The results of this study will be extremely important to the zoo community: if there is a visitor effect on ape behaviour, then the extent to which this is so should be fully recognised by anyone involved in the keeping of zoo animals. Do zoo animals seem to perceive their human visitors as enrichment “devices”, who are there to entertain the animals and keep them interested in their captive environment? Or are visitors an aversive presence, who create too much noise and invade the animals’ privacy, resulting in harmful activities that do not represent the sorts of behaviour that one might expect to see in the wild? These are the kinds of issues that today’s zoos have to consider. The modern zoo must aim to reconcile the welfare needs of the animals with the accurate education of the visitors. In addition, if human visitors do affect ape behaviour then zoo biologists must ensure that this variable is taken into account when conducting research projects otherwise they could be confounding their results.

Our knowledge about the behavioural flexibility of wild populations of primates^{1.1} and other non-human animals can be supplemented by data from captivity. Wild chimpanzees, for example, exhibit “cultures” that differ from site to site, including different techniques for processing oil palm nuts (see McGrew, 1992, for a more detailed review). Just as the behaviour of wild chimpanzees can vary between communities, so too might captive chimpanzees exhibit novel behaviours that are not usually seen in the wild, because captivity presents them with different niches and opportunities to those in nature. These novel behaviours might be beneficial to the animals (for example, playing with toys such as rubber balls or “fishing” for food in a converted drainpipe) or harmful (such as self-

^{1.1}. The word “primate” is used throughout this study in reference to the non-human primates.



mutilation). Either way, zoo-based studies enable us to gain a better understanding of the behavioural adaptations that animals are capable of.

Primates - especially the great apes - are extremely popular with the zoo-visiting public, probably because of their obvious similarities to our own species. The behaviour of zoo-housed primates certainly seems to be affected by the presence of visitors – anyone who has ever been to a zoo will have their own anecdotes - but it is not well documented (Waters, S., personal communication). However, some researchers believe that zoo animals become habituated to the presence of human visitors, and it has even been argued that zoo visitors are “invariably ignored” by animals unless they cross the safety barriers or enter the zoo before or after normal zoo hours (Snyder, 1975, p. 48).

On the contrary, more recent literature in the field of zoo biology provides evidence to support the notion that visitors do influence primate behaviour, although these studies have tended to focus on the more explicit effects such as visitor-directed aggression and human-animal interactions. Research into some of the more subtle effects of visitors, such as how they might affect the typical daily behaviour of primates, has not been well documented until now. The data presented in this study go some way towards filling the gap in the literature on visitor effects.

Ideally, zoo animals should be ambassadors for their conspecifics in nature (Goodall, J., personal communication), but in reality they have no control over the ways in which they are presented by zoos. Moreover, the animals cannot regulate how many visitors stand at the enclosure nor how the visitors behave; the animals must simply adapt or not. Zoo visitors are a dynamic part of the animals' environment, because the composition of crowds can of course change by the minute. Studies such as this one will raise awareness among zoo officials regarding the specific effects – if any – that visitors have on the animals. Zoo management would want to know the welfare implications that these changes have for the animals themselves, and how this might affect the potential for conservation education of the visitors. When visitors leave the zoo at the end of

their visit, what impression of these animals do they take away with them? Is this impression likely to encourage visitors to contribute towards saving endangered species and threatened habitats, or will the visitors have little respect or concern for these animals?

It is unlikely that many visitors go to a zoo for the explicit purpose of being educated about the animals, rather a zoo visit is more likely to be for recreational purposes. However, it is inevitable that visitors will gain some sort of impression about animals as a result of their visit, regardless of whether or not they are conscious of being educated. If visitors have only ever seen chimpanzees behaving like spoilt human children (for example, throwing tantrums in an effort to get visitors to give them food) or like institutionalised people (performing stereotypic or self-mutilating activities), then that is all they will know about the species. Such an impression is hardly likely to encourage anyone to find out more about the species or to support *in situ* conservation projects. In contrast, if visitors see chimpanzees performing species-typical behaviour such as grooming, “fishing” in an artificial termite mound or engaging in social interaction, with little or no obvious regard for the visitors’ presence, they will probably gain a completely different perspective of the animals.

Several studies have shown that visitors prefer to see animals in naturalistic habitats, performing more species-typical behaviour (e.g. Price *et al.*, 1994; Stoinski *et al.*, 1997). These visitors are more likely to take an interest in supporting conservation projects in the wild. I discuss the importance of these issues in greater detail in Chapter 2.

The general aim of this study is to generate quantitative data detailing the enriching and aversive influence of zoo visitors on the typical daily behaviour of zoo-housed gorillas and chimpanzees. Ultimately the conclusions generated from this research can be used to assess the validity of further investigation into visitor

effects, and to offer zoos some recommendations regarding:

- i) the provision of appropriate habitat designs
- ii) the “use” of zoo visitors as “enrichment devices”
- iii) the promotion of a greater understanding among the visitors of how to behave in front of the enclosure.

Hypotheses and Predictions: An Overview

Throughout this study, the assumption is made that small or quiet visitor groups are more likely to elicit the sort of ape behaviour that one could expect if no visitors were present. The working hypotheses and predictions that follow are based on four models given below. These models are expected to operate more strongly for chimpanzees than for gorillas, because “...the chimpanzee [...] is famous for its mimicry, aggressiveness and human-like behaviour and the gorilla [...] for its gentleness and private nature...” (Markowitz, 1982, p. 137). I tentatively predict that if there is any association between the specified zoo visitor variables and ape behaviour, then chimpanzees will be affected to a greater extent than will gorillas (i.e. gorilla behaviour is less likely to change under the variables of crowd size and noisiness than chimpanzee behaviour is)^{1,2}.

If these zoo-housed apes do demonstrate behavioural responses to human zoo visitors, it is likely to be because visitors have an enriching or aversive influence on the animals. To illustrate this, visitors might provide a source of entertainment for zoo animals and could thus be “used” as a type of enrichment “device.” Alternatively, the presence of zoo visitors might be stressful to animals due to the noise levels or crowd size, which over a prolonged period of time may cause harm to the animals (these visitor conditions might be more annoying or threatening). The data might reveal that the members of one ape species experience zoo visitors as enrichment whilst members of the other species experience them as an aversive presence, or that the behaviour of certain ape

^{1,2} This study does not deal with statistical analyses of this particular issue (see Chapters 3 and 5).

categories (based on zoo, sex and dominance) is affected by visitors whilst others are not.

Visitor noise level models

Two models are presented here, based on the assumption that noisy visitors will disturb ape behaviour more than quiet visitors do (in the same way that most humans are more likely to be aware of the presence of noisy people rather than quiet ones). This visitor effect on ape behaviour might enrich the apes' lives, or alternatively might compromise their well-being. In addition, if noisy or quiet visitor groups affect the behaviour of the animals, this can have implications for the success of the zoo as a medium for conservation education.

1. "Noisy Visitors as Aversive" Model

Under this model, the disruption caused by human noisiness is not beneficial to the apes, and as such they perceive noisy groups of zoo visitors as more threatening or annoying than quiet ones. This model suggests that apes will engage in more bouts of behaviour that are possibly associated with stress (such as more self-grooming or abnormal behaviour) in the presence of noisy visitors, who are thus an aversive presence.

2. "Noisy Visitors as Enrichment" Model

Alternatively, zoo apes might not be very stimulated by their captive environment and might therefore enjoy the distraction that noisy visitor groups can offer. In the presence of noisy visitors, one would therefore expect apes to perform fewer bouts of behaviour that are possibly associated with stress (e.g. self-grooming), because they are less bored and more stimulated by their surroundings.

Visitor crowd size models

The following two models assume that the presence of a large number of zoo visitors (20 or more people) will cause a greater disturbance (enriching or aversive) to ape behaviour than will a small group of visitors (5 or fewer people). Presumably the presence of zoo visitors is more obvious when large crowds are standing at the enclosure, just as most humans would find large groups of people more noticeable than small ones.

3. “Large Crowds as Aversive” Model

This model deals with the possibility that a large group of visitors might be more threatening, or invade the apes’ privacy to a greater degree than a small group does. Therefore, when a large group of people is present apes might be less relaxed, exhibiting more bouts of behaviour that are possibly associated with stress (e.g. more self-grooming). Large crowds would thus be an aversive presence.

4. “Large Crowds as Enrichment” Model

In contrast, this model assumes that the apes’ captive environment will be less boring when a large crowd of visitors is present. When people are at the enclosure in large numbers, they might enrich the apes’ lives to a greater extent by providing something for the apes to watch or even interact with. Under this model, one would expect apes to exhibit fewer bouts of behaviour that are possibly associated with stress (e.g. self-grooming) in the presence of a large crowd of visitors, who provide a form of enrichment.

Working hypotheses and predictions

Hypothesis 1: The influence of visitor conditions on ape behaviour

Large (20 or more people) or noisy groups of zoo visitors will affect the behaviour of zoo-housed gorillas and chimpanzees differently from small (5 or fewer people) or quiet groups of visitors.

Prediction 1.1

- a. The presence of noisy zoo visitors will be associated with fewer than expected bouts of social affiliative behaviour among apes**
- b. The presence of large groups of zoo visitors will be associated with fewer than expected bouts of social affiliative behaviour among apes**

Predictions 1.1.a and 1.1.b refer to Models 1 and 3 described above, that noisy or large groups of zoo visitors are an aversive presence. Previous studies into the effects of zoo visitors on primate behaviour suggest that primates engage in fewer affiliative interactions in the presence of large groups of visitors (e.g. Glatson *et al.*, 1984). This could indicate stress, perhaps because the animals perceive large crowds as being more of a threat or annoyance (e.g. less privacy) than small ones. If noisy visitor groups are also perceived as aversive, one would predict that there would be fewer bouts of social affiliative behaviour than expected.

- c. The presence of noisy visitors is associated with more bouts of social affiliation among apes than one would expect**
- d. The presence of large groups of visitors is associated with more bouts of social affiliation among apes than one would expect**

Predictions 1.1.c and 1.1.d also refer to Models 1 and 3, but from a different perspective. They address the possibility that apes might engage in more social affiliative bouts than expected when they feel more threatened or stressed, as a form of reassurance to one another. In this case, apes might engage in more social affiliative bouts than expected when large or noisy crowds are present, if these are more aversive visitor conditions.

Prediction 1.2

- a. The presence of noisy visitors will be associated with more social aggressive bouts than expected among apes**
- b. The presence of large groups of visitors will be associated with more social aggressive bouts than expected among apes**

Predictions 1.2.a and 1.2.b are based on previous work by other researchers (e.g. Mitchell *et al.*, 1992) and from personal observations of captive primates acquired prior to undertaking this study. A rise in levels of social aggression is usually associated with an increase in stress or tension. If these predictions are supported by the data, then it can be inferred that apes find large or noisy groups of visitors more threatening/annoying than small or quiet ones. This would fit Models 1 and 3, that the presence of noisy or large crowds does not benefit the apes.

- c. The presence of quiet visitors is associated with more social aggressive bouts among apes than expected**
- d. The presence of small groups of visitors is associated with more social aggressive bouts among apes than expected**

Alternatively, if zoo visitors are a source of enrichment to apes then one would predict that the apes would feel more tension (perhaps due to boredom) when the visitor presence is barely felt, i.e. when there is a small or quiet group of visitors at the enclosure. It is predicted here that there will be more bouts of social aggression than expected in the presence of quiet or small visitor groups, as per Models 2 and 4 (that noisy or large crowds provide more enrichment than quiet or small ones).

Prediction 1.3

- a. The presence of noisy zoo visitors is associated with more bouts of active behaviour in apes than one would expect (i.e. more travelling bouts and fewer resting bouts than expected)**
- b. The presence of large groups of zoo visitors is associated with more bouts of active behaviour in apes than one would expect (i.e. more travelling bouts and fewer resting bouts than expected)**

It is predicted here that apes will be engaged in more travelling bouts and fewer resting bouts than one would expect in the presence of large or noisy groups of visitors. If these predictions are supported by the data, one might conclude that noisy or large crowds cause more of a diversion or interruption for apes than do small or quiet ones. If visitors are a source of enrichment (from Models 2 and 4), apes might be too preoccupied to rest; if visitors have an aversive effect on apes (under Models 1 and 3), the apes might be too agitated to rest so often.

- c. The presence of quiet zoo visitors is associated with more bouts of active behaviour in apes than one would expect (i.e. more travelling bouts and fewer resting bouts than expected)**
- d. The presence of small groups of zoo visitors is associated with more bouts of active behaviour in apes than one would expect (i.e. more travelling bouts and fewer resting bouts than expected)**

Under these predictions, apes would be engaged in more travelling bouts and fewer resting bouts than expected in the presence of small or quiet groups of zoo visitors. Should the data support these predictions, one might conclude that apes are more able to relax in the presence of large or noisy crowds of visitors. This could be enriching (see Models 2 and 4) by providing a more relaxed environment. Alternatively, excessive passivity (lethargy) might indicate that the apes are undergoing some form of stress or psychological depression due to the presence of large or noisy groups of visitors (Models 1 and 3).

Prediction 1.4

- a. Apes will be engaged in more visitor-directed bouts of behaviour than expected in the presence of noisy zoo visitors**
- b. Apes will be engaged in more visitor-directed bouts of behaviour than expected in the presence of large groups of visitors**

A study by Hosey and Druck in 1987 found that captive monkeys attempted to engage in significantly more interactions with zoo visitors when the visitors were in large active groups. It is predicted here that there will be more visitor-directed bouts of behaviour (not only ape-human interactions) than expected by apes when large or noisy crowds are present, because these visitor conditions are presumably more noticeable than small or quiet groups.

The types of visitor-directed behaviour that the apes engage in might be enriching, such as stick-passing or simply watching the visitors (“watching the world go by”), as per Models 2 and 4. Alternatively such bouts might have a potentially aversive effect (as per Models 1 and 3), if apes engage in so much visitor-directed behaviour that they do not interact fully with members of their own social group. Visitors would gain an inaccurate impression of the behaviour of the species (this issue is discussed in greater detail in Chapters 2 and 5).

Prediction 1.5

- a. Apes will be engaged in more bouts of abnormal behaviour than one would expect in the presence of noisy zoo visitors**
- b. Apes will be engaged in more bouts of abnormal behaviour than one would expect in the presence of large groups of visitors**

Abnormal behaviour is usually associated with an impoverished or stressful environment, both physically and socially (e.g. Poole, 1988; Meyer-Holzapfel, 1968). Predictions 1.5.a and 1.5.b state that if noisy or large groups of visitors are threatening or annoying to apes, then apes would be expected to engage in more

bouts of abnormal behaviour than expected in the presence of visitor groups displaying these conditions. These predictions come under Models 1 and 3, that noisy or large crowds of zoo visitors are an aversive presence.

- c. Apes will be engaged in more bouts of abnormal behaviour than expected in the presence of quiet visitors**
- d. Apes will be engaged in more bouts of abnormal behaviour than expected in the presence of small groups of visitors**

Alternatively, if noisy or large groups of visitors are a source of enrichment for apes (as per Models 2 and 4) then one would predict a greater number of abnormal bouts of behaviour than expected when visitors are being quiet or are in a small group. The lack of visitor-based enrichment associated with small or quiet groups of people might produce a more boring (and therefore potentially more stressful) captive environment.

Prediction 1.6

- a. Noisy zoo visitors will be associated with more self-grooming bouts than expected in apes**
- b. Large groups of zoo visitors will be associated with more self-grooming bouts than expected in apes**

Previous research has suggested that high levels of self-grooming can be associated with an increase in stress levels and boredom in primates (e.g. Maple, 1980; Castles and Whiten, 1998). If apes engage in more bouts of self-grooming than one would expect when noisy or large crowds are present, one can assume that these visitor conditions are aversive (as per Models 1 and 3).

- c. **Quiet groups of visitors will be associated with more self-grooming bouts in apes than expected**
- d. **Small groups of visitors will be associated with more self-grooming bouts in apes than expected**

Alternatively, if apes' lives are enriched by the presence of noisy or large groups of visitors then the number of self-grooming bouts in apes might increase over that expected if visitors are being quiet or are in small groups. These less-stimulating visitor conditions might produce a situation where apes are bored, which can be stressful and perhaps encourage them to engage in excessive self-grooming. These predictions follow Models 2 and 4, that noisy or large groups of visitors have enrichment potential.

Hypothesis 2: The effect of visitor conditions on the apes' spatial use of their enclosures

The presence of large (20 or more people) or noisy groups of zoo visitors will affect the apes' spatial use of their enclosures differently from small (5 or fewer people) or quiet groups of visitors.

Prediction 2.1

- a. **The presence of noisy visitors is associated with fewer behavioural bouts observed at the front of the enclosure (i.e. nearest to the visitors' viewing areas) than expected**
- b. **The presence of large groups of visitors is associated with fewer behavioural bouts observed at the front of the enclosure (i.e. nearest to the visitors' viewing areas) than expected**

Predictions 2.1.a and 2.1.b refer to Models 1 and 3, that large or noisy crowds of zoo visitors are an aversive presence. These predictions assume these visitor conditions will be more threatening or annoying (e.g., invading privacy) to apes

than will small or quiet visitor groups. Apes will be discouraged from spending time at the front of the enclosure (i.e. nearest to the visitors' viewing area) when people are in large or noisy groups, thus will engage in more bouts of behaviour than expected in the middle or back of the enclosure.

- c. The presence of noisy visitors will be associated with more behavioural bouts observed at the front of the enclosure (i.e. nearest to the visitors' viewing areas) than expected**
- d. The presence of large groups of visitors will be associated with more behavioural bouts observed at the front of the enclosure (i.e. nearest to the visitors' viewing areas) than one would expect**

Alternatively, it may be the case that noisy or large crowds entertain the apes or at least arouse their interest in the visitors (from Models 2 and 4, i.e. these visitor conditions are enriching). Therefore, Predictions 2.1.c and 2.1.d state that apes will be encouraged to spend more time at the front of the enclosure than expected when large or noisy crowds are present, and will engage in fewer bouts of behaviour than expected in the middle or back of the enclosure.

Prediction 2.2

- a. The presence of noisy zoo visitors is associated with fewer than expected behavioural bouts observed at ground level (i.e. at the same level as the visitors)**
- b. The presence of large groups of visitors is associated with fewer than expected behavioural bouts observed at ground level (i.e. at the same level as the visitors)**

Previous research has suggested that humans and other animals perceive themselves as being dominant if they are physically elevated from other beings around them (e.g. Coe, 1985). Animals are also known to seek safety in the height of trees if they feel threatened. Using this information, it is predicted here

that apes will be observed at ground level less often than expected in the presence of large or noisy groups of zoo visitors, thus they will be encouraged to perform their daily activities on structures above the ground (above the visitors). These predictions follow Models 1 and 3, that noisy or large crowds are an aversive presence.

- c. The presence of noisy zoo visitors is associated with more behavioural bouts observed at ground level (i.e. at the same level as the visitors) than one would expect**
- d. The presence of large groups of visitors is associated with more behavioural bouts observed at ground level (i.e. at the same level as the visitors) than one would expect**

Alternatively, apes might be observed on the ground more often than expected in the presence of noisy or large groups of visitors. If these predictions are supported, one can infer that these more obvious groups of visitors are probably better sources of enrichment for the apes (referring to Models 2 and 4) than are quiet or small groups, because the apes have not sought the relative safety of the “trees.”

Summary

This thesis deals with some of the effects of captivity (particularly the influences of zoo visitor crowd size and noisiness) on the behaviour of gorillas and chimpanzees. In Chapter 2 there follows a review of the relevant literature in this field of “zoo biology”, including an examination of some of the issues that face the modern zoo. In Chapter 3 I present a detailed account of the methodology used in this research project, including details on the sampling techniques, recording rules and data analyses.

I present and describe the results of the data analyses in Chapter 4, dealing with each working hypothesis in turn. Firstly I test the hypothesis that large or noisy

groups of zoo visitors will affect the behaviour of apes differently from small or quiet groups. I go on to test the hypothesis that large or noisy groups of visitors will influence the apes' spatial use of their enclosure differently from small or quiet groups. In each case, gorillas are grouped into two categories per zoo (the females and the silverback male) and chimpanzees into three categories per zoo (the females, non-dominant males and the dominant male). Chapter 5 comprises a discussion of the methods and major findings of the research. In addition I suggest possible areas for further investigation in this field. In Chapter 6 I present the overall conclusions of this study.

Chapter 2 - Literature Review

Overview

Studies in the fields of zoo biology and animal welfare have become more commonplace over the past two or three decades. My study, investigating some of the effects of captivity on the behaviour of captive chimpanzees and western lowland gorillas, focuses primarily on the possibility that zoo visitors, as part of the captive environment, affect the behaviour of these apes. In this chapter I present a review of the pertinent literature in this field.

I begin by giving an overview of the important role that zoo biology has to play, followed by a brief history of wild animal keeping and the functions of the modern zoo. I go on to discuss some of the potential implications - both positive and negative - of allowing human visitors into zoos, with regards to promoting the well-being of zoo animals and the conservation education of visitors. I discuss some of the possible misconceptions that zoo visitors can acquire from a trip to the zoo, as well as some specific examples of naturalistic zoo exhibits that have been designed to promote a more accurate representation of captive animals. I examine some cases where zoos have tried to encourage interactions between humans and animals through behavioural engineering, and I go on to review studies regarding the effect of zoo visitors on certain types of behaviour in primates. The typical daily behaviour of wild chimpanzees and western lowland gorillas is then discussed, as well as the types of environmental and behavioural constraints that captive animals usually have to cope with. Finally, I discuss the behavioural priorities of captive animals, and describe stereotypic and other abnormal behaviour as a response to captivity.

The importance of zoo biology

Scientific interest in the behaviour of captive animals, and especially primates, has become increasingly popular this century. As one of the most prominent workers in this field has stated, "... captive studies in isolation [cannot] replace research in the natural habitat, but they do complement it in one very important respect: *detail*" (de Waal, 1991, p. 32). Such studies have previously covered the sorts of issues already dealt with in wild or laboratory settings such as mother-infant interactions, social dominance hierarchies and cognitive ability. Zoos can utilise these sorts of research topics as part of their justification for the keeping of wild animals in captivity (research is usually cited as one of the functions of zoos). Research undertaken in zoos can also provide information on technologies for the breeding, handling and transporting of primates, which can then be applied to conservation efforts for wild-living populations if necessary (Mittermeier, 1997).

Interest in the welfare of captive animals has also risen during the last thirty or so years, among professionals in this field and the general public. Studies undertaken in the wild have introduced us to how these animals behave under natural conditions (Goodall, J., personal communication), and in the United States, the introduction of Animal Care and Use Committees have also contributed to the rising interest in captive animal welfare (Ball, H., personal communication). In addition, televised nature documentaries and other such media can make information about the lives of wild-living species readily available to the general public. This has put moral and financial pressure on zoo management to provide their animals with more naturalistic enclosures, as this is what most of today's zoo visitors expect to see^{2.1}. Zoo biology, therefore, can provide a scientific foundation for the care taking of captive animals under optimal and behaviourally relevant conditions (i.e. captive environments that enable the animal to demonstrate as much of its natural behaviour as possible, in an appropriate context) as emphasised by Hediger (1969).

^{2.1} Realistically, however, most zoos cannot adapt quickly enough in response to this, because of a lack of funding (McKenna, 1987).

In spite of the remarkable behavioural flexibility of many species and their ability to adapt to different environments, most people are no longer content to see captive animals in sterile environments. There seems to be a general consensus that zoo exhibits should emulate the natural setting to as great an extent as possible, not only for the sake of the animals' welfare but also for the education (and enjoyment) of the visitors. Furthermore, zoo visitors constitute a dynamic aspect of the exhibits, as a constantly changing part of the captive animals' environment. Therefore it is important to assess whether visitors actually influence animal behaviour, and if so, to examine some of the potential implications of this.

Applied studies such as those assessing zoo animal welfare or the animals' response to the captive environment serve an extremely important function as a by-product of the keeping of wild animals in captivity. It is the responsibility of all those who work in zoos to be familiar with the effects of the captive environment on animal behaviour. In addition to the welfare implications of zoo-based studies, data collected in the zoo setting can supplement our understanding of the wild behaviour of the species, and can raise new questions as to the extent of human and environmental influences on the behaviour of captive animals. With this in mind, this study aims to contribute to our knowledge of some of the effects of captivity on gorilla and chimpanzee behaviour, focussing specifically on the influence of zoo visitors.

The changing role of zoos

Early collections of captive wild animals

Animals are very much a part of human evolutionary history and our interest in them - scientific or otherwise - presumably originated as an essential survival technique: humans were both the hunter and the hunted. The earliest recorded collections of captive wild animals include those of various Egyptian kings as long ago as 2500 BC and the Ling-Yu collection in China some 1000 years BC. The education role of modern zoos is not a recent phenomenon: Greek students

in the 4th century BC were taken to see collections of wild animals as part of their education (Hatley, 1980).

Animals have also been seen as symbols of power and given as diplomatic gifts. For example, a lion was presented to Charlemagne by Pope Leo X in 800 AD, and Emperor Frederick II gave a polar bear to his brother-in-law Henry III of England (Cherfas, 1984). The Romans believed that the greatest show of power was to keep an animal captive, especially if it was then killed, such as in gladiatorial games. In 106 AD, for example, 11,000 animals died in a four month period of games staged by Trojan to mark the conquest of Dacia (Cherfas, 1984).

From the 1500s through until the 1800s, most European zoos were royal or aristocratic and were not, therefore, open to the general public. King Louis XIV of France is credited with founding the first modern zoo at Versailles in 1664, which was open to scientists and the general public (Rybot, 1972). This menagerie played a part in the then-developing science of comparative anatomy, and another zoo founded by Louis XIV at the Jardin du Roi in Paris was opened to a wider range of visitors. In around 1792, following the French Revolution, the surviving animals at Versailles were sent to the Jardin du Roi, which then became known as the Jardin des Plantes.

In Britain, it was illegal for anyone but the monarch to exhibit wild animals until the 18th century (Rybot, 1972). London Zoo (founded by Sir Stamford Raffles, as discussed below) was set up as a scientific institution in 1826 and was officially opened to the public in 1846. Following this, other zoos sprang up across Europe and the rest of the world, the main purpose being to draw in the crowds to raise the funds necessary to keep the animals (Maier and Page, 1990). It was therefore of great importance to keep the visitors happy with the display of “charismatic fundraisers” such as big cats and elephants, and so the main role of zoos was to be a popular attraction. Enclosures were designed to allow maximum viewing opportunities for the visitors, and cages were barren because this was deemed easier to clean and keep free from harmful germs and bacteria. Zoo animals were not expected to live for very long, and if an animal died it could easily be

replaced with another one from the wild. As we have gained a greater understanding of animal welfare and conservation issues, these old menagerie style zoos are no longer deemed appropriate^{2.2}.

The modern zoo

In most cases, the modern zoo has changed a great deal since the first collections of captive wild animals such as those described above, but further changes are still essential if animal welfare and the conservation education of zoo visitors are to be taken more seriously. Today, we use animals for our own needs to make human life easier, as pets, clothing, food, experimentation and “entertainment.” Nonetheless, there seems to be a widespread unease regarding the human-animal relationship. This can probably be attributed – at least in part – to Charles Darwin’s theories of evolution, which revolutionised our thinking. Instead of continuing in the beliefs that humans and animals were separately created and that animals are simply automatons, we now accept our shared evolutionary heritage. Today, the majority of people believe that (at least some) animals are sentient beings. There is a growing belief that there should be a sense of moral duty to ensure that once humans interfere with animals, the stresses that these animals experience should be no more severe than they would be in the wild (Animals and Ethics Working Party, 1980). In addition, there is increasing interest regarding the protection of the natural world. Reflecting this change in attitudes, the word “conservation” has only really been in general use for the past 30 or so years (Kirkwood, J., personal communication).

^{2.2} Many authors have summarised the history of zoos and the keeping of animals (e.g. Bostock, 1993; Maier and Page, 1990; Mullan and Marvin, 1987), and readers are invited to refer to such texts for a more detailed review than is given here.

The role of zoo visitors

The advantages and disadvantages of human visitors

With regards to zoo animal welfare (and, indeed, the welfare of all captive animals) there are some basic needs, including social contact with conspecifics and a healthy diet, to name but two. In addition, it is important that zoo animals should have the ability to perform daily routines of natural activities (such as would normally be observed in the wild) and have the minimum spatial and territorial requirements, including provisions for privacy (Animals and Ethics Working Party, 1980).

With this in mind, this study investigates the possibility that zoo visitors are a type of enrichment “device” for captive apes, or that they are an aversive presence. Another possibility is that zoo animals will become completely habituated to their captive environment and ignore the visitors entirely. As a consequence of this study, zoos will have a better understanding of how best to deal with their visitors: if visitors can be “used” as an enrichment “device,” zoos should maximise this potential, and if visitors are an aversive presence, zoos should take measures to reduce the negative effects. If animals are completely habituated to the visitors, then zoos need take no further action in this matter and we will have increased our knowledge about the apes’ ability to adapt to their environment. I expand upon these issues throughout this study.

Animals, staff and visitors form the backbone of every zoo. Zoo management must aim to reconcile the demands of the public, whose financial support they rely heavily upon, with the physiological and psychological requirements of the animals. There is a great potential for a conflict of interest here. Hal Markowitz describes the influx of zoo visitors as “pollution” (particularly on weekends) and states that this “produces unnecessary hardships for the animals” (Markowitz, 1982, p. 114). Nevertheless, as discussed below, Markowitz’s zoo was able to raise quite substantial funds from their visitors by encouraging them to engage in organised games with some of the animals.

John Aspinall believes that the absence of the visiting public would be beneficial to the gorillas at his two wild animal parks, Howletts and Port Lympne (Aspinall, 1986). He argues that the advantages of stimulation and diversion that the apes might receive from visitor presence are outweighed by the dangers associated with visitors transmitting infectious diseases to the apes, and by the time, space and costs incurred in catering for the public. However, he does recognize that the revenue from zoo visitors covers an all-too-important one third of his zoos' total running costs, making visitors an absolute necessity. Therefore, even if my study shows that visitors are an aversive presence, it is obvious that zoos must reconcile the demands of the visitors with the needs of the animals because visitors are so financially important.

In addition to the danger associated with the transmission of harmful diseases to zoo animals, there is also a more sinister risk – zoo visitor misconduct. This usually stems from a lack of knowledge and understanding on the visitors' part, and inadequate information provided by zoos regarding appropriate visitor behaviour. This problem can be highlighted by many cases, several of which are discussed more fully in Chapter 5. Visitors are often so keen to interact with zoo animals that they will throw food or other objects into the enclosure without realising the damage they might be doing. Zoo animals can perpetuate the problem by begging to the crowd, thus making visitors believe that they are “doing the right thing” by feeding the apparently “hungry” animals. Zoo visitors seem to have a strong desire to interact with the animals, in a variety of ways (personal observation), possibly because modern life removes a great many people from contact with the natural world to which we are adapted (e.g. Hediger, 1969).

Molly Badham (Twycross Zoo) is quoted as saying, “...the public are a great trial. We don't put up with any nonsense, but it's hard to watch them every minute; not long ago I caught a boy shooting at our little grey seal with a slingshot. ...I'm willing to admit that a few visitors are good for the animals – to keep them interested...” (Hahn, 1968, p. 285). Zoo personnel are frequently astounded by the apparent lack of common sense that the average zoo visitor

seems to possess (personal observation, 1998, this study). Heini Hediger also comments on this, relating an incident that involved the moving of an extremely distressed African Barbary wild sheep from one enclosure to another. The animal was displaying seemingly obvious signs of distress such as very flared nostrils, foaming at the mouth, pilo-erection, running frantically to and fro, and wild-looking eyes. In spite of these physical signs, a female zoo visitor came along with a group of children and, "...blissfully ignorant of what was going on, cheerfully held out a piece of bread to the foam-flecked maned sheep, as it dashed by her" (Hediger, 1955, p. 140). This zoo visitor had failed to observe that the animal was in a state of extreme excitement and was not simply playing or exercising. If this type of scenario is common, where visitors totally misunderstand (or ignore) what the animals do, then zoos are failing in their accurate education of the visitors. I discuss this issue in the following section.

Conservation education in zoos – visitors' (mis)conceptions

Wallis (1997) gives a review of the changing world of zoo-based primate conservation and of the plight of primates earlier this century, both in captivity (as a result of substandard animal husbandry) and in the wild (at the hands of hunters). As for today's situation in the wild, wide-scale habitat destruction and the commercial bushmeat trade are the main threats to primate populations and are a real cause for concern. For example, the Ape Alliance coalition (1998) suggests that 5-7% of Congo-Brazzaville's chimpanzee and gorilla populations are killed each year for bushmeat; in one 12-month period, 293 chimpanzee carcasses were counted in a Brazzaville market. The bushmeat issue is rife with socio-political problems, and so it certainly cannot be solved overnight. There is a great need, nonetheless, for today's zoos to move further towards assisting in the conservation of species threatened by this crisis and others. Zoos have a great potential to become more directly and indirectly involved in conserving wild populations. However, "despite excellent intentions, even the best zoo may be creating animal stereotypes that are not only incorrect but that actually work against the interests of wildlife conservation" (Sommer, 1972, Pp. 28-29). It is for this reason that the ways in which animals are portrayed in captivity by the

zoo environment need to be critically explored. My assessment of the influence of zoo visitors on species-typical chimpanzee and gorilla behaviour can contribute towards this.

Today's zoos usually claim four main roles for themselves: visitor education and enjoyment^{2,3}, and species research and conservation, given here in no particular order of importance (e.g., Margodt, 1999). Regarding visitor education, zoos can hardly be regarded as establishments for education if they fail to transmit to the public the appreciation of naturalistic behaviour and its significance in the lives of animals in nature. It is of great importance that zoo visitors should enjoy their trip – zoos rely heavily upon the financial support of visitors and happy visitors are more likely to return to the zoo in the future. Furthermore, people who have enjoyed their visit might be encouraged to become financially involved in the support of *in situ* conservation projects.

One of the factors that makes visitors stay longer at the enclosure seems to be animal activity (e.g. Bitgood *et al.*, 1985) or visitor participation/interaction (e.g. Jones-Davis, 1996). It should alarm zoo management that “the average visitor spends as little as 12 seconds to two minutes at the typical animal exhibit” (Altman, 1998, p. 12). Even chimpanzees, who are widely believed to be very popular with zoo-goers, are observed by visitors for an average of 3.5 minutes at Arnhem Zoo in the Netherlands (de Waal, 1991). Even then, de Waal notes that many of these short-stay visitors regularly exclaim that they could watch the animals for hours. Altman's own study assesses differences in zoo visitors' responses (i.e. their interest) at three bear exhibits, and has found that certain types of bear activity hold the visitors' attention longer than others. In addition, she reviews some of the literature that suggests that “the general visitor does not go to the zoo to be educated” but goes to have a good day out, or because of a general affection for animals (Altman, 1998, p. 12).

^{2,3} “Visitor enjoyment” is usually referred to as “entertainment,” but this word can give the misleading impression of circus-type performances. I believe that zoos should try to avoid using the word “entertainment” *per se*, for the sake of their education and conservation roles, and for the animals' welfare.

Furthermore, a survey involving 100 randomly selected people was conducted in four shopping centres in Tulsa, Oklahoma (Kawata and Hendy, 1978). These people had to answer 14 questions on various subjects regarding zoos, including reasons for going to the zoo. A total of only 6 people (i.e. 6%) answered that they would go to the zoo so that they or their children could learn about animals, with the most common reason (38 people, or 38%) being simply to see the animals. These 38 people rejected “learning” as a reason for going to the zoo, but it is highly likely that they would learn *something* from seeing these animals during their zoo visit. Whether this “something” accurately represents the species-typical behaviour of the animals or portrays them as circus performers or unhappy prisoners, is in the hands of the zoo. Zoos undoubtedly influence public attitudes regarding conservation of these species in the wild. In addition to the possible effects on conservation education, a zoo environment that does not give its animals the opportunity to engage in species typical behaviour (and in appropriate contexts) is probably not providing conditions that are conducive to welfare. These sorts of issues need to be explored in more detail in future studies to enable zoos to maximise the public's enjoyment of their visit without compromising the psychological and physiological well-being of the animals, whilst also getting the conservation message across to visitors.

The study presented in this thesis deals with the behaviour of chimpanzees and western lowland gorillas in captivity. All three sub-species of chimpanzee and gorilla respectively have the status “endangered;” the 1996 IUCN estimated population of *Gorilla gorilla gorilla* stands at 110,000 and for the three chimpanzee sub-species combined, the estimate stands at 105,000 (Ape Alliance, 1998). Some people argue in favour of maintaining the gene pools of endangered species such as gorillas and chimpanzees by keeping them in captivity, but these efforts will be in vain if the species are not conserved in their fast disappearing natural habitats.

Zoo animals become heavily reliant upon the care of people, despite the best intentions, and this is just one of the factors that makes it extremely difficult to re-release them into the wild. Therefore, species preserved in the modern zoo (a

kind of “Noah’s ark”) will most probably have nowhere else to go, and so one cannot really justify the existence of zoos as genetic pools of endangered species. Instead, zoos must try to encourage their visitors to become active financial supporters of *in situ* conservation of endangered species and threatened habitats. However, if visitors are leaving the zoo after their tour with a lack of respect and awe for the animals that they have spent the day viewing, then something is very much amiss. If they leave the zoo understanding no more about the species’ natural behaviour and capabilities than if they had gone to a side-show or circus, then zoos are far from reaching their conservation education goals.

Malamud describes how zoos are “...generally thought to be as important to any city as a good symphony orchestra or a well-developed system of parks” (Malamud, 1998, p. 1). Zoos are often credited with offering the experience of the natural world to people who live far from it. However, “... a caged animal, in the heart of a city, perhaps thousands of miles from its habitat, really offers little insight into the natural condition of that species” (Malamud, 1998, p. 1). As Sommer states, “... by itself, the sight of caged animals does not engender respect for animals” (Sommer, 1972, p. 26).

Zoos, therefore, have the potential to create a negative or inaccurate impression, possibly instilling in visitors the notion that humans are entitled to capture wild animals and keep them in captivity for our own gains. These notions are unlikely to encourage visitors to engage in conservation efforts such as financial support for *in situ* projects. Many similarities have also been drawn between colonial ideas of supremacy over other races and the zoo-goers’ attitudes towards the captive animals that they are watching. Malamud (1998) presents a review of such beliefs, taken from various literary sources. During colonial times, some European travellers became animal collectors, appropriating exotic wild animals for captivity in the West. “Free-ranging animals [were] turned into specimens of possession/subjection,” writes Malamud, and these collectors were the “great imperialists” such as Sir Stamford Raffles, founder of the Zoological Society of London (Malamud, 1998, Pp. 59-60). Malamud argues that one could follow the

spread of colonialism with the founding of zoos such as London in the nineteenth century.

To Malamud, therefore, the keeping of wild animals in captivity seems to symbolize power, and zoo managers need to ensure that modern zoos do not make the visitors believe that conquering nature is permissible or desirable. The type of enclosure (e.g. cage) might also reinforce the subconscious notion that zoo animals “deserve” to be kept in captivity in the same way that human criminals “deserve” to be kept in prison. There is also the danger that visitors might (if they consider it at all) be led to believe that we do not even need to conserve species in the wild, because animals are readily available to view in captivity. Zoos might unwittingly portray themselves as the “be all and end all” safety net for these species, which is a highly unrealistic scenario.

As I have already mentioned, Malamud argues that there is the danger that many zoo exhibits seem to rationalise the keeping of captive animals by subconsciously presenting them as prisoners who actually deserve to be held captive. In everyday English language, the word “zoo” is often used when describing places of confusion and disorder, and this stresses the fact that to many people, zoos might be seen more as a prison or asylum than as a centre for conservation and education. Comparisons have been drawn between the noisy and disorderly behaviour of some zoo visitors who taunt or endanger the animals, and people in the 1600s and 1700s who would visit the Bethlehem Hospital (from which we get the word “bedlam”) specifically to try to enrage the mental patients (Malamud, 1998).

Although Malamud’s opinions are a little extreme (being that he completely disapproves of all zoos), he does raise an important point: it is essential that the impressions conveyed to visitors by modern zoo enclosures, and the behavioural responses of the animals to captivity, should contribute towards zoos’ conservation education ideals. The study presented in this thesis is important in this respect because we will have a greater understanding of the change (if any)

in “behavioural priorities” in gorillas and chimpanzees as a result of the presence of zoo visitors, and some of the likely implications of this.

Some examples of exhibits conducive to conservation education and animal welfare

Various important studies have already been conducted to investigate whether or not zoo habitats that elicit species-typical behaviour from their animals are more likely to promote human appreciation for the wild members of the species.

Golden lion tamarins (*Leontopithecus rosalia*) in a free-ranging exhibit at the National Zoo, Washington, were of great interest to the public who enjoyed the arboreal presence of the monkeys (Stoinski *et al.*, 1997).

Price *et al.* (1994) have compared zoo visitors’ reactions to two groups of cotton-top tamarins, *Saguinus oedipus oedipus* (one group being free-ranging and the other caged), at Jersey Zoo. Their study assessed the potential of the two types of exhibit for promoting conservation education, and for raising the fascination, awareness and enjoyment of the zoo visitors. The results showed that zoo visitors spent on average ten times longer searching for the free-ranging monkeys and twice as long actually observing them, than did visitors at the caged exhibit. From questionnaires, it was also found that visitors believed that there was an improvement in the welfare of the monkeys in the wood compared with their caged conspecifics, because the free-ranging ones were able to roam in the trees. Visitors also felt that they could learn more about the species by observing the monkeys in the more naturalistic habitat, and this increased their personal enjoyment of the exhibit. It seems, therefore, that the naturalistic wooded exhibit has a greater potential for keeping the visitors’ interest than does the traditional cage, and visitors were more likely to consider wider issues such as animal welfare and *in situ* conservation.

With visitors contributing crucial finances to zoological establishments, zoo management must endeavour to reach a compromise between the demands of the visitors and the needs of the animals. One can sympathise with zoo officials who

are somewhat reluctant to create more naturalistic enclosures for their animals in case visitors are not impressed with having to actively seek out the animals. However, studies such as that done by Price *et al.* (1994), as discussed above, positively reinforce the ability of zoos to satisfy their visitors by keeping the animals in more naturalistic enclosures. These types of enclosure simulate aspects of the natural habitats that zoo visitors are likely to have seen in nature documentaries and magazines. Even though visitors would have to spend more time searching for the animals in a naturalistic enclosure, it might encourage an interest in conserving the species that they have observed in the zoo, *in situ*. Through a scientific investigation of these aspects of zoo biology, improvements in enclosure design can and should be made.

The architect, Coe, applies theories of both human and animal behaviour to his enclosure designs for zoo animals. He argues that zoo visitors are environmentally predisposed to learn from and enjoy what they experience, and that zoos have the opportunity to display their animals “in such a way that their right to exist is intuitively self-evident to the visitors” (Coe, 1985, p. 198). Because such exhibits are designed to communicate with visitors at both the conscious and the subconscious level, there is a great potential that these types of exhibit may enhance visitor awareness and appreciation for the *in situ* conservation of species and their habitats.

Coe argues that there are eight fundamental concepts in the provision of a behavioural basis to exhibit design in zoos (Coe, 1985). The first, that of getting attention, is aimed at encouraging visitors to spend longer at the enclosure than the average range of a few seconds to a few minutes. Coe tries to achieve this by presenting the animals in such a way that makes them appear unrestrained and therefore dangerous, expanding upon the early ideas of Carl Hagenbeck, “the inventor of the cage without bars” (Cherfas, 1984, p. 37). This in turn makes the zoo experience more memorable, Coe argues, due to the surprise and awe induced by coming across an apparently unrestrained animal. He explores the issue further by stating the importance of first impressions. The right first impression can create a vivid memory in a child, and can predispose that child to

support the protection of that species and its habitat when he or she reaches adulthood. Conversely, the wrong first impression can create so strong a prejudice that it might never be overcome (for example, the contrast between a silverback gorilla being perceived as a violent monster who directs aggression at visitors, or as a peaceful animal foraging in a lush habitat, surrounded by his family).

The fourth concept offered by Coe is that of subordination: in most human societies, posture and relative position can be indicative of the perceived dominance, such as the throne of royalty or teachers on podiums. He argues that it is possible for the lowered position to predispose the subordinate individuals to learn. Hence, zoo visitors who surround a group of zoo animals or are elevated above them might perceive themselves as being dominant over the animals (he uses the analogy of Masai hunters surrounding their prey) and thus their learning may be inhibited. Therefore, it follows that if a zoo enclosure is designed such that the visitors are in the subordinate position of looking up at the animals, then visitors may be predisposed to learn about the animals, and be more attentive and respectful towards them. In addition, if animals are positioned higher up than the visitors are, the animals might be less threatened or annoyed by the visitors because they too might perceive themselves as being in a dominant position. Coe's other concepts involve making the zoo experience both more enjoyable and more realistic for the zoo visitors, using so-called immersion exhibits. The overall notion revolves around the likelihood that an exhibit that the animals find boring will almost certainly bore the visitors, which will most certainly hamper the success of conservation education.

Some of Coe's ideals have been put into practice in two gorilla enclosures, one at Zoo Atlanta and the other at Dallas Zoo. These enclosures take into account a combination of the needs of the zoos' animals, visitors and staff, and were designed with the intention of providing the gorillas "with as many components of their natural environment as possible" (Bruner and Meller, 1992, p. 213). A variety of zoo staff from each of the two zoos, including education, veterinary

and research staff, were involved in the planning procedures to gain a more holistic insight into the requirements of the exhibits.

Dallas Zoo held a three-day symposium with the participants being split into several groups, each with the task of creating an optimal habitat for zoo-housed gorillas. Zoo Atlanta gained outside sponsorship to send architects and some of the zoo's key staff to Central and Western Africa to view and study natural gorilla habitats firsthand. Throughout the design process, each zoo encouraged regular consultations with zoo personnel. Bruner and Meller (1992) report that the resulting enclosures are naturalistic, and provide the gorillas with places where they can get out of sight from visitors and conspecifics. The exhibits are based on the notion of immersion (where there are no perceivable barriers between the visitors and gorillas), thus making the visitors' experience more realistic. Both zoos designed multiple-group exhibits to reflect the territoriality of wild gorilla groups. The zoo gorillas could thus interact with members of another group at the enclosures' boundaries, whilst still maintaining physical separation for safety reasons.

Some effects of zoo visitors

Engineered human-animal interactions in zoos

I have already discussed the notion that zoo visitors are much more likely to gain a greater respect for the animal if they see them performing species-typical behaviour (even if this is in the "unnatural" context of the zoo enclosure). Enrichment tasks can be given to the animals to encourage them to engage in more active behaviours that demonstrate their natural behavioural capabilities. Some zoos have developed enrichment devices to actively encourage visitor-animal interactions by the implementation of competitive "games" between human and animal. The efforts of Hal Markowitz are particularly well known in this field. He and his colleagues at the Portland Zoo, USA, devised various means for zoo visitors to interact with animals in such a way so as not to be

humiliating or otherwise detrimental to the animals (by not encouraging visitor-directed begging or excessive food intake, for instance)^{2,4}.

The following examples of Markowitz's behavioural engineering devices are taken from his book, *Behavioural Enrichment in the Zoo* (Markowitz, 1982). One such system was designed for gibbons (*Hylobates lar*). Two stations were built, each with a stimulus light and lever, and a food chute at the second station. When the light was lit on the first station, visitors could put a 10 cents coin into the machine. This would trigger the light to come on at the second station – if a gibbon then responded to this light by using the lever, the ape would receive a measured quantity of food. Following a period of initial training, the gibbons almost always chose to work for their food rather than just being given it for nothing. The zoo received positive feedback from their visitors regarding this “game,” and in the first year this machine alone raised \$3000 worth of dimes from participating visitors. This contraption enabled gibbons to work for their food and reduce their boredom. In addition, the visitors witnessed more active animals engaged in interesting activities that showed their natural behavioural capabilities (even if the context in which they were performed was “unnatural”: wild animals obviously do not play with such devices).

Also at the Portland Zoo, Markowitz and colleagues devised a speed game to entertain their male mandrill (*Papio sphinx*), Blue. A console was positioned in a door of his cage, with an identical one placed in the visitor viewing area so that people could follow his progress during the game. A light would appear on Blue's console and would remain lit until he responded (because the game was designed mainly to entertain him). When he chose to play, his response to the light would activate a light on the visitors' console. Visitors were then invited to pay a dime if they wanted to compete with Blue in the game. If no one deposited a dime, he could play against the computer (but apparently he rarely played against the computer, even if there were no willing visitors; he seemed to prefer playing against people). Once the game was initiated, the aim was to touch a

^{2,4}. Unfortunately, the behavioural engineering apparatus were removed from the Portland Zoo when a new director was appointed in 1977 (Hutchings *et al.*, 1978).

randomly lit square in one of three possible locations on the console screen (the lit square would appear simultaneously on both Blue's and the visitors' console). Premature responses resulted in an automatic loss. Whoever touched the light first was the winner. The first participant to gain three wins was rewarded (a piece of food for the mandrill, or an announcement on the scoreboard for the visitor). Interestingly, Blue won over 70% of the games, apparently in fair competition with his human visitors. Spider monkeys (*Ateles ater*) at the Panaewa Rain Forest Zoo, Hawaii, also received this speed game and were noted for beating many of their visitors.

However, not all of the enrichment devices devised by Markowitz and his colleagues were as successful as was originally intended. One such example was at the Honolulu Zoo, where they were invited to make a piece of equipment for visitors at the bear enclosure. The enclosure housed one male grizzly bear (*Ursus arctos horribilis*), and the equipment was designed in response to complaints from visitors that they were not allowed to feed him. Previously, the zoo had allowed visitors to throw food into the enclosure, but had changed its policy for the sake of the bear's welfare. The zoo also planted a lot of vegetation around the enclosure, so that the visitors could still see the animal but could not throw food to him without it hitting the trees. So, to keep the visitors happy without compromising the bear's welfare, visitors could push a button that would catapult a piece of suitable food into the enclosure, landing in random locations. In theory, the bear's activity should have increased because he had to move around the enclosure to obtain this food. Initially, this did happen and the visitors were entertained by their interaction with the animal. However, the bear soon realised that if he waited until several visitors had catapulted food into the enclosure, he could collect it with minimum effort.

Another example is that of Willy B, a gorilla at Zoo Atlanta, who was given a rope with which to play "tug-of-war" with the visitors. The gorilla destroyed the first rope that he was given, and so a second rope had to be brought in. The zoo then decided that there was too great a potential for human injury and thus the

human-gorilla test of strength was no longer available except during certain publicity events (Maple and Hoff, 1982).

Today, most British zoos do not provide special facilities to enable (or encourage) human-animal interactions to occur (personal observation). Nevertheless, zoo visitors do seem to want to experience an interaction with exotic animals, perhaps because the modern way of life removes us from nature to a great extent (Hediger, 1969). In the absence of special facilities enabling human-animal interactions, zoo visitors who feel the need for interaction often resort to shouting or clapping at the animals to attract their attention, or throwing unsuitable food items into the enclosure.

Some zoo visitors might think that above all else they have paid to be entertained, and they will often go to great lengths to try to provoke a passive animal to get up and do something, to “perform” for them (McKenna, 1987). Only when the captive environment stimulates zoo animals to behave in some natural or unnatural way will the visitors want to stay and watch. What sort of influence do zoo visitors have on the animals? Whether visitors are trying to interact with zoo animals or not, their mere presence at the enclosure or the noise they make might elicit behavioural responses in the animals that one would not see in the absence of visitors. The following section reviews the literature regarding the non-engineered influence that human zoo visitors can have on primate behaviour.

The effects of zoo visitors on primate behaviour

Some researchers have argued that zoo animals become habituated to the presence of zoo visitors, leading to a situation in which visitors are completely ignored by the animals (e.g. Snyder, 1975; Adams and Babladelis, 1977). In contrast, the results of several other studies suggest that animals are indeed affected by human visitors. Galbraith (1996) compared the effects of varying audience size and composition on the behaviour of adult and infant chimpanzees at Edinburgh Zoo, to determine whether or not the apes’ interest in the visitors

decreases with increasing age. His results showed that the chimpanzees' interest in the zoo visitors did not decrease with age, and so these apes did not seem to become habituated to the presence of visitors over time.

Presumably, if an animal is housed alone or in an otherwise sterile environment then he or she will be even more eager for visitor interaction. One such example is that of an adult male chimpanzee, Sebastian, who was housed alone in a zoo enclosure in Nairobi because he had killed his two cagemates (Goodall, J., personal communication). When the zoo temporarily closed down for repairs, he went into a deep depression that was thought to be brought on by the lack of stimulation provided by zoo visitors. Zoo visitors would usually tease this chimpanzee a great deal, and although this type of visitor behaviour would be deemed inappropriate by many zoos, this animal had adapted to it and seemed to suffer more as a result of the lack of this stimulation.

One study has assessed the influence of the zoo environment on the social behaviour of cotton-topped tamarins, *Sanguinus oedipus oedipus*, to try to ascertain whether or not the zoo situation is responsible for the poor breeding record for this species (Glatson *et al.*, 1984). Captive breeding of cotton-topped tamarins is vital due to the severity of the threat of extinction, but at the time that their study was done zoos were having little success in the captive propagation of this species. By rotating groups of cotton-topped tamarins around various enclosures, the researchers discovered that animals on display to the public exhibited less social behaviour than animals that were off-exhibit. Of particular importance to their study was the finding that while on display to zoo visitors the breeding pairs were less sociable towards each other and their offspring. When off-display, the tamarins were significantly more affiliative and less agonistic towards one another. Enclosure type also seemed to play a role, as there was more affiliation in the larger mesh-fronted cage than the smaller glass-fronted one, even though both cages were on display to zoo visitors. Thus the authors conclude that this study demonstrates a strong difference in the behaviour of these primates when housed on- and off-display, influenced both by the presence of zoo visitors and cage design.

In spite of Hagenbeck's revolutionary enclosure designs and Coe's adoption of these discussed previously), it may be the case that animals in "open" enclosures including islands are more aware of the zoo visitors than animals in cages are, as there is no obvious physical barrier between them. As a result, the animals on islands might feel less protected or more intruded upon by the visitors. Over the long term, this might have harmful effects and would therefore need to be investigated further. In nature, all animals have adapted mechanisms to cope with the stress of their daily lives, such as escape from predators or finding food, and they can respond accordingly as and when the situation arises. In captivity, whilst the need for protection from predators or food seeking is removed, animals are potentially subjected to long-term ongoing stressors in their captive environment. A study by Chamove and Moodie (1990), illustrating this, is discussed later in this chapter.

Researchers involved with a study on the interactions between chimpanzees and human zoo visitors at Chester Zoo argue that the willingness of chimpanzees to interact with visitors might alleviate boredom (Cook and Hosey, 1995). Early stages of chimpanzee-initiated interaction sequences involved "attention-seeking" behaviours whereas in the later stages of the sequence most of the chimpanzee behaviours comprised begging, usually a "food-soliciting gesture" (Cook and Hosey, 1995, p. 439). Despite the fact that 25% of human-initiated interactions and 9% of chimpanzee-initiated interactions resulted in these apes being given food, the solicitation of food might not be the driving force behind these interactions, as chimpanzees did not always take the food that was given to them. Instead, the chimpanzees might have been interacting with visitors for social reasons.

Even if the presence of visitors does provide these chimpanzees with a distraction from an otherwise boring life in captivity, the predominance of visitor-directed begging does not seem to fit in with the zoo's education aims. The study presented in this thesis will be important in this respect, by helping to assess the "normality" of ape behaviour that zoo visitors are likely to observe during their visit. When chimpanzees beg during official feeding times or to

encourage visitors to “illegally” throw food into the enclosure, visitors often comment on the chimpanzees’ circus clown-like behaviour and describe these apes (“monkeys”) using derogatory words such as “stupid” or “ugly” (personal observation, 1998, this study). There is the danger that “...one would learn from watching zoo animals ‘that the chimpanzee, for example, is a neurotic humanoid that cadges food from humans, and throws tantrums and excreta should this not materialize...’” (Batten, P. cited in Malamud, 1998, p. 8).

Mitchell *et al.* (1992) undertook research on the relationship between the number of zoo visitors and frequency of aggressive facial displays by three groups of golden-bellied mangabeys (*Cercocebus galeritus chrysogaster*) at the Sacramento Zoo. These monkeys frequently threatened zoo visitors, primates of other species in nearby enclosures and conspecifics, using facial displays. One group of monkeys that was moved from a cage with few visitors to one that had a higher rate of visitation paid significantly more attention to the visitors and to conspecifics within the cage, but less to neighbouring primates. Likewise, the reverse was true in that when a group of mangabeys was moved from a highly visited enclosure to one having few visitors, they showed a significant decrease in visitor-directed threats and an increase in threats to neighbouring primates. The introduction of an aggressive female mangabey to one of the other mangabey groups caused an increase in intra-group threats in the receiver group, although visitor-directed threats were reduced even when there were many visitors present. The donor group engaged in fewer aggressive interactions within the group following the removal of this aggressive female. The results from this study show that zoo visitors do elicit aggressive responses from the mangabeys, and so the notion of zoo animals becoming habituated to visitors cannot be supported in this case either.

Hosey and Druck (1987) have studied the influence of human visitors on the behaviour of twelve captive primate species at Chester Zoo. Zoo visitors were rated in terms of group size and activity. Group sizes were rated as “no visitors”, “small groups” comprising of 1-5 visitors and “large groups” of more than 6 visitors. Group activity was split into “active” groups (being those in which at

least one person attempted to interact with an animal) and “passive” groups (in which no one attempted an interaction). The observers recorded all occurrences of certain primate behaviours (behaviour directed at the visitors, behaviour directed at other members of the primate social group, the level of primate locomotory activity and the spatial dispersions of the primates in the cage) for observation periods lasting one minute.

The results of the study by Hosey and Druck showed that the animals directed significantly more behaviours at large active groups of visitors than at small active groups. Overall, there were significantly more behaviours directed at active groups than at passive groups. Under the different audience conditions, there was no significant difference in the rate of intra-group interactions. Active groups of visitors (both large and small) caused significantly more locomotory activities in the animals than did the no-visitors condition, but passive audiences did not affect locomotion. In addition, the spatial distribution of all of the primates was significantly different from the no-visitors condition, and they tended to spend most of their time at the front of the enclosure when visitor groups were large and active. The authors conclude, therefore, that it is wrong to assume that zoo animals become habituated to visitors.

Another study demonstrating the effects of visitors on primate behaviour was undertaken by Chamove *et al.* (1988). They conducted a two-part study to assess the effects of zoo visitors on primate social behaviour for fifteen species at Edinburgh Zoo. In the first part of the study, they observed the three species of primate under two audience conditions: no visitors present, and more than six visitors present (this number of people was enough to fill the viewing window). Observations were made on each animal for two 10-minute sessions separated by two weeks, for each visitor condition. Four behaviour categories were recorded at 10-second intervals (agonistic, grooming, affiliation and inactivity). The results showed that primates were significantly less affiliative, significantly less inactive, groomed significantly less often and were engaged in significantly more aggression (five-fold) when zoo visitors were present (i.e. at least six visitors).

From this, Chamove *et al.* have inferred that visitors cause behavioural changes in these primates that are consistent with an interpretation of stress. One way that zoo management could rectify this would be to reduce the number of visitors that are allowed to observe the animals. Most zoo managers are likely to find this course of action impractical and out of the question, particularly because zoos have to keep their visitors “happy” for financial reasons. Restricting the visitors’ access to zoo enclosures is unlikely to be a popular course of action.

In the second part of their study, Chamove *et al.* assessed an alternative method for reducing stress. Eight volunteer groups of at least five zoo visitors were used to manipulate an audience condition. These people would either stand as tall as possible at the viewing window or crouch down with only their heads visible above the base of the window, watching the animals for at least five minutes. Observations were made on individual animals for one-minute each, with the same behaviour categories as in Part 1 recorded every five seconds. Visitor-directed vigilance was also noted as and when it occurred.

The results of this part of their study showed that when visitors were crouching down there was a significant change in primate behaviour, which was reduced to half of that observed in the first part of the study for visitors being present. The behaviour of the primates when visitors stood as tall as possible did not differ significantly from the results in the first part of the study for visitor presence. Therefore, this work by Chamove *et al.* also shows that visitors change the behaviour of primates in zoos, and their work supports the argument that captive primates do not become habituated to zoo visitors. In addition, with an increase in aggressive behaviours and activity, and a reduction in amicable behaviour among the primates, it would appear that the presence of zoo visitors is more stressful than enriching. This seems to go beyond the levels of “positive” stress as discussed later in this chapter (Chamove and Moodie, 1990), which lead to reductions in aggression.

The results of the studies discussed above disagree with the argument by Snyder (1995) and others that zoo animals become completely habituated to human

visitors. However, there is still a lack of data on the extent to which visitors influence the typical daily behaviour of captive animals. The study presented in this thesis aims to address the validity of studying this particular issue, regarding the captive behaviour of gorillas and chimpanzees.

The behaviour of *Pan troglodytes* and *Gorilla gorilla* in nature

Before the behaviour of captive chimpanzees and gorillas can be discussed in relation to this study, it is first necessary to describe the behaviour of their wild conspecifics. In doing this, we will have a greater understanding about the sorts of activities that zoo apes would ideally be able to engage in within their captive environments. If my data show that apes are behaving very differently than they would be in the wild (especially in relation to the influence (if any) of zoo visitors) then the welfare and conservation education implications of these behavioural changes must be discussed.

To date, the social behaviour of chimpanzees (*Pan troglodytes*) has been more fully studied in the wild than in captivity (de Waal, 1996), although the Jane Goodall Institute's "ChimpanZoo" programme is helping to encourage zoo-based studies of chimpanzee behaviour (personal observation). In addition, Arnhem Zoo, in the Netherlands, is famous world wide for its chimpanzee colony and for the behavioural research conducted there by Frans de Waal and others (de Waal, 1991). Many studies have also been conducted on the mountain gorilla (*Gorilla gorilla beringei*) in its natural habitat (e.g., Schaller, 1963; Fossey, 1988; Fossey and Harcourt, 1977), whereas the western lowland gorilla (*G. g. gorilla*) and eastern lowland gorilla (*G. g. graueri*) have not been studied in such great depth. The western lowland gorilla, pertinent to this study, has proved to be difficult to study intensively in the wild. This is mainly due to their lowland rainforest habitat, which can make it difficult for an observer to follow the apes successfully and collect reliable data (Jones and Sabater Pi, 1971; Sabater Pi, 1993; Rogers, E., personal communication; Remis, M., personal communication). Even in long-term study sites such as the Lopé Reserve, central

Gabon, where gorilla studies have been running since 1984, habituation to human observers has proved limited and so it is hard to follow the gorillas under observation.

Gorillas

A study of mitochondrial DNA diversity in the three subspecies of *Gorilla* has revealed that the genetic differences between western lowland and eastern lowland or mountain gorillas seem to be greater than the differences between published sequences from *Pan troglodytes* and *Pan paniscus* (Garner and Ryder, 1996). Therefore, just as *P. troglodytes* and *P. paniscus* are recognised as being distinct species, having obvious differences in their ecology and behaviour (as well as morphology), western lowland gorillas may well behave differently from their mountain gorilla cousins. It is suggested that eastern and western gorillas may also be two different species. Doran and McNeilage (1998) support this by suggesting that from what is known of western lowland and mountain gorillas there are considerable differences particularly in their habitat and diet, as well as morphology. Therefore, one cannot be totally confident that western lowland and mountain gorillas should have the same time budgets just because they are both gorillas, due to the genetic and behavioural differences that have been suggested.

Sabater Pi is one of the few people to have been involved with the long-term study of wild western lowland gorillas. He has been involved in field studies of chimpanzees and western lowland gorillas in the area of Rio Muni, Republic of Equatorial Guinea, since 1956 (Sabater Pi, 1993). The information that I give here regarding the daily behaviour of western lowland gorillas is based upon Sabater Pi's work. In western lowland gorillas, the silverback initiates the making of night nests between about 1730 and 1830 hours, when darkness sets in. Nest making is usually completed by 1835 hours. Nocturnal activities (such as chest beating, belch vocalisations and other noises and vocalisations) take place from then until about 2200 hours, and start again at about 0400 hours. Gorilla vocalisations tend to be at their peak around the times of going to "bed" at night and getting up in the morning, and are intentionally aimed at intra-group

members. The gorillas get up from their night nests between about 0555-0650 hours when visibility is good enough to enable them to search for food (if the weather is particularly bad or during the rainy season, the gorillas tend to get up later than this). There is a main period of travelling or movement between about 0600 and 0700 hours. The major period of feeding is between 1000 and 1300 hours, overlapping with their period of resting during the middle of the day (roughly between 1100 and 1400 hours) for which they may construct simple day nests. Following this siesta, the gorillas engage in more feeding. Between 1700 and 1800, the gorillas have another main period of movement before making their night nests.

Regarding social structure, western lowland gorillas seem to resemble mountain gorillas. They live in cohesive groups estimated to comprise an average of ten individuals (Tutin, 1997), and are quite peaceful by nature. There is typically only one fully adult male per group (the silverback), several adult females, and their offspring. Younger males usually leave their natal group shortly before sexual maturity (when they are still blackbacks) or sometimes as young silverbacks. A young male will then either join a bachelor group, or eventually start his own breeding group by encouraging females from other bands to join him. It is the responsibility of the silverback male to protect his family from danger, to protect his breeding rights against other males and to decide when to move to another feeding area. Silverback gorillas will usually respond to a threatening outside stimulus (gorilla or non-gorilla) with aggressive displays (e.g. Tutin and Fernandez, 1987), protecting their females and offspring. Usually the intimidation of this display is enough to end the encounter (physical aggression is rarely needed but does occur when necessary). Aggressive interactions among group members are rare, and seem to be associated with food shortage (Tutin, 1997).

Female gorillas leave their natal band seemingly by choice, unlike chimpanzee females who are coerced (Richards, 1985). If a female gorilla transfers, she will usually do so before she has ever given birth, and will then usually stay in her chosen group for life, although some females have been known to transfer

several times. Females are never solitary, probably because they and their offspring need the protection of the silverback (Richards, 1985).

Chimpanzees

Many field studies have been undertaken on wild chimpanzees, the most famous being those of Jane Goodall at the Gombe Stream National Park, Tanzania. Data from full-day follows on Gombe chimpanzees reveal that these apes spend between 35% and 65% of their time each month in feeding-related activities (Goodall, 1986), with the highest percentage of time spent feeding being between May and July. This is the result of the seasonal availability of particular seeds cased in hard pods and fruits that are widely dispersed. On a typical day, the Gombe chimpanzees get up at dawn and set off to look for food. Intense feeding can last for several hours and then across the hottest midday hours the chimpanzees rest and engage in relaxing activities such as social grooming (Lemmon, 1994). The afternoon consists of more feeding and travelling, and they make their night nests before sunset. Gombe chimpanzees nest early in wet weather and may make day nests as well.

Sabater Pi (1993) has recorded a similar pattern of behaviour in the chimpanzees in Rio Muni. At night, Rio Muni chimpanzees begin nesting at about 1805-1845 hours, before the sun goes down completely. Like the Rio Muni gorillas described above, Rio Muni chimpanzees have a period of nocturnal communicative activity from then until 0100 hours, which starts again at 0400 hours. These vocalisations tend to be distributed throughout the whole of the night, rather than just being concentrated on times of going to "bed" and getting up, as in the gorillas. The chimpanzees communicate their state of mind or emotions to other groups who are further away, and obtain vocal answers that calm the noise down. This communicative activity then escalates until they leave their nests, typically between 0531-0650 hours (again depending upon light levels and the weather). A period of travelling or movement then follows until about 0800 hours. They eat intensively from 0800 to 1100 hours. Rio Muni chimpanzees also make day nests for their inactive period during the heat of the

day between about 1100-1500 hours, slightly longer than in the Rio Muni gorillas. Feeding activity decreases noticeably in the afternoon, although the chimpanzees continue to eat in moderation from 1400 to 1800 hours. Travelling increases between 1600 and 1800 hours. Night nests are then constructed and the chimpanzees settle down again for their nocturnal activities.

A typical day for the chimpanzees in the Budongo Forest, Uganda, also involves getting up at dawn, then spending a few hours feeding high up in the trees. Across the middle hours of the day, the chimpanzees forage for food on the forest floor or doze in the top canopy of the trees (Reynolds, 1965). Another period of feeding then follows. At times when food is plentiful, these apes also engage in periods of rest and social behaviour, and at times of scarcity they travel a great deal throughout the day to look for food. The Budongo chimpanzees spend roughly 50-75% of the daylight hours in the trees. At nightfall, these chimpanzees retire to freshly made night nests in the trees. Reynolds also refers to the work of Henry Nissen in western Guinea during the 1930s (Reynolds, 1968). Nissen's observations of chimpanzees were similar to those of Reynolds, in that the apes get up at dawn and are most active during the early morning and later in the afternoon, with resting being the main activity in the middle of the day. Nissen's chimpanzees made day nests on the ground for their midday rest.

Chimpanzees are known for being more gregarious than gorillas are, which is perhaps due to the fact that they live in fission-fusion groups. Chimpanzees can live in groups of up to 80 or more individuals, but are usually dispersed (fission-fusion), with individuals from the group coming and going on a daily basis (Napier and Napier, 1985). Thus by dispersing themselves over a greater distance, members of the group have more access to food items because they are foraging in different areas. Tutin argues that the "flexible association patterns of the chimpanzee community demand complex social relationships" (Tutin, 1996, p. 187). Chimpanzees may go for several days without seeing particular group members (Goodall, 1986) and they engage in social affiliative behaviours such as allo-grooming, hugging and so forth when they meet up.

Chimpanzees live in multi-male groups. The alpha or dominant male chimpanzee has preferential mating rights, but all males in the community are allowed to mate with females. Tension can build up within the group due to competition for females in oestrus. This does not happen in gorillas, because they usually live in one-male groups (see above), with the silverback protecting his mating rights against outside males. Therefore, the differences in social structure in gorillas and chimpanzees can probably explain the fact that chimpanzees are much more excitable and sociable than the passive gorillas.

Female and male chimpanzees will usually leave their natal group as late adolescents or young adults, to avoid inbreeding within the group. Females will transfer between groups, getting to know the group first by making short visits to them (Goodall, 1986; Lemmon, 1994). Resident females usually regard the outsider as a threat to their resources, and are often very aggressive towards her. Males, in contrast, are usually very welcoming to the new female, as she is a potential sexual partner (males usually protect the new female until the other females have accepted her, which can take months) (Lemmon 1994). Female chimpanzees are at their most sociable when in oestrus, and are more solitary at other times (Goodall, 1986). Goodall (1986) describes how chimpanzees have “what appears to be an inherent dislike or ‘hatred’ of strangers” (p. 331). Chimpanzees will respond to outsiders (male or female, chimpanzee or non-chimpanzee) with intimidation displays, subordinate males in the group usually backing up their dominant male. As in the gorilla, intimidation displays are more common than actual physical confrontation unless necessary. Female chimpanzees usually join in with the display in response to an outside stimulus, raising their arms and giving “waa-barks”. Females usually grab their young offspring first, to try to protect them (Goodall, 1986).

Infanticide has been recorded in mountain gorillas (e.g., Fossey, 1988) but has not been observed in western lowland gorillas, probably because of a general lack of data (Yamagiwa *et al.*, 1997). When infanticide occurs in mountain gorillas, it is usually when a silverback takes over (or attempts to take over) an already established family group. It is argued that infanticide by males occurs

because this will bring the mother back into oestrus, and so the new leader can sire offspring and not have to invest time and energy in protecting another male's genes (e.g. Richard, 1985). Infanticide probably occurs in western lowland gorillas as well.

Infanticide has also been recorded in chimpanzees, by both male and female aggressors, and they have even been recorded eating the infants (Goodall, 1986). In chimpanzees, it would appear that infanticide occurs as a means of reducing competition for resources. When an unhabituated female attempts to join the group, resident females (and sometimes males) often attack her and her infant. When a male chimpanzee kills another male's infant, it is probably for the same reason as given above in relation to gorillas. The mother will come into oestrus again quickly following the death of her offspring, thus increasing the aggressor's reproductive fitness over the male whose infant he has killed (Richards, 1985). It is argued that females carry out infanticide to eliminate the infant as a competitor for food resources that their own offspring require.

The African ape model

From the descriptions given above of the typical daily behaviour of chimpanzees and western lowland gorillas in the wild, there would appear to be a general model of activity that can be applied to all groups of African apes (Sabater Pi, 1993). To summarise a typical day, African apes rise from their night nests in the early morning at around dawn (later if the weather is unfavourable or during the rainy season)^{2.5}. They then feed intensely until the middle of the day and engage in social behaviour and resting during the hot midday hours. The apes have another period of intense feeding throughout the afternoon, from about 1400-1700 hours. Night nests are then made, and the day's activities are over. Chimpanzees are more sociable than gorillas, probably due to the differences in social structure as outlined above.

^{2.5} Baldwin (1979) found that chimpanzees at Mt. Assirik, Senegal, would even leave their nests in complete darkness before dawn (cited in Sabater Pi, 1993).

Captive apes

Zoos then, should surely follow the African ape model and aim for this sort of daily routine for their captive western lowland gorillas and chimpanzees.

However, if captive apes are given their feeds at predetermined times throughout the day, as is often the case, then there is no opportunity for the apes to engage in intense periods of foraging and other feeding-related activities throughout the day. In addition, captive apes cannot travel very far to find a suitable feeding area or site for the construction of night nests. This can leave long periods of time where the apes effectively have little or nothing with which to keep themselves occupied. In addition, the temperate climate in Britain might not encourage apes housed in British zoos to rest over the midday hours (which would be the hottest time of the day in their natural habitat).

In such circumstances, the presence of zoo visitors might be a welcome distraction in an otherwise uneventful day. Alternatively, if apes live in a boring environment the presence of visitors could perhaps have more of an aversive influence, as the apes have nothing to distract themselves from the visitors' stares and noisiness. For example, a study by Wood regarding the occupational therapy of chimpanzees at the Los Angeles Zoo has shown that "fresh enrichment served as a compelling diversion to the impact of high crowds" (Wood, 1995, p. 177). Data from the study presented in this thesis will give us an insight into how captive chimpanzees and gorillas typically spend their day, and how the presence of large or noisy groups of people might affect this.

If the captive apes look bored because they are not given the opportunity to engage in activities throughout the day (such as time-consuming feeding-related activities such as foraging), visitors are unlikely to be interested in learning more about these animals. In consequence, visitors might leave the zoo with a negative impression of zoos, as places that house unhappy animals. However, the model of wild African ape behaviour tells us that chimpanzees and gorillas typically rest over the midday period – zoos should perhaps inform their visitors that a certain amount of inactivity during the day is healthy and "normal." It is the zoos' responsibility to ensure that captive apes do not have to sit around and do nothing

for the rest of the day. We need to compare the behaviour of apes in zoos with ape data collected in the wild so that we understand the extent of the influence of the captive environment on ape behaviour.

Behavioural priorities of captive animals

The provisions that a zoo makes for its animals should be based upon information that we have from the wild. Therefore zoos should give their animals the opportunity to engage in species-typical behaviour, because this is what the animal has adapted to throughout evolution (Hediger, 1969). For example, chimpanzees in zoos should be given fake termite mounds and sticks with which to “fish” for food such as peanut butter or honey as they would “fish” for termites in the wild. Zoos that house their animals in poorly enriched enclosures, or that have animals demonstrating abnormal behaviours, usually do so because of financial constraints or a lack of understanding of zoo biology, and not because of an indifference to the needs of animals.

For zoo visitors to get really excited and to be accurately educated about the species they are observing, naturalistic exhibits need to bring out naturalistic behaviour in the animals (Markowitz, 1982). The importance of applying the behavioural knowledge that we have of wild animals to their captive relatives, for the purpose of improving the well-being of these species, has only recently been recognised and utilised widely (Bitnoff, 1996). However, Yerkes demonstrated his understanding of this principle in the 1920s (Yerkes, 1925, cited in Bitnoff, 1986).

In a captive setting, animals have different priorities than they would have in the wild. Not only are food and water provided by their human caregivers, but they are also provided with a territory, protection against predators, shelter, and mates. In the wild, the rule is very much variety and change, and nature provides stimulation in this unpredictability (Markowitz, 1982). Hediger has argued that one should not regard zoo animals as captive, but as “property owners,” who live

within their territory as defined by the boundaries of their enclosure (Hediger, 1969, p. 56).

Wild, so-called "free-living" animals are in fact far from free - they are potentially under much more stress than their captive relatives, due to the necessity of constant vigilance, the need to search for food and water, and spatial constraints associated with territory, to list the main factors. It would appear that many captive animals prefer to work for their food when given the choice (assuming the effort required is not too great), even when "free" food is simultaneously offered to them. Markowitz (1982) describes an anecdotal event involving a group of captive ostriches. These birds were involved in a behavioural engineering experiment where they had to peck a button in order to obtain peanuts. A keeper, unaware that the experiment was taking place at that time, filled the ostriches' feeding trough with peanuts (from the same batch as the experimental nuts), thereby providing the birds with "free" peanuts. The birds went over and sampled a few of these free peanuts but then returned and began to peck the button again, preferring to "earn" their food.

As a result of being provisioned by human care givers, primates housed in zoos have significantly more time to devote to certain activities such as social behaviours, than they would in the wild (e.g. Wrangham *et al.*, 1996). As Wrangham points out, with zoo primates being continuously associated with one another, one would expect that this could potentially intensify their social relationships, for example by checking male power and violence against females by the formation of group-strong female alliance parties. Zoo animals usually move about less than their wild counterparts, as they do not need to have to travel to find food or to defend their territory. To exemplify the change in behavioural priorities as a result of human provisioning, a study comparing the time budgets of wild-feeding and semiprovisioned baboons (*Papio cynocephalus*) demonstrates the increase in "slack" time that animals have when there is a human nutritional interference. The semiprovisioned group fed for about 20% of the time and rested for 50% of the time, compared with 60% and 10%, respectively, for wild-feeding baboons (Altmann and Muruthi, 1988).

Wilson (1982) conducted a study of environmental influences on the activity of gorillas and orang-utans (*Pongo pygmaeus*) in a total of 41 zoological parks in Europe. Her research suggests that the number of animals and objects (stationary, temporary (i.e. short-term) and moveable) within the enclosure were factors relating highly to activity level. Neither the frequency of feeding times, the size of enclosure or the enclosure's usable surface area seemed to be related to activity levels. Therefore, to reduce the chance that these apes may become bored or inactive in captivity and to improve captive environments, she argues that it is more important that environmental complexity should be increased, rather than simply enclosure size. Gorillas preferred stationary and temporary (short-term) objects whereas orang-utans preferred stationary and moveable objects, and so the particular items that are used to increase the complexity of the environment should be species-specific.

Perkins (1992) extended Wilson's study using orang-utans as her subjects, but her results did not support those of Wilson. However, different methods were used in each study, and Perkins collected more data. The results from Perkins' study showed a strong association between orang-utan activity levels and the number of social partners, the number of moveable objects, and enclosure size (including both volume and usable surface area). Therefore, Perkins concludes that captive orang-utans are encouraged to demonstrate active behaviours in enclosures that are large, with many moveable objects and social members to interact with (although in the wild orang-utans are known for being solitary).

A comparative study has been undertaken in three Californian zoos investigating the effect of the physical environment on the behaviour of captive chimpanzees (Bitnoff, 1996). The results of this study show that the different habitats affect chimpanzee behaviour in a variety of ways. Some types of behaviour were obviously feature-dependent, such as gymnastics. Chimpanzees spent most of their time (approximately 61%) off the ground in two of the zoos (San Francisco and Sacramento zoos), although the third zoo (Oakland Zoo) had more features suitable for off-ground use. One possible reason for this is that the ground in the Oakland Zoo enclosure is covered with grass, and so it is softer and presumably

more comfortable to be on than the concrete floor at San Francisco Zoo and the dirt floor at Sacramento Zoo.

Of particular relevance to the study presented in this thesis are Bitnoff's data on publicly oriented behaviour. The chimpanzees at Sacramento and Oakland zoos used to live in open enclosures with large visitor viewing areas, in close proximity to the public, and would respond to visitors with activities such as the throwing of faeces, spitting or begging. Today Sacramento Zoo's chimpanzee enclosure is glass-fronted, which lowers the transmission of visitor noise, and prevents the animals from begging, throwing objects and so on. Positive responses have emerged including human-ape "hide and seek" games and through-the-glass hand touching. Likewise, Oakland Zoo now has a mesh cage that prevents the passing of food or other objects into (or out of) the enclosure, and negative public interactions have now decreased. At San Francisco Zoo, however, the chimpanzees are separated from the visitors by a dry moat. Therefore the main barrier between apes and visitors is air (rather than a more substantial physical structure), which is perhaps responsible for the negative responses of chimpanzees to visitors who taunt and yell at the apes (Bitnoff, 1996).

Bitnoff suggests, therefore, that the type of enclosure can influence the effects of zoo visitors on ape behaviour. In addition, she noticed that visitors to the most naturalistic of the three chimpanzee enclosures (at Sacramento Zoo) were more likely to simply stand and observe the apes rather than to try to attract the apes' attention and elicit a response from them. This supports the idea that naturalistic enclosures, in which animals are more likely to demonstrate species-typical behaviour, will contribute to the success of conservation education by enticing the visitors to pay more respectful attention to the animals. However, even in today's zoos many animals do not demonstrate naturalistic behaviour.

Stereotypic and abnormal behaviour as responses to captivity

Where captive environments are not very complex, unnatural stereotypic and self-directed behaviours (such as rocking, self-depilation, self-biting and over-eating) can ensue to alleviate boredom and to fulfil the need to release energy and endorphins (unnatural behaviours are not typically observed in the wild (Poole, 1988)). The well-being of animals is usually measured in terms of successful bearing and rearing of offspring, but it is argued that these objectives are far too narrow (Maple, 1980). The presence of stereotypies and other abnormal behaviour patterns would perhaps be better welfare indicators.

Most zoo visitors are probably aware of the stereotyped motor reactions that can occur in zoo animals. This sort of behaviour is not only unpleasant to witness because of the underlying notion that the animal is unhappy, but might also give an incorrect message to the visitors that all zoos are invariably bad places that should not be supported. It is in zoos' best interests, therefore, to try to eradicate stereotypies. Meyer-Holzapfel discusses the possibility that freedom of choice is instrumental in alleviating stereotypic behaviours by stating that an animal will usually stop such behaviour as soon as it can move about freely (Meyer-Holzapfel, 1968). She argues that if an animal housed in a large and well-enriched enclosure still displays stereotypic behaviour, then one can guess at the past experience of the animal, in a similar way to the persistence of human neuroses. As discussed previously, all of these sorts of changes in "behavioural priorities" consequently have ramifications for the impression that zoo visitors gain from the species they observe, and as a result can influence public attitudes and (mis)conceptions.

At North Carolina Zoo, researchers found that the stereotypic pacing and swimming of their polar bears (*Thalarctos maritimus*) was virtually eliminated by simply giving these animals the option of being "on exhibit" or "off exhibit" during the day (Gregor, G., personal communication), a notion discussed by Meyer-Holzapfel (see above). North Carolina Zoo's bears used to perform stereotypic behaviours constantly, in spite of the enclosure being relatively good.

The enclosure contains features that include a large swimming pool, rocks for climbing on (including a large rock from which the bears could jump into the pool), a variety of enrichment “toys” which were frequently changed, and a waterfall. Zoo officials made several attempts to reduce the stereotypies, such as by slowing down the speed of the waterfall in case it was too noisy, rotating the “toys” more frequently, and scattering fish all over the enclosure to encourage the animals to actively seek food. The enrichment helped improve the situation in the short term, but as soon as the bears got used to the changes the stereotypies returned to their previous extent.

In the end, North Carolina Zoo researchers tried leaving the door to the inside quarters open, to give the bears their choice of being in or outdoors. The stereotypies disappeared almost immediately, and have apparently not returned. Incidentally, even though the doors to the inside quarters are left open, these bears still spend most of their time outdoors, despite the fact that they do not have to. Zoo visitors can still view the bears, which is obviously good news for zoo officials. The simple freedom of choice that these polar bears now have seems to have alleviated their stereotypies and visitors have a better chance of observing more species-typical behaviour.

As mentioned previously, life in the wild is far from stress-free. Can stressful situations in captivity therefore be of benefit to the animals, because they have adapted some coping mechanisms? If stress is beneficial to captive animals, and the presence of zoo visitors is a source of tension, could one conclude that this visitor-induced stress is healthy and should therefore be encouraged rather than stopped? A study by Chamove and Moodie (1990) has found that laboratory-housed cotton-top tamarins (*Sanguinus oedipus oedipus*) respond well to low-intensity arousal. This sort of brief stress seems to be adaptive and presumably, therefore, healthy for the monkeys. These intense but brief arousing experiences involved the capture (taking no more than five minutes) and removal (again for about five minutes) of the chosen focal monkey from the cage, and fake birds “flying” overhead (the removal of monkeys was only done when necessary for animal husbandry). The tamarins’ behavioural responses to the brief arousing

experiences were compared with their behavioural responses to long-term stressors (classified as aversive, such as the presence of zoo visitors) and to environmental enrichment (classified as beneficial). This was necessary to see if a wider range of normal behaviours (i.e. behaviours that are seen in the wild) was produced when low-level stressors were experienced.

The results of Chamove and Moodie's study showed that the effects of brief arousal are similar to the effects of enrichment, and are dissimilar to the effects of long-term stressors such as zoo visitors. Therefore, it would appear that captive zoo animals respond positively to low level stressors because they have evolved to deal with short-term stressful situations in the wild, which can occur regularly. However, long-term stressors (including the presence of zoo visitors) had a negative effect on the tamarins' behaviour. Therefore, the on-going tension that zoo visitors can create is probably not beneficial to the captive animals. I discuss this issue further in Chapter 5.

Summary

The literature that I have cited in this chapter reveals the importance of zoo biology research in the modern zoo. I have documented studies supporting the claim that zoo visitors influence the behaviour of captive primates (and probably other animals too). I have also provided evidence to support the suggestion that zoo visitors can be a source of non-beneficial stress to captive animals, which is obviously an important welfare issue. In addition, I have presented evidence from the literature to suggest that the way that animals are represented by zoos, and the type of behaviour that the animals engage in, have important implications for the conservation education of the human visitors. These matters are of great importance if today's zoos are going to play a positive role in the conservation of endangered species.

The results of this study will contribute further to the issue, by providing valuable information to zoos regarding the ways in which human visitors can

affect the behaviour of gorillas and chimpanzees, and whether zoo visitors are an enriching or aversive presence to these apes. Alternatively, my study might show that zoo visitors do not affect ape behaviour and are therefore an inert environmental feature.

Chapter 3 - Methods

Study Site Details

Data for this study were collected between 26th March and 1st September 1998 at four zoological establishments: Chester Zoo, Howletts Wild Animal Park, Colchester Zoo and Jersey Zoo. British zoos were chosen so as to keep the constraints of time and finance to a minimum. This particular time period was chosen in the expectation of relatively good weather: during these months the animals were more likely to spend the day in their outdoor enclosures and human visitors were more likely to go to the zoo (unlike during the winter when zoos are typically quieter). These factors are obviously important in the study of visitor effects, as the animals must be likely to be visible (to enable behavioural data to be collected) and the zoo visitors likely to be present (to provide the various audience conditions).

I selected the four zoos on the basis of the type of enclosure (“cage” versus “island”)^{3.1} and the ape species held within them. Western lowland gorillas (*Gorilla gorilla gorilla*) were housed in a cage at Howletts Wild Animal Park and on an island at Jersey Zoo. Chimpanzees (*Pan troglodytes* spp) were in a cage at Colchester Zoo and on an island at Chester Zoo (see Tables 3.1 and 3.2 for a brief description of each enclosure, and Figures 3.1-3.7 for photographs of the enclosures). Even though parts of the chimpanzee enclosures at both Chester and Colchester zoos were glass-fronted, which would reduce noise from the visitors, visitors could still be heard through the glass and so “noisy visitors” were still louder than “quiet visitors.”

Chimpanzees and gorillas are closely related to each other but have adapted to inhabit different niches in the wild. In captivity both species are popular with zoo visitors, probably due to the obvious similarities between these species and ourselves. Therefore, in this study I compare the behavioural responses of

^{3.1.} I decided against statistically testing the differences in behavioural responses between apes in cages and apes on islands because of the many confounding factors. For example, even within the categories of “cage” and “island,” the enclosures’ facilities differed greatly from one another.

gorillas and chimpanzees to human zoo visitors (one caged and one island group per ape species) to investigate some of the effects of captivity on ape behaviour.

Pilot Study

Prior to the main period of data collection, preliminary observations were made on the gorillas and zoo visitors at Howletts Wild Animal Park (during a surprisingly warm spell in February 1998, with temperatures in the 70s). This initial period of observation allowed me to practice the recording methods and to refine the hypotheses and predictions. During that short pilot study, both continuous focal sampling (Altmann, 1974) and focal instantaneous sampling with intervals of 20-seconds (discussed later) were used. However, continuous focal sampling was eliminated from the study, as it was difficult to record all of the relevant data (thus reducing reliability). In addition the 20-second intervals for instantaneous sampling were deemed too short as some observations were missed due to the animal moving out of the observer's sight (rather than the animal being totally hidden from visitors). This problem was intensified by the fact that there was a high volume of visitors as a result of the good weather, making it difficult for me to move quickly into a better viewing position. As a result of these difficulties the interval length was increased (see below).

Some researchers studying visitor effects in primates have previously suggested that observers should try to stay out of the animals' sight during observation sessions (e.g. Chamove *et. al.*, 1988; Hosey and Druck, 1987; Cook and Hosey, 1995). However, I did not find it practical to try to hide at these four zoos, as it was too restrictive in terms of viewing the animals adequately or following them if they moved to another part of the enclosure. Instead I tried to be as unobtrusive as possible, both to the visitors and the animals, and I counted myself as a zoo visitor when recording visitor conditions. In the event of me being the only "visitor" present, it was very rare that I was alone at the enclosure for more than a few consecutive observations.

Table 3.1. Description of the gorilla enclosures at Howletts and Jersey zoos.

ZOO	SPECIES	ENCLOSURE TYPE	DESCRIPTION
Howletts	Western lowland gorilla	Mesh cage	<p>Large 3-D climbing-frame type enclosure with visitor viewing areas on 2 of 4 sides.</p> <p>Enrichment items include: a deep straw "carpet" for nesting and foraging, water taps, shallow water pool, slides, climbing structures, nesting platforms, pots in which to "fish" for honey/peanut butter.</p> <p>Food is thrown into the straw, encouraging gorillas to actively forage for food.</p> <p>Apes have no access to indoor night-areas during the day.</p> <p>14 group members (data were analysed for 4 gorillas).</p>
Jersey	Western lowland gorilla	Walled island	<p>Large grassy enclosure surrounded by walls on 3 of 4 sides, that visitors look over into the enclosure.</p> <p>Enrichment items include climbing structures, naturally growing vegetation, hills and tunnels in the landscape.</p> <p>Food is given by keepers at designated times, each animal receiving its own portion directly (rather than having to engage in active food-seeking).</p> <p>Apes have no access to indoor night-areas during the day.</p> <p>7 group members (data were analysed for 5 gorillas).</p>

Table 3.2. Description of the chimpanzee enclosures at Chester and Colchester zoos.

ZOO	SPECIES	ENCLOSURE TYPE	DESCRIPTION
Colchester	Chimpanzee	Glass-fronted cage	<p>Fairly large glass-fronted enclosure, with wire mesh above the glass panels and around the back of the enclosure in the keepers' area.</p> <p>Enrichment items include climbing structures, clothing and boxes (to play with), caves, tubes to "fish" for food.</p> <p>Food is thrown into the enclosure from the roof to encourage the apes to forage.</p> <p>Apes have access to a glass-fronted indoor enclosure when raining (some data were collected indoors).</p> <p>9 group members (data were analysed for 6 chimpanzees).</p>
Chester	Chimpanzee	Moated island	<p>Large enclosure with visitor viewing areas on 2 of 4 sides (water moat and electric fence separate visitors and apes).</p> <p>Enrichment items include climbing structures, fake termite mound, wood-wool, tunnel.</p> <p>Food is thrown over the moat by the keepers at designated times, and so the apes do not forage for food throughout the day.</p> <p>Apes also have access to a glass-fronted indoor enclosure during the day (some data were collected indoors).</p> <p>28 group members (data were analysed for 8 chimpanzees).</p>

Figure 3.1. Interior view of Howletts' gorilla enclosure.

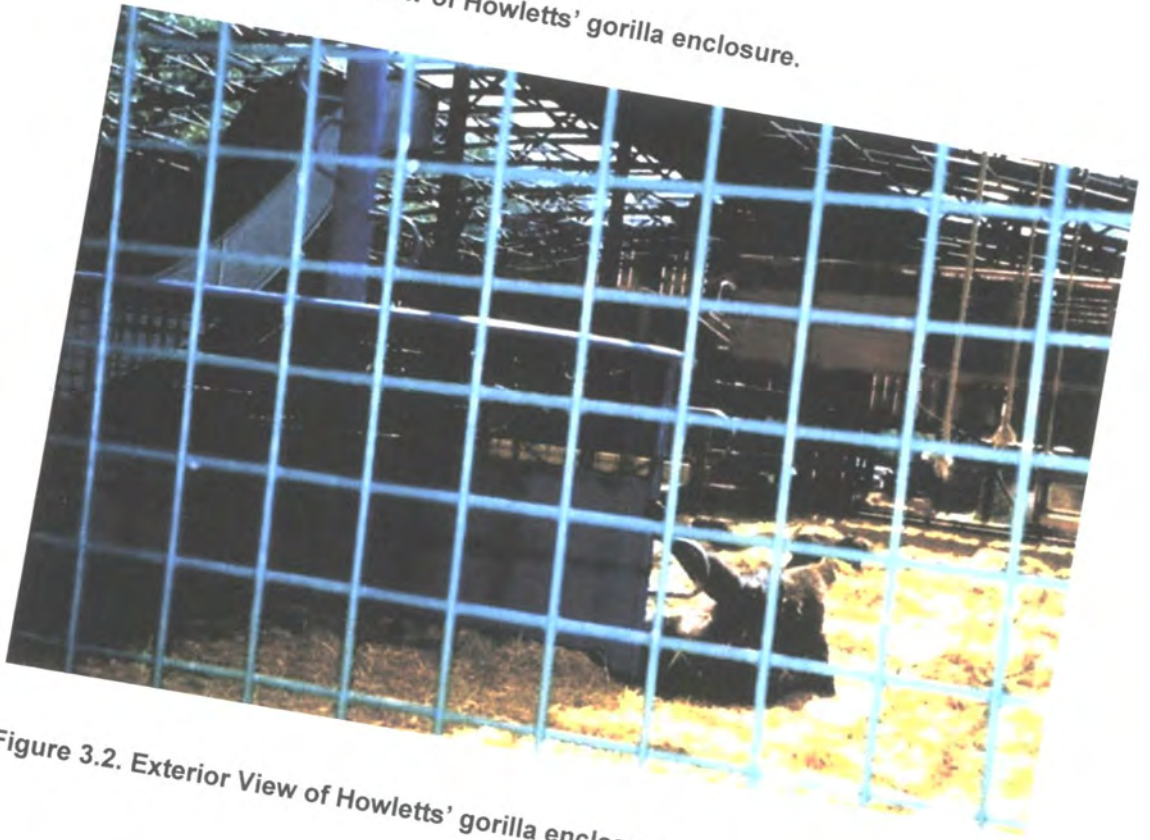


Figure 3.2. Exterior View of Howletts' gorilla enclosure.



Figure 3.3. Silverback gorilla in Jersey Zoo's enclosure.



Figure 3.4. Visitors at the perimeter wall of Jersey Zoo's gorilla enclosure.



Figure 3.5. Colchester Zoo's chimpanzee enclosure.



Figure 3.6. Feeding time for Chester Zoo's chimpanzees.



Figure 3.7. A view of the chimpanzee enclosure at Chester Zoo.



Subjects

Subjects were 14 captive adult chimpanzees (8 out of 28 chimpanzees at Chester Zoo, 6 out of 9 chimpanzees at Colchester Zoo), and 9 captive adult western lowland gorillas (4 out of a group of 14 gorillas at Howletts Wild Animal Park, 5 out of 7 gorillas at Jersey Zoo). Apes were housed in a purpose-built enclosure at each of the four zoos (more information about the focal animals can be found in Tables 3.3-3.6). Unfortunately, one of the zoos involved in the study refused to give me any background information regarding the age and sex of their apes, prior to me collecting data there. As a result of this, I was prevented from being able to make an informed decision before the start of data collection as to which age/sex groups that I should be studying in this research project. I collected data on adults, juveniles and infants at the first zoo, but I could only use the adult data in the analyses; the age/sex ratio of animals at the “problem” zoo did not fit in with my initial plans (there were no juveniles). I can only assume that the zoo that I had problems with were suspicious, for whatever reason, of researchers (and indeed, of other zoos) wanting information about their animals.

All of the animals had been housed in their respective zoos for at least several years, and so none of the subjects were new to their enclosures. The social groups were also well established. The focal apes were individually recognisable by natural physical differences such as body size and facial features. Tables 3.3-3.6 give a brief life history of each subject, from information provided by the zoo keepers. At Howletts and Chester zoos, where there were many potential focal apes to choose from, the keepers’ suggestions were very useful. At Chester Zoo, animals were selected on the basis of ease of recognition. The keepers advised me against studying particular animals that look very similar to other individuals in the group, in case I misidentified an individual during my relatively short time at the zoo. Some of the animals did resemble one another closely, and more time would have been needed to confidently identify each individual than I had available to me. At Howletts, four of the five potential study groups were discounted. Three of these eliminated groups were housed in older enclosures that were being renovated, which would have been potentially disruptive to the gorillas, zoo visitors and myself. The fourth gorilla group comprised mainly

Subjects

Subjects were 14 captive adult chimpanzees (8 females, 6 males) and 9 captive adult western lowland gorillas (7 females, 2 silverback males), housed in a purpose-built enclosure at each of the four zoos. Unfortunately, one of the zoos involved in the study refused to give me any background information regarding the age and sex of their apes, prior to me collecting data there. As a result of this, I was prevented from being able to make an informed decision before the start of data collection as to which age/sex groups that I should be studying in this research project. I collected data on adults, juveniles and infants at the first zoo, but I could only use the adult data in the analyses; the age/sex ratio of animals at the "problem" zoo did not fit in with my initial plans (there were no juveniles). I can only assume that the zoo that I had problems with were suspicious, for whatever reason, of researchers (and indeed, of other zoos) wanting information about their animals.

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hand-reared gorillas, whose behavioural responses to visitors may have been biased due to their more humanised upbringing.

Table 3.3. A brief life history of the focal gorillas at Howletts Wild Animal Park.

NAME	SEX (M/F)	DATE OF BIRTH	CAPTIVE BORN (CB) OR WILD BORN (WB)	COMMENTS
Kijo*	M	02-Apr-75	CB	
Founa	F	1971	WB	Wild-caught in Congo-Brazzaville.
Dihi	F	27-Apr-89	CB	
Mushie	F	1969	WB	Wild-caught in southern Cameroons.

* Silverback male

Table 3.4. A brief life history of the focal gorillas at Jersey Zoo.

NAME	SEX (M/F)	DATE OF BIRTH	CAPTIVE BORN (CB) OR WILD BORN (WB)	COMMENTS
Ya Kwanza*	M	03-Jun-84	CB	Second gorilla to be born by artificial insemination, first to survive.
Kishka	F	09-Sep-78	CB	
Sakina	F	14-Jul-86	CB	
Hlala Kahilli	F	23-Mar-88	CB	
N'Pongo	F	1957	WB	Wild-caught. Arrived from Cameroons in 1959.

* Silverback male

Table 3.5. A brief life history of the focal chimpanzees at Colchester Zoo.

NAME	SEX (M/F)	DATE OF BIRTH	CAPTIVE BORN (CB) OR WILD BORN (WB)	COMMENTS
Bobby*	M	12-Aug-74	CB	
Pipin	M	23-Jun-86	CB	
Billy Jo	F	Unknown	Unknown	Thought to be wild born.
Hannah	F	Unknown	Unknown	Thought to be an ex-lab chimpanzee.
Mandy	F	Unknown	Unknown	
Tara	F	08-Oct-85	CB	

*Dominant male

Table 3.6. A brief life history of the focal chimpanzees at Chester Zoo.

NAME	SEX (M/F)	DATE OF BIRTH	CAPTIVE BORN (CB) OR WILD BORN (WB)	COMMENTS
Boris*	M	1966	WB	Was a pet in an apartment in USA; donated to Chester Zoo in 1969.
Dylan	M	09-Apr-87	CB	
Wilson	M	20-Feb-68	CB	
Friday	M	06-Feb-76	CB	
Kate	F	23-Dec-70	CB	
Half Penny	F	20-May-75	CB	
Mandy	F	19-Sep-77	CB	
Heidi	F	30-Jun-72	CB	

* Dominant male

Procedure

As a consequence of my experience during the brief pilot study, I decided upon the following strategies. Using instantaneous focal time sampling (e.g. Altmann, 1974; Martin and Bateson, 1994; Patterson, 1992), each animal was observed for at least 13 thirty-minute sessions, at one-minute intervals (marked by the stopwatch's "beep"), over a period of four weeks per zoo.

On the first day of data collection at each zoo, I randomly chose the order in which to observe the focal animals (by pulling names out of a "hat") and then observed these animals in the order that they appeared on the list. On the second day the order of animals to be observed was then rotated, still following the original list order (i.e. the second animal from Day 1 would be the first animal on Day 2, the last animal on Day 3, and so on). This ensured that observation sessions were balanced across all days of the week and across the zoos' opening hours (data were collected between approximately 1000h and 1700h). Such precautions were taken to reduce the biases that might ensue due to the typical daily routine of the animals, keeper regimes such as feeding times, and variations in human visitation. In the event that the animal due to be observed next was not visible to the observer on a particular day, that individual was put to the end of the list (just for that day). The observation order would then continue as normal with the next animal in line.

Behavioural data on the subjects were recorded onto check sheets, along with data on the visitor conditions corresponding with each sample point (the check sheet layout is shown in Table 3.7). The ethogram of ape behaviour used in the data analyses is shown in Table 3.8 (the ethogram used in data collection was far more complex, and had to be re-coded to simplify it for the analyses). The descriptions of the apes' spatial location codes are given in Table 3.9. Visitor conditions were recorded in terms of visitor crowd size and crowd noisiness. "Small" crowds consisted of five or fewer visitors and "large" crowds comprised at least twenty people. Quiet visitor groups ("Q") were classified as people who were whispering or being silent, and noisy groups ("N") comprised people who were talking loudly or shouting (see Table 3.10).

Table 3.7. The layout of the check sheets.

Focal ape: Sheet no:		Weather: Date:		Time (start-end):	
INTERVAL	APE LOCATION	APE BEHAVIOUR	NO. OF VISITORS	VISITOR NOISINESS	COMMENTS
0					
1					
2					
3					
4					
5					
▶					
26					
27					
28					
29					
30					

Table 3.8. Ethogram of ape behaviour.

BEHAVIOUR	DESCRIPTION	SOME EXAMPLES
Abnormal bouts (ABNL)*	The focal ape is engaged in an activity that is rarely observed (if ever) in the wild, and does not seem to be beneficial to the animal. The animal is not engaged in any other obvious activity simultaneously.	Locomotor stereotypes (e.g. rocking), hair-plucking, masturbation, regurgitation/reingestion of food (R/R).
Resting bouts (REST)*	The ape is lying down or sitting, inactive.	Sitting inactive, lying down inactive, sleeping.
Visitor-directed bouts (VISD)*	Ape behaviour that is actively aimed towards the zoo visitors, when the ape is not engaged in any other obvious activity simultaneously.	Begging at, staring at, displaying at, interacting with zoo visitors.
Social affiliative bouts (SOAF)**	The focal ape is engaged in a non-aggressive interaction with at least one other member of the social group.	Allo-grooming, copulation, play.
Social aggressive bouts (SOAG)**	The focal ape is engaged in an agonistic interaction with at least one other member of the social group.	Displaying, biting, smacking.
Self-grooming bouts (SGRO)**	The focal animal is engaged in self-grooming.	Finger-brushing through hair, nose-picking, teeth-picking.
Travelling bouts (TRAV)**	The focal ape is engaged in locomotory activities.	Climbing, knuckle-walking, modified brachiation.
Miscellaneous (MISC)	All other activities that are not included in the above (not analysed in this study).	Feeding-related behaviour, keeper-directed behaviour.

* ABNL, REST AND VISD are mutually exclusive in their own right.

** SOAF/SOAG>SGRO>TRAV, resulting in mutually exclusive categories.

Table 3.9. Codes for the spatial location of apes within the enclosure.

CODE	DESCRIPTION
GROUND*	The focal ape is located at ground level, or is within touching distance of the ground ^{3.2} .
ABOVE*	The focal ape is located on a substrate above the ground and is not within touching distance of the ground.
FRONT**	The focal ape is located at the front of the enclosure, i.e. nearest to the visitors' viewing area.
BACK**	The focal ape is located in the middle or back of the enclosure, i.e. furthest away from the visitors' viewing area.

* GROUND and ABOVE are mutually exclusive categories

** FRONT and BACK are mutually exclusive categories.

Table 3.10. Visitor condition codes.

VISITOR CODE	DESCRIPTION
S*	5 or fewer visitors are present at the enclosure.
L*	20 or more visitors are present at the enclosure.
Q**	Visitors are being quiet (silent or whispering).
N**	Visitors are being noisy (loud talking or shouting)

* S and L are mutually exclusive categories regarding visitor crowd size.

** Q and N are mutually exclusive categories regarding visitor noisiness.

^{3.2} In the case of Jersey's gorillas, in a "pit" enclosure, there were occasions when they would be on the ground but at a lower level than the zoo visitors were. These areas were recorded as "Ground" (i.e. ground level) and any areas of the enclosure above the visitor area were recorded as "Above" (i.e. off the ground).

Data Analyses

Raw data from the check sheets were entered into a Microsoft Excel spreadsheet. Data were then reorganised such that within any one observation session, all consecutively repeated observations of any of the four variables being tested (i.e. ape behaviour, spatial location of the ape within the enclosure, visitor crowd size and visitor noisiness) were removed. By doing this I am assuming that if an ape is engaged in only one type of behaviour in one area of the enclosure, with constant visitor conditions, for several consecutive observations (marked by “beeps” of the stopwatch), then he or she is engaged in a behavioural bout rather than several discrete events. This bout would then end if any of the four variables had changed since the last sample point. As Altmann states, “the number of consecutive samples exhibiting differing states does give a crude lower bound for the number of transitions” (Altmann, p. 260, 1974).

The data are reorganised in this way to ensure that data in each observation session are statistically independent (Martin and Bateson, 1994); if all consecutively repeated observations had been included in the analysis, the results would be heavily dominated by bouts of behaviours that are time-consuming. In addition, if an animal was engaged in one type of behaviour for a certain length of time, the visitor conditions at each sample point (i.e. “on the beep”) within that time period may vary. There might be a small group of visitors at the onset of that behaviour, for example, but a large crowd by the time the animal ceases that behaviour. In such an instance, one would not be able to assess the effect of visitors on ape behaviour, because only the visitor conditions at the onset of the behaviour would have been recorded. Thus, by defining a behavioural bout as being when the animal is engaged in the same activity without changes to its spatial location or the visitor conditions, we obtain the number of bouts of behaviour. These are an approximate frequency (i.e. an approximate number of occurrences) of each type of ape behaviour and spatial distribution within the enclosure.

Using this reorganised data set, the four variables (ape behaviour, ape location, visitor crowd size and visitor noisiness) were then re-coded into mutually

exclusive categories in another spreadsheet to reduce the number of variables for analysis into a more manageable data set, without losing any of the data. It is from this spreadsheet that the data presented in this study have been taken (see Table 3.8, the ethogram of ape behaviour used in the analyses). Observations made when crowds contained between 6 and 19 people were eliminated from analysis because it was often hard to be sure whether a crowd of visitors was “medium” or “large” in size. Using the extremes of “small and “large” crowds ensures that the visitor crowd size data are reliable.

Approximately 450 hours were spent collecting data, and the results presented here are based on 149.5 hours of observation (6.5 hours per individual ape, i.e. 13 observation sessions per animal). Therefore, the data analyses are based upon a uniform amount of observation time per animal (the working hypotheses and predictions that are tested in this study are explained in Chapter 1). The chi-squared test for two independent samples was used in the analyses to determine whether or not the observed number of bouts of certain types of ape behaviour changes significantly under the specified zoo visitor conditions. The equation used for this test is given below (from Siegel and Castellan, 1988):

$$\chi^2 = \sum_{i=1}^r \sum_{j=1}^c \frac{(O_{ij} - E_{ij})^2}{E_{ij}}$$

Where expected values were smaller than 5, Yates’ Correction for Continuity was applied to remove the imprecision in approximation that may arise from such small expected frequencies. The equation is given below (from Siegel and Castellan, 1988):

$$\chi^2 = \frac{N(|AD - BC| - N/2)^2}{(A + B)(C + D)(A + C)(B + D)}$$

Where significant chi-squared results were obtained, the Kendall partial rank-order correlation coefficients were calculated. This two-tailed test was used because the observed association between the two variables (visitor crowd size or noisiness, and ape behaviour) might be due to the link between each of these two

variables and a third variable, the time of day at which the observations were made. An animal's own daily behaviour patterns might coincide with the time of day at which zoo visitor attendance is particularly high, and so any behavioural changes may not necessarily be associated with the visitors. Although data were collected in a rotated order (described above) in an effort to experimentally reduce the biases associated with time of day, this statistical control is applied to further strengthen the validity of the results. A statistically significant Kendall correlation means that one cannot necessarily claim that zoo visitors are responsible for a change in ape behaviour. The equation is given below (from Siegel and Castellan, 1988):

$$T_{xy.z} = \frac{AD - BC}{\sqrt{(A + B)(C + D)(A + C)(B + D)}}$$

Chapter 4 - Data analyses

Objectives

In this chapter I examine the data collected at the four zoos, in order to assess the changes in behaviour for each of the ten ape categories under the variables of visitor crowd size and noisiness. The analyses test the working hypotheses and predictions (see Chapter 1), that zoo visitors influence the typical daily behaviour of captive chimpanzees and western lowland gorillas, and the apes' spatial location within the enclosure. Apes are grouped into one of 10 categories based on their sex, zoo and dominance (dominance for males only). There are three chimpanzee categories for each of Chester and Colchester zoos (females, non-dominant males and dominant male) and two categories of gorilla for each of Jersey and Howletts zoos (females and silverback male).

The results of the analyses are presented in three ways. The chi-squared test for two independent samples is used to calculate whether or not the number of bouts of certain types of ape behaviour change significantly under the specified zoo visitor conditions (relating to visitor crowd size and visitor noisiness). The chi-squared test is also used to calculate whether or not there is a significant association between the visitor conditions and the apes' spatial use of their enclosures. Thirdly, where significant chi-squared results are obtained for an ape category the Kendall partial rank-order correlation coefficients are then calculated to consider the potentially confounding factor of time of day. The equations for the statistical tests are given in Chapter 3.

Graphs corresponding to the data are given in Figures 4.1-4.34 below, showing the observed numbers of bouts of behaviour upon which the chi-squared test results are based (coloured columns). In addition the calculated expected values are displayed on these graphs for comparison purposes only (expected values are shown by a transparent overlay for each column of data). These graphs show the absolute number of bouts rather than proportional representations of the data: some types of behaviour occurred very infrequently and so by using actual values

the graphs can be compared with one another. In addition, the data were analysed using the chi-squared test, requiring the observed and expected values to be used in the calculations. These graphs therefore demonstrate the chi-squared results, allowing the reader to compare the differences between observed and expected values. Statistically significant chi-squared results are marked on the graphs with an asterisk (*) for each relevant ape category.

Changes in the number of bouts of social affiliation (SOAF)

Gorillas

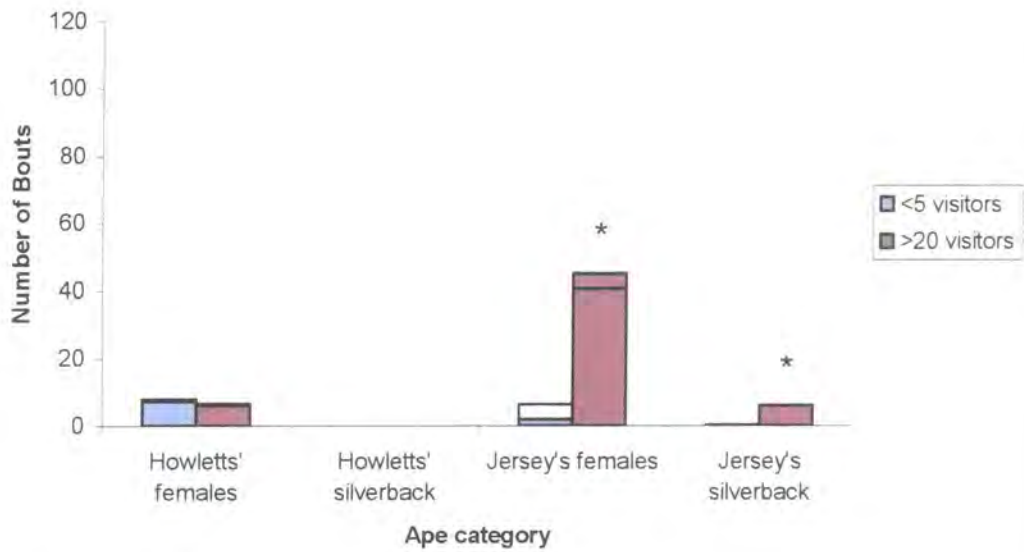
In general, social affiliative bouts were not very commonly observed in the gorillas, as Figures 4.1 and 4.2 show. Regarding visitor crowd size, statistically significant chi-squared results have been obtained for Jersey Zoo's gorillas (females, $\chi^2=3.86$, $df=1$, $p<0.05$; silverback, $\chi^2=11.98$, $df=1$, $p<0.001$), with Yates' Correction for Continuity being used for the silverback's data. In both of these cases the data support Prediction 1.1.d, that the presence of a large crowd of visitors is associated with more social affiliative bouts among apes than one would expect.

Under the variable of visitor noisiness, chi-squared results were significant for Howletts' females ($\chi^2=4.44$, $df=1$, $p<0.05$), Howletts' silverback ($\chi^2=8.24$, $df=1$, $p<0.01$, using Yates' Correction for Continuity) and Jersey's silverback ($\chi^2=5.97$, $df=1$, $p<0.05$, again using Yates' Correction). In each of these cases, the presence of noisy visitors is associated with more social affiliative bouts than expected, supporting Prediction 1.1.c.

The Kendall partial rank-order correlation coefficient results were non-significant in each of the cases described above, and so the time of day is not influential here.

Figure 4.1

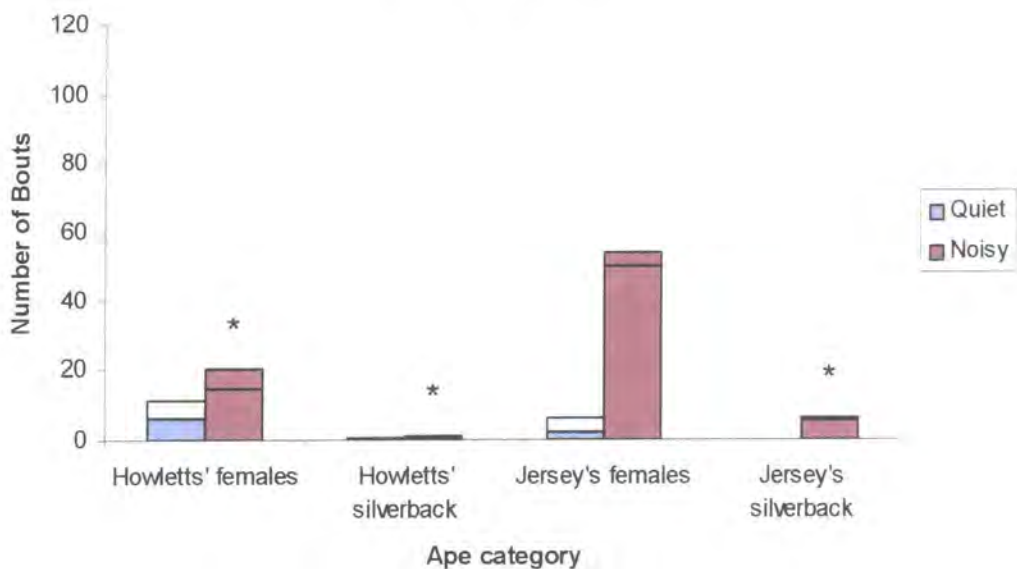
The effect of visitor crowd size on social affiliative behaviour in captive gorillas



Please note that the data presented in these and subsequent graphs are frequencies, not percentages, and therefore visibly perceived differences between zoos and/or age sex classes in the height of the bars are not representative of actual differences between these classes.

Figure 4.2

The effect of visitor noisiness on social affiliative behaviour in captive gorillas



Chimpanzees

The chimpanzees at Chester and Colchester zoos were observed in bouts of social affiliation, as shown in Figures 4.3 and 4.4. Significant chi-squared results have only been obtained for Colchester Zoo's female chimpanzees, who were observed in more bouts of social affiliation than expected when large crowds of visitors were present ($\chi^2=6.36$, $df=1$, $p<0.05$), and when visitors were being noisy ($\chi^2=12.66$, $df=1$, $p<0.001$). These data support Predictions 1.1.c and 1.1.d, that there is an association between the presence of noisy (1.1.c) or large (1.1.d) groups of zoo visitors and more social affiliative bouts than one would expect. These results are independent of the time of day.

Figure 4.3

The effect of visitor crowd size on social affiliative behaviour in captive chimpanzees

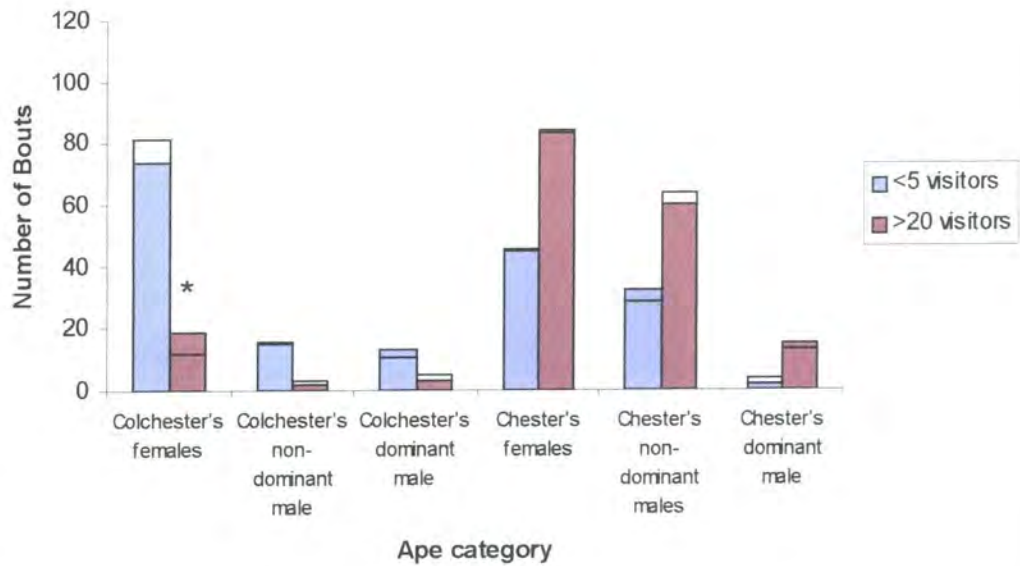
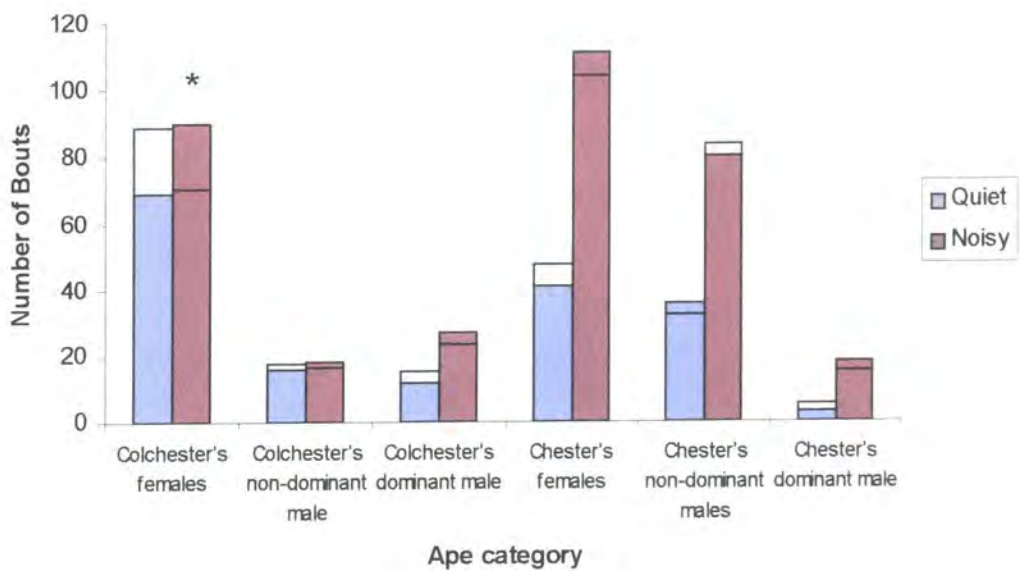


Figure 4.4

The effect of visitor noisiness on social affiliative behaviour in captive chimpanzees



Changes in the number of social aggressive bouts (SOAG)

Gorillas

Social aggressive bouts were absent in the gorillas at both Howletts and Jersey zoos. Therefore there are no data with which to test Predictions 1.2.a-d.

Chimpanzees

Bouts of social aggression in chimpanzees at Chester and Colchester zoos were rare (see Figures 4.5 and 4.6). This type of behaviour was never observed in Colchester Zoo's non-dominant or dominant male chimpanzees. Where bouts of social aggression did occur, they are not associated with the specified zoo visitor conditions. Therefore Predictions 1.2.a-d are not supported by the data.

Figure 4.5

The effect of visitor crowd size on social aggression in captive chimpanzees

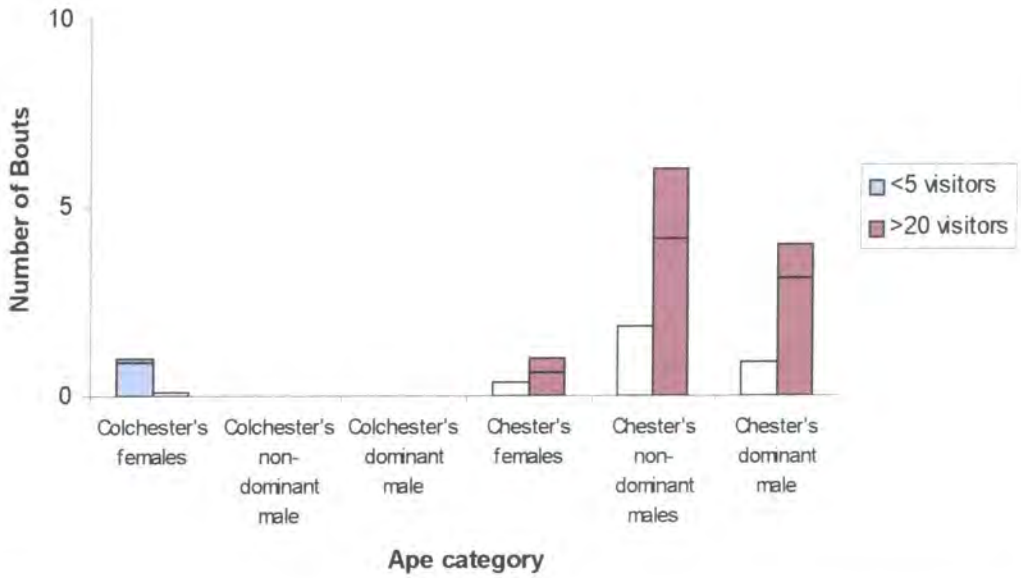
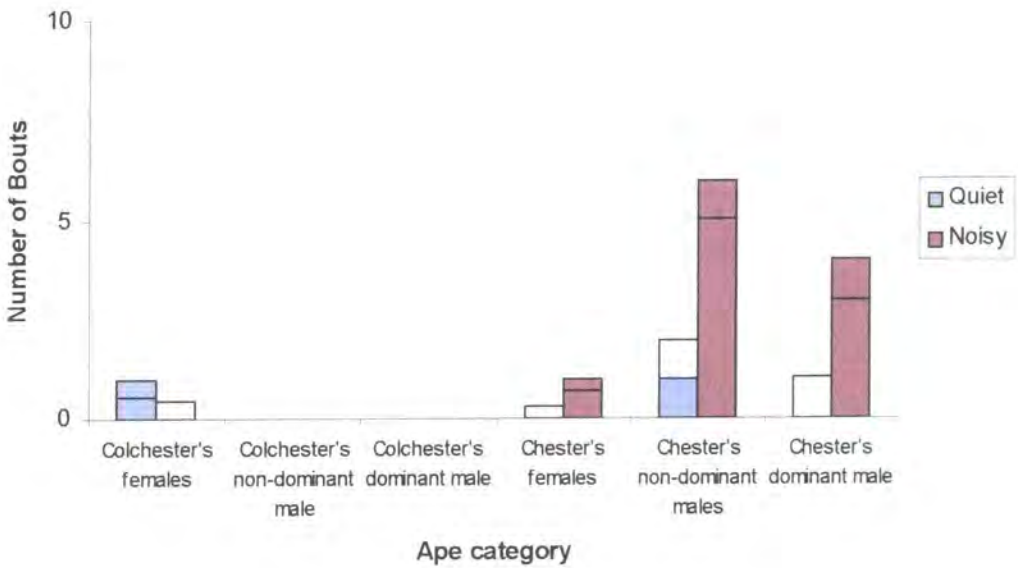


Figure 4.6

The effect of visitor noisiness on social aggression in captive chimpanzees



Changes in the number of bouts of travelling (TRAV)

Gorillas

Gorillas at both Howletts and Jersey zoos were observed in bouts of travelling, but overall these bouts were not very common (see Figures 4.7 and 4.8). There is no evidence of a link between the specified zoo visitor conditions and the number of bouts of travelling in the female gorillas at Howletts and Jersey zoos, or in Howletts' silverback.

Using Yates' Correction for Continuity, the data for Jersey Zoo's silverback gorilla support Predictions 1.3.a, with an association between the presence of a noisy crowd of visitors and an increase in the number of bouts of travelling over that expected ($\chi^2=4.56$, $df=1$, $p<0.05$). There is also an association between the presence of a large crowd of visitors and more bouts of travelling than expected, again using Yates' Correction ($\chi^2=8.98$ $df=1$, $p<0.01$). Thus Prediction 1.3.b is also supported by the data. These results are independent of the time of day.

Figure 4.7

The effect of visitor crowd size on travelling in captive gorillas

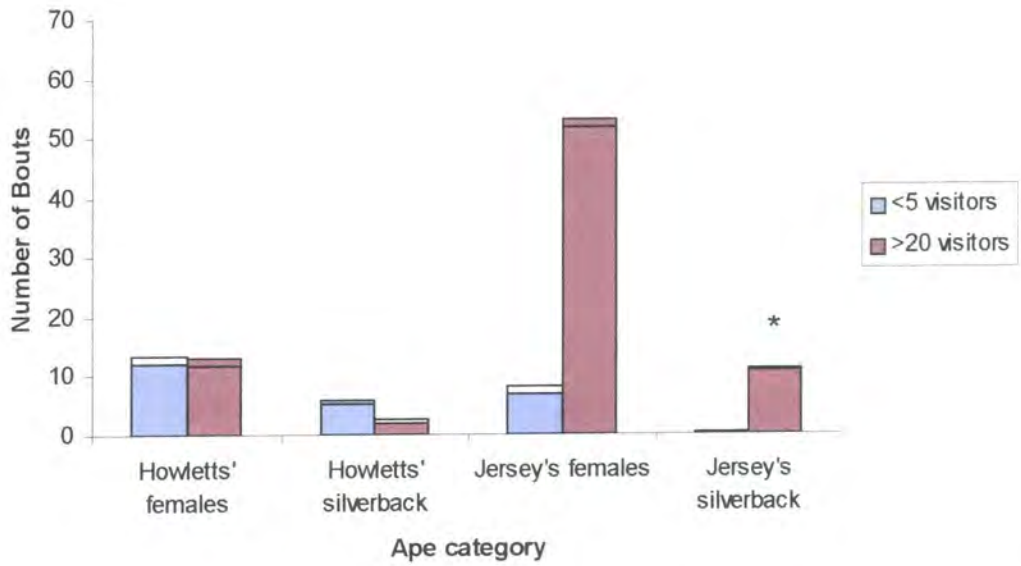
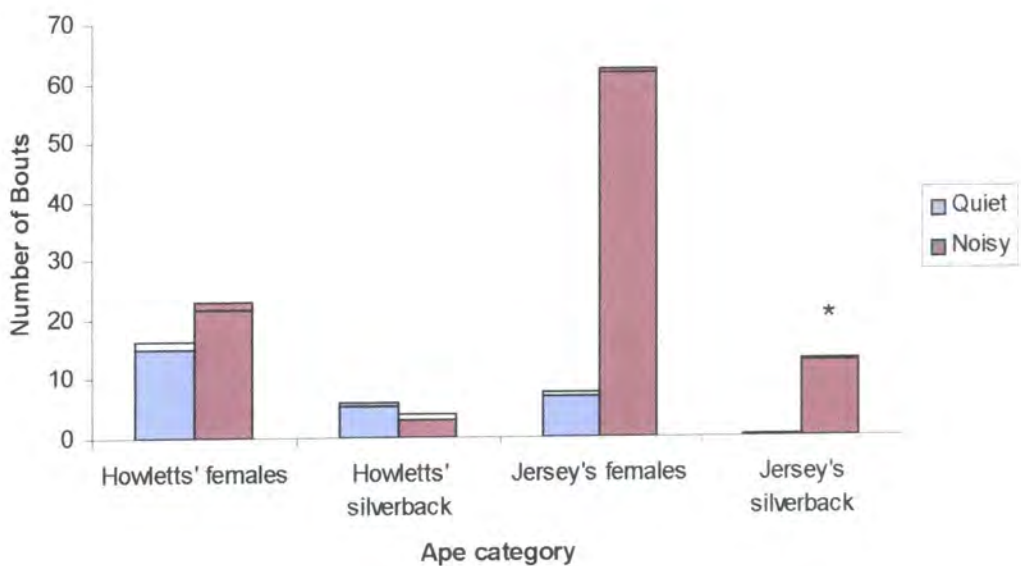


Figure 4.8

The effect of visitor noisiness on travelling in captive gorillas



Chimpanzees

Travelling bouts occurred in all categories of chimpanzee, as the graphs in Figures 4.9 and 4.10 show. There is no evidence of an association between the specified visitor conditions and the number of bouts of travelling observed in Colchester Zoo's chimpanzees and the male chimpanzees at Chester Zoo.

Conversely, Chester Zoo's female chimpanzees performed fewer bouts of travelling than expected in the presence of a large group of visitors, which is highly significant ($\chi^2=22.93$, $df=1$, $p<0.001$). This result is independent of the time of day and so Prediction 1.3.d is supported. There is no evidence of a link between visitor noisiness and bouts of travelling in these females.

Figure 4.9

The effect of visitor crowd size on travelling in captive chimpanzees

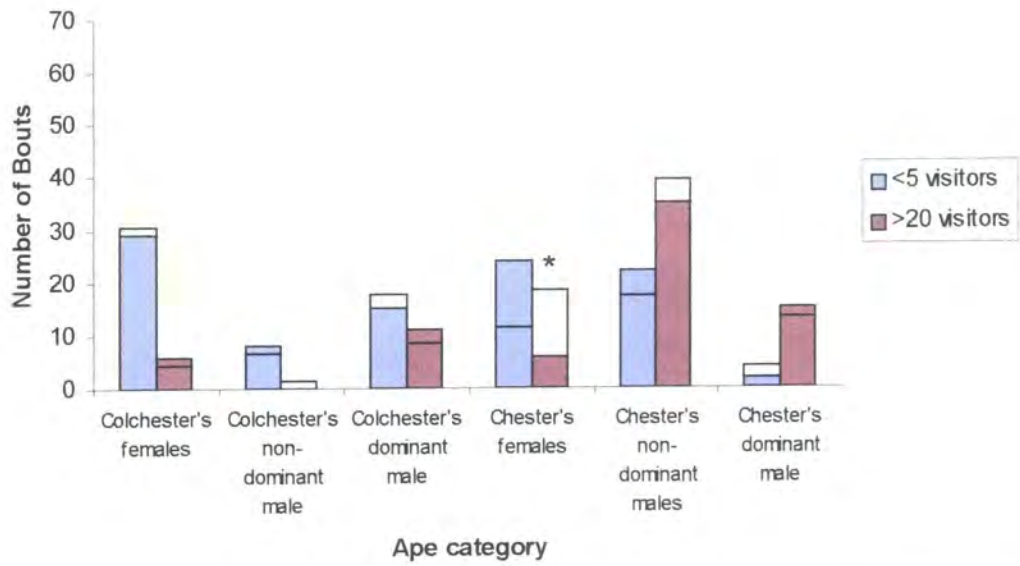
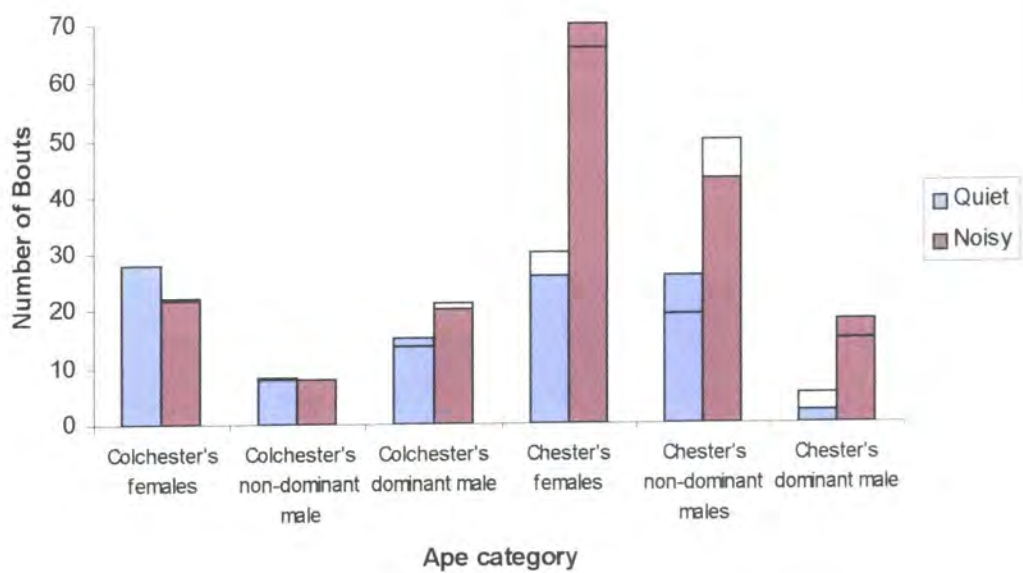


Figure 4.10

The effect of visitor noisiness on travelling in captive chimpanzees



Changes in the number of bouts of resting (REST)

Gorillas

In general, resting was a common behaviour for the gorillas at both Howletts and Jersey zoos, as the graphs in Figures 4.11 and 4.12 show. Under the variable of visitor crowd size, significant results were obtained for the females at both Howletts ($\chi^2=7.97$, $df=1$, $p<0.01$) and Jersey ($\chi^2=6.94$, $df=1$, $p<0.01$) zoos, and also for Jersey's silverback ($\chi^2=5.02$, $df=1$, $p<0.05$, using Yates' Correction). In each of these cases, there is an association between the presence of a large group of visitors and fewer than expected resting bouts observed. These data support Prediction 1.3.b.

In relation to visitor noisiness, a significant chi-squared result has been obtained for Howletts' female gorillas, who were observed in fewer bouts of rest than expected when visitors were being noisy ($\chi^2=7.89$, $df=1$, $p<0.01$). This result supports Prediction 1.3.a (that noisy visitors are associated with fewer resting bouts than one would expect).

Non-significant results were obtained for the Kendall partial rank-order correlation test in each of these cases, and so the time of day has no influence on these results.

Figure 4.11

The effect of visitor crowd size on resting in captive gorillas

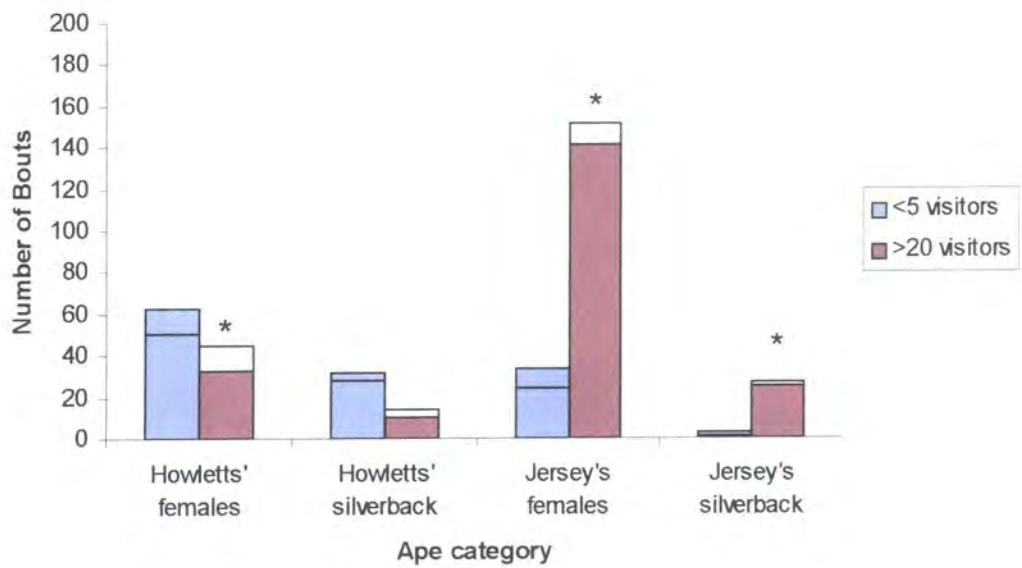
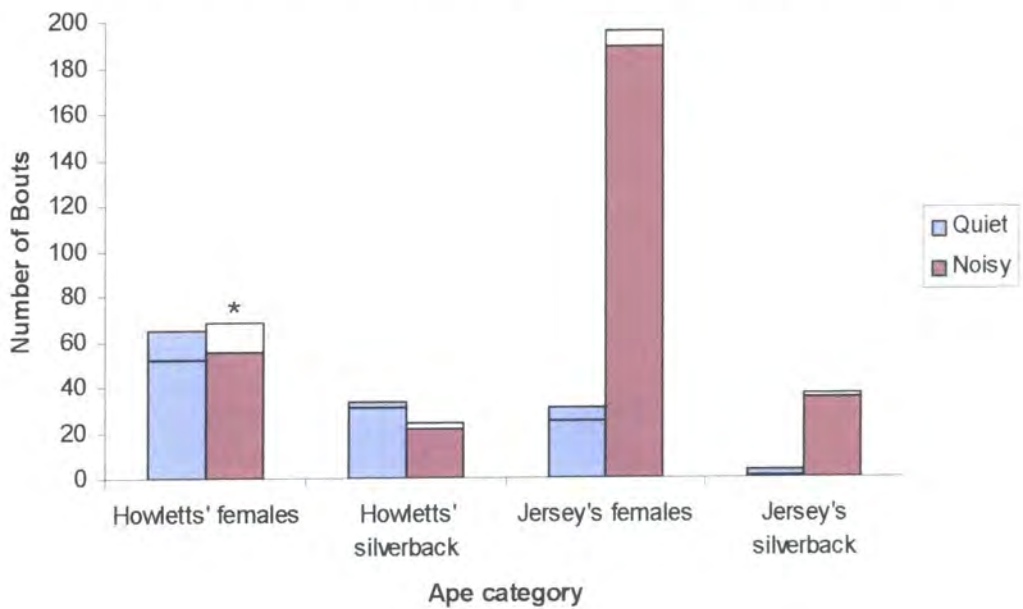


Figure 4.12

The effect of visitor noisiness on resting in captive gorillas



Chimpanzees

On the whole, resting bouts were also commonly observed in chimpanzees at Chester and Colchester zoos, as with gorillas (described above). Overall, the female chimpanzees at Colchester Zoo were observed resting more often than the other chimpanzee categories were (see Figures 4.13 and 4.14).

The data for female chimpanzees at both zoos support Prediction 1.3.b. These females were observed in fewer bouts of rest than expected in the presence of large crowds of visitors (Colchester's females, $\chi^2=6.49$, $df=1$, $p<0.05$; Chester's females, $\chi^2=12.40$, $df=1$, $p<0.001$).

Similarly, the data show that both categories of female chimpanzee were observed in fewer resting bouts than expected when visitors were being noisy (Colchester's females, $\chi^2=18.39$, $df=1$, $p<0.001$; Chester's females, $\chi^2=8.62$, $df=1$, $p<0.01$). These data support Prediction 1.3.a, thus resting bouts are similarly affected by noisy and large groups of visitors in both female gorillas and chimpanzees.

The results of the Kendall partial rank-order correlation tests are non-significant for female chimpanzees at both zoos, and so the time of day does not influence these results.

Figure 4.13

The effect of visitor crowd size on resting in captive chimpanzees

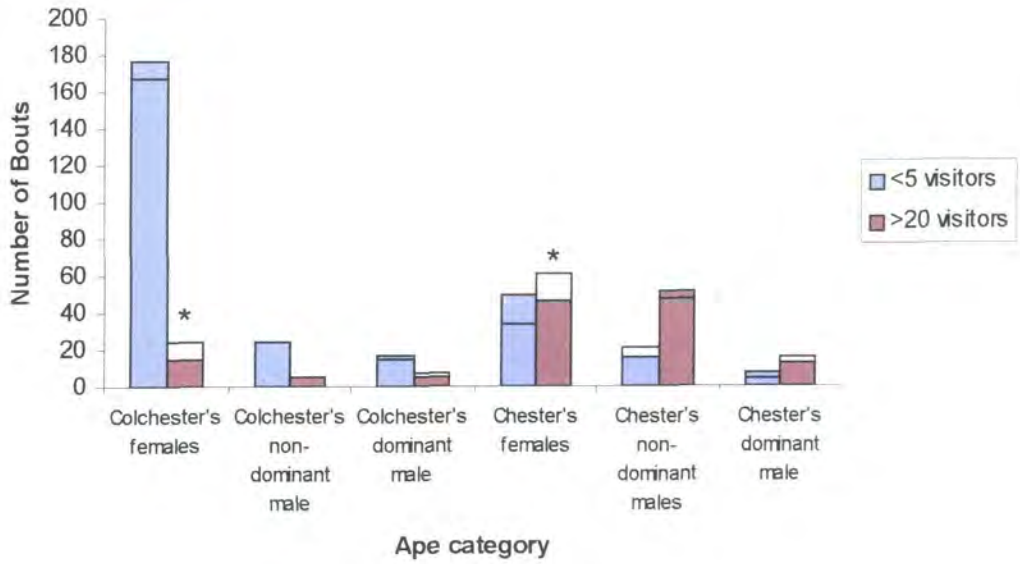
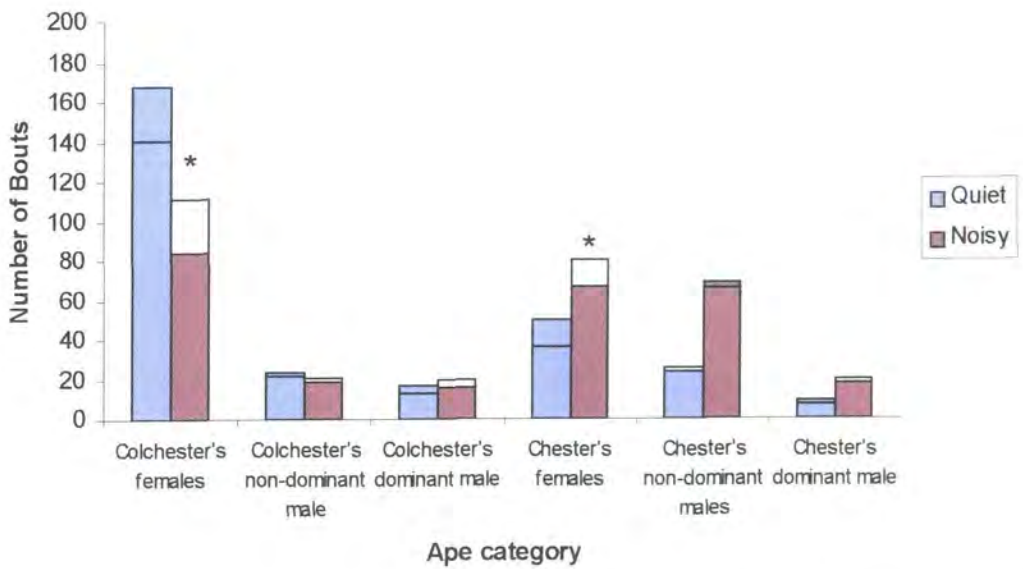


Figure 4.14

The effect of visitor noisiness on resting in captive chimpanzees



Changes in the number of visitor-directed bouts of behaviour (VISD)

Gorillas

All gorillas at Howletts and Jersey zoos were observed performing bouts of visitor-directed behaviour, as the graphs in Figures 4.15 and 4.16 demonstrate. Under the visitor crowd size variable, statistically significant results were obtained in all gorilla categories bar Howletts' silverback.

The data show that there is an association between the presence of a large crowd of visitors and an increase in the number of visitor-directed bouts of behaviour in Howletts' female gorillas, compared with the number expected ($\chi^2=5.52$, $df=1$, $p<0.05$). Jersey Zoo's gorillas followed the same pattern (Jersey's females, $\chi^2=5.96$, $df=1$, $p<0.05$; Jersey's silverback, $\chi^2=8.66$, $df=1$, $p<0.01$, using Yates' Correction). All of the data presented here are independent of the time of day. Therefore the results for these three gorilla categories support Prediction 1.4.b, that there is a link between the presence of a large number of visitors and more visitor-directed bouts by apes than one would expect.

In relation to zoo visitor noisiness, a very similar pattern emerged. Significant chi-squared results were obtained for the same three gorilla categories (Howletts' females, $\chi^2=8.87$, $df=1$, $p<0.01$; Jersey's females, $\chi^2=5.16$, $df=1$, $p<0.05$; Jersey's silverback, $\chi^2=5.42$, $df=1$, $p<0.05$, using Yates' Correction). In each of these cases, there is an association between the presence of noisy visitors and more visitor-directed bouts of behaviour by apes, compared with the number expected. Again, these data are independent of the time of day and so Prediction 1.4.a is supported.

Figure 4.15

The effect of visitor crowd size on visitor-directed behaviour in captive gorillas

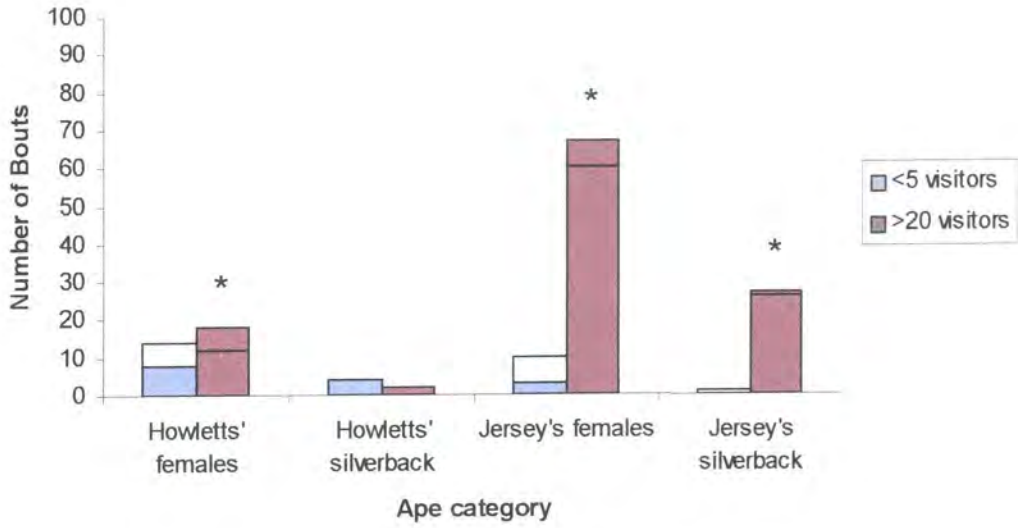
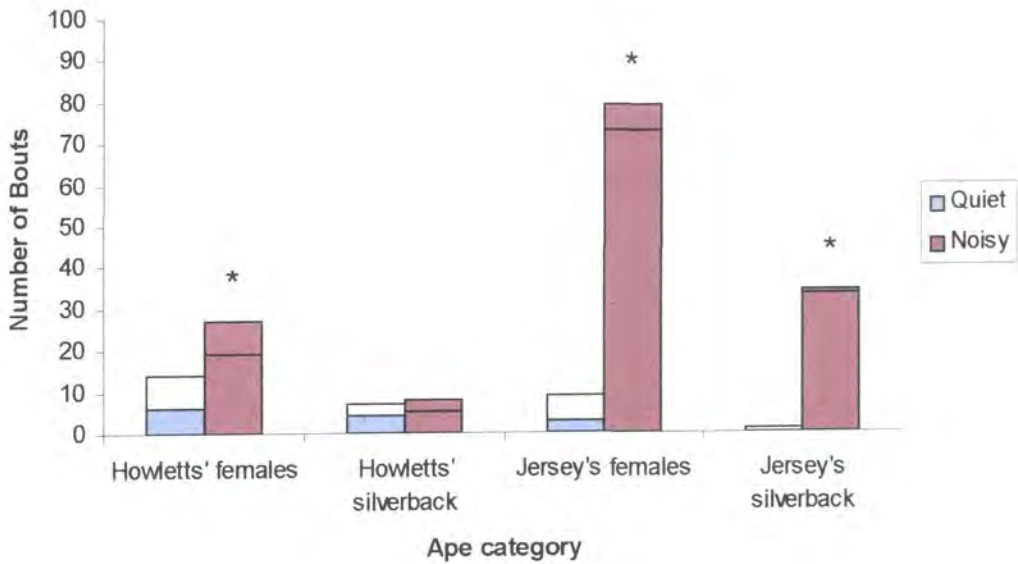


Figure 4.16

The effect of visitor noisiness on visitor-directed behaviour in captive gorillas



Chimpanzees

All chimpanzees were observed in bouts of visitor-directed behaviour, as can be seen in Figures 4.17 and 4.18. There is evidence of an association between large crowds of visitors and more visitor-directed bouts of behaviour than expected in Chester Zoo's female chimpanzees ($\chi^2=12.39$, $df=1$, $p<0.001$). This result is independent of the time day and so Prediction 1.4.b is supported by the data. There is no evidence of such an association in the other chimpanzee categories.

The presence of noisy visitors is also associated with more visitor-directed bouts of behaviour than expected in female chimpanzees at Chester Zoo ($\chi^2=12.86$, $df=1$, $p<0.001$). This result is independent of the time of day and so Prediction 1.4.a is supported by the data.

A significant chi-squared result has been obtained for female chimpanzees at Colchester Zoo ($\chi^2=5.66$, $df=1$, $p<0.05$). These females also engaged in more visitor-directed bouts of behaviour than expected in the presence of noisy zoo visitors (the same pattern as was observed in Chester Zoo's females). However, the Kendall partial correlation is statistically significant in this particular case ($T_{xy.z}=0.67$, $p/2<0.025$). This means that the association between noisy visitors and more visitor-directed bouts of behaviour than expected is also linked to a third variable, the time of day. Consequently, the data do not necessarily support Prediction 1.4.a in this particular case.

Figure 4.17

The effect of visitor crowd size on visitor-directed behaviour in captive chimpanzees

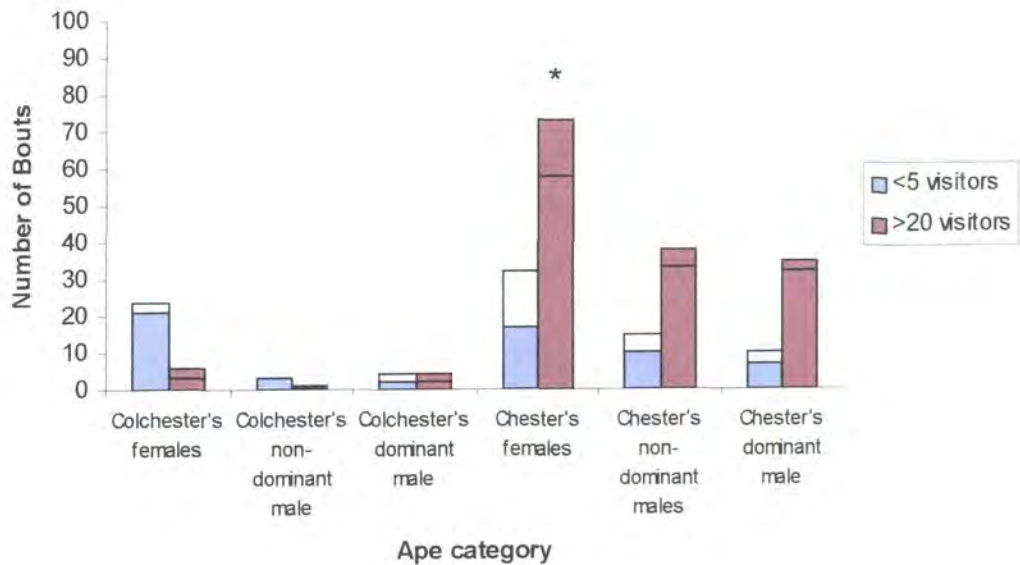
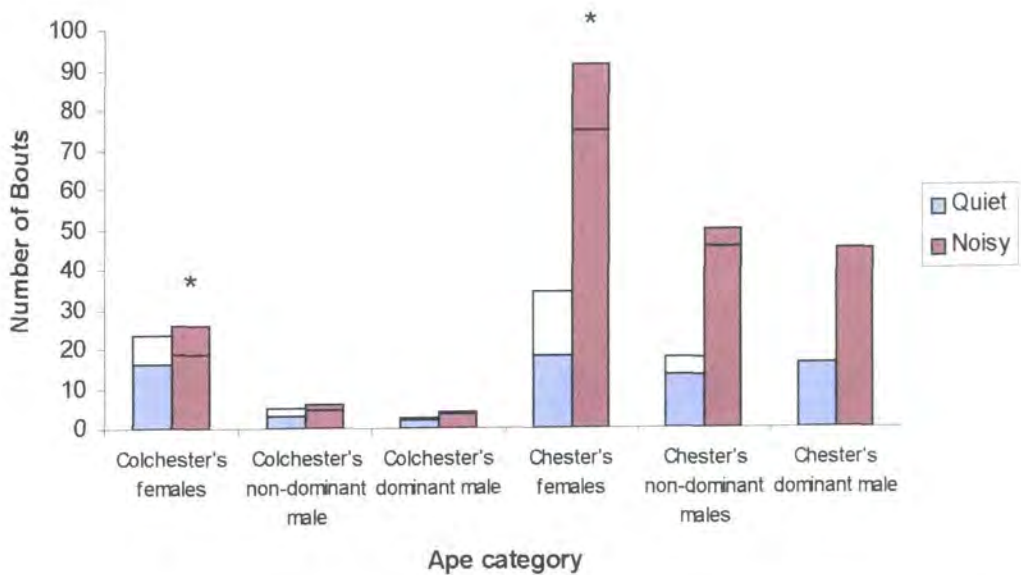


Figure 4.18

The effect of visitor noisiness on visitor-directed behaviour in captive chimpanzees



Changes in the number of bouts of abnormal behaviour (ABNL)

Gorillas

The gorillas at both Howletts and Jersey zoos displayed very few bouts of abnormal behaviour. As Figures 4.19 and 4.20 show, bouts of abnormal behaviour were absent in all silverbacks, and Jersey's females only had one occurrence. These results mean that there are not enough observations of abnormal behaviour to statistically show any relation to either crowd size or noisiness. Therefore, there are insufficient data with which to test Predictions 1.5.a-d for these gorillas.

Howletts' females displayed more bouts of abnormal behaviour than the other gorilla categories overall, but as these were not significantly linked with the specified visitor conditions, Predictions 1.5.a-d are not supported by these data either.

Figure 4.19

The effect of visitor crowd size on abnormal behaviour in captive gorillas

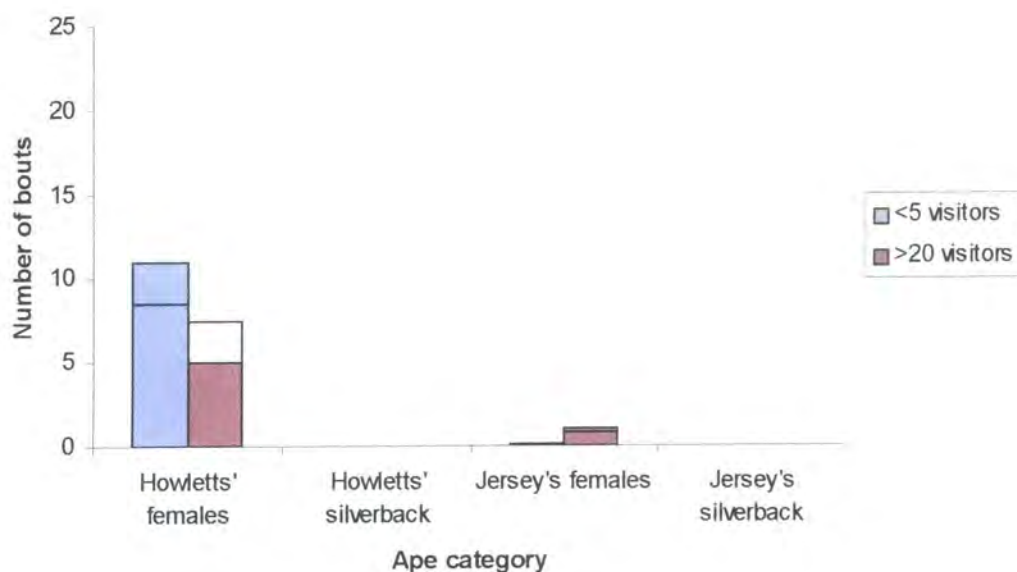
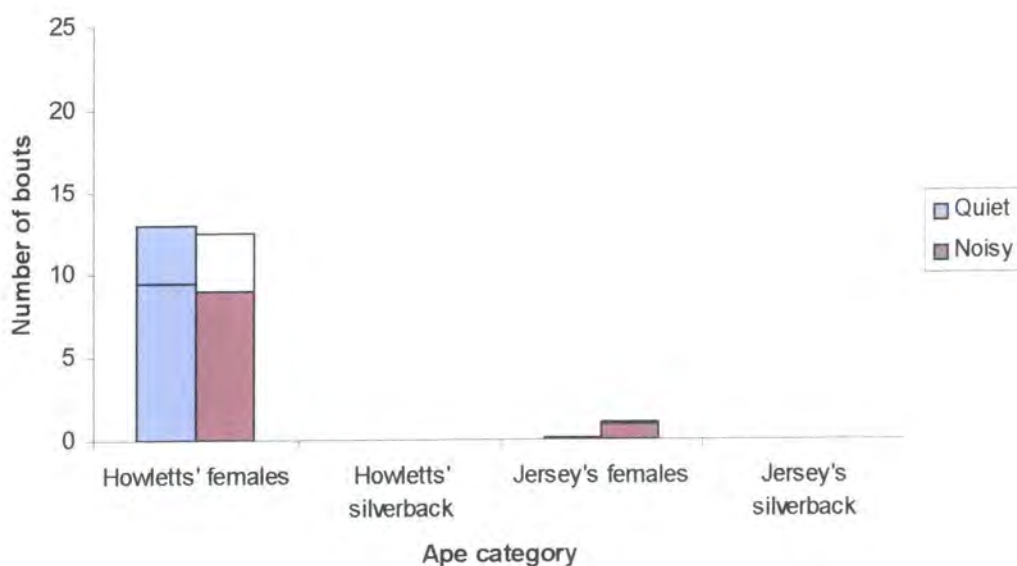


Figure 4.20

The effect of visitor noisiness on abnormal behaviour in captive gorillas



Chimpanzees

As Figures 4.21 and 4.22 show, all chimpanzees were observed performing some bouts of abnormal behaviour. One category of chimpanzee (Chester Zoo's females) did not engage in abnormal behaviour unless large or noisy groups of visitors were present, but the observed number of these bouts was not significantly different than one would expect.

Some statistically significant chi-squared results were obtained for two of the chimpanzee categories. The presence of large groups of zoo visitors is associated with fewer bouts of abnormal behaviour than expected in Chester's Zoo's dominant male ($\chi^2=4.41$, $df=1$, $p<0.05$, using Yates' Correction). Prediction 1.5.d is supported by this result. Noisy visitors did not affect the number of abnormal bouts in Chester's dominant male and so Prediction 1.5.c is not supported by the data.

The opposite was observed in the non-dominant male at Colchester Zoo. In this case, the presence of noisy or large groups of visitors is associated with more bouts of abnormal behaviour than expected (noisiness, $\chi^2=10.80$, $df=1$, $p<0.01$; crowd size, $\chi^2=22.62$, $df=1$, $p<0.001$, using Yates' Correction). These results thus support Predictions 1.5.a and 1.5.b, respectively.

The Kendall partial rank-order correlation coefficients are non-significant and so time of day is not a factor in these cases.

Figure 4.21

The effect of visitor crowd size on abnormal behaviour in captive chimpanzees

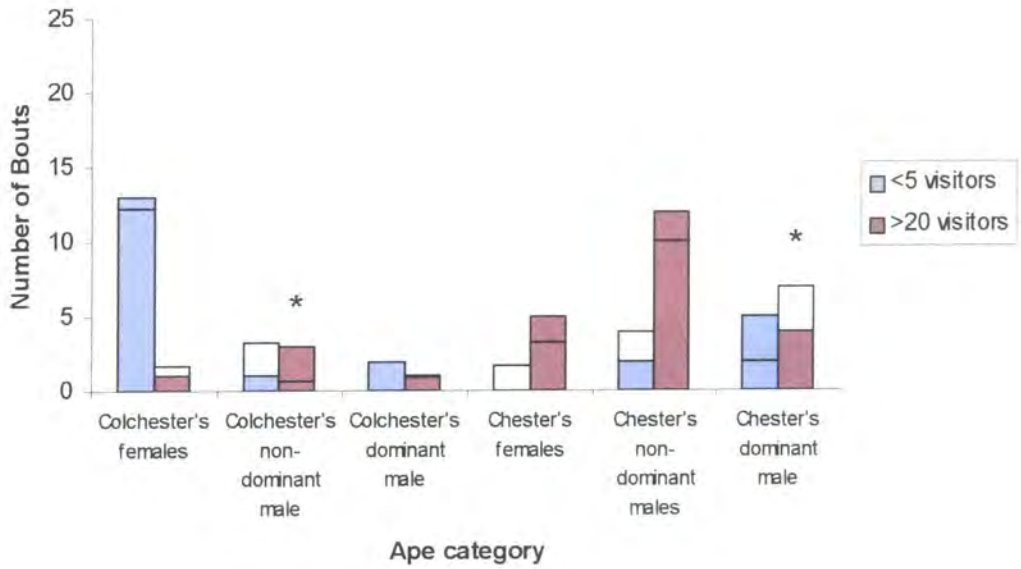
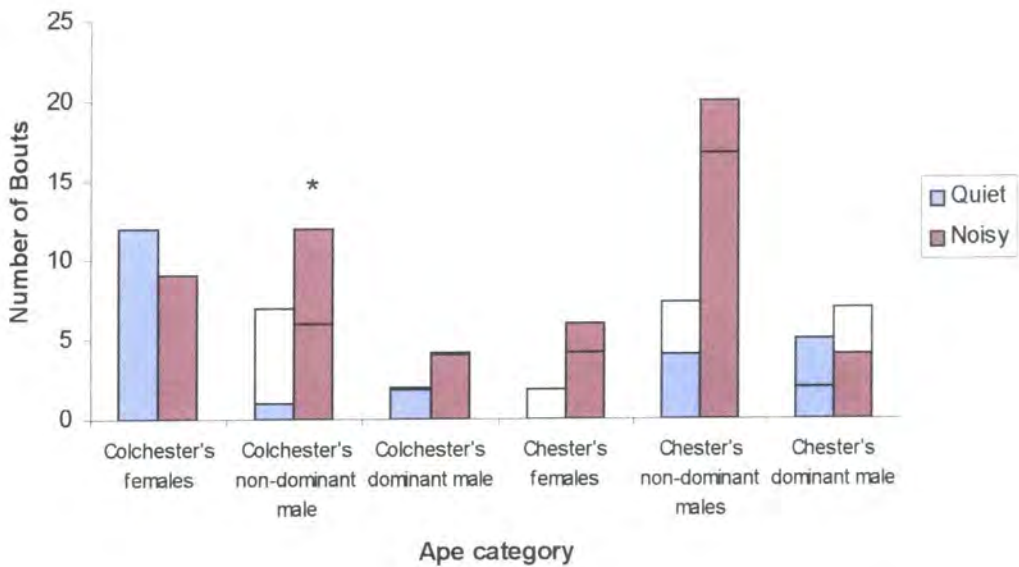


Figure 4.22

The effect of visitor noisiness on abnormal behaviour in captive chimpanzees



Changes in the number of bouts of self-grooming (SGRO)

Gorillas

Bouts of self-grooming were rarely observed among gorillas at Howletts and Jersey zoos, as the graphs in Figures 4.23 and 4.24 show. The presence of small groups of visitors is associated with more self-grooming bouts than expected in Howletts' females ($\chi^2=5.32$, $df=1$, $p<0.05$), which supports Prediction 1.6.d. In contrast, there is an association between large crowds of visitors and more bouts of self-grooming than expected in Jersey's silverback ($\chi^2=50.40$, $df=1$, $p<0.001$, using Yates' Correction).

Jersey's silverback was also observed in more bouts of self-grooming than expected in the presence of noisy zoo visitors ($\chi^2=7.61$, $df=1$, $p<0.01$, using Yates' Correction). These results support Predictions 1.6.b and 1.6.a respectively, that there is an association between the presence of large or noisy groups of zoo visitors and a greater number of self-grooming bouts than expected.

The associations between the specified visitor conditions and self-grooming in Howletts' females and Jersey's silverback occurred independently of the time of day.

Figure 4.23

The effect of visitor crowd size on self-grooming in captive gorillas

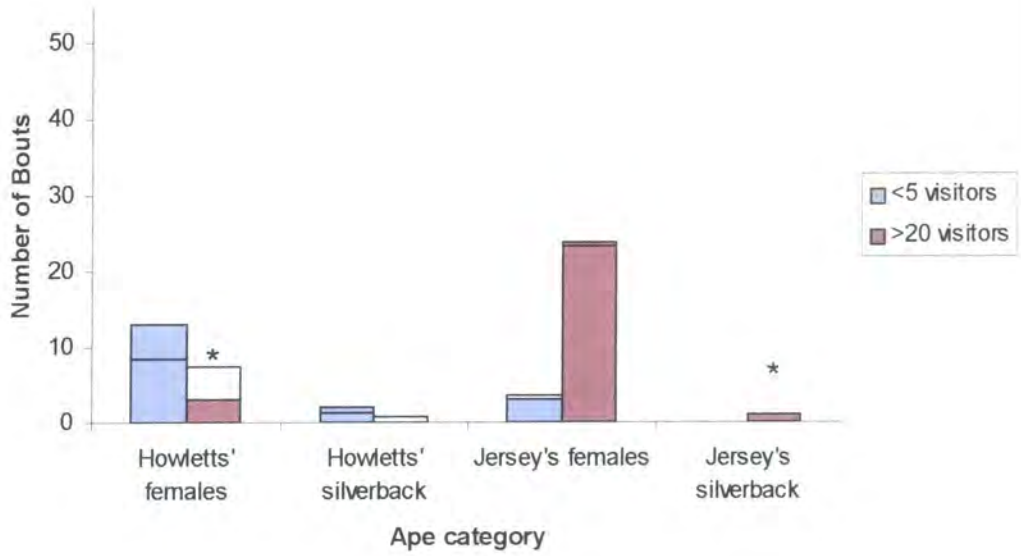
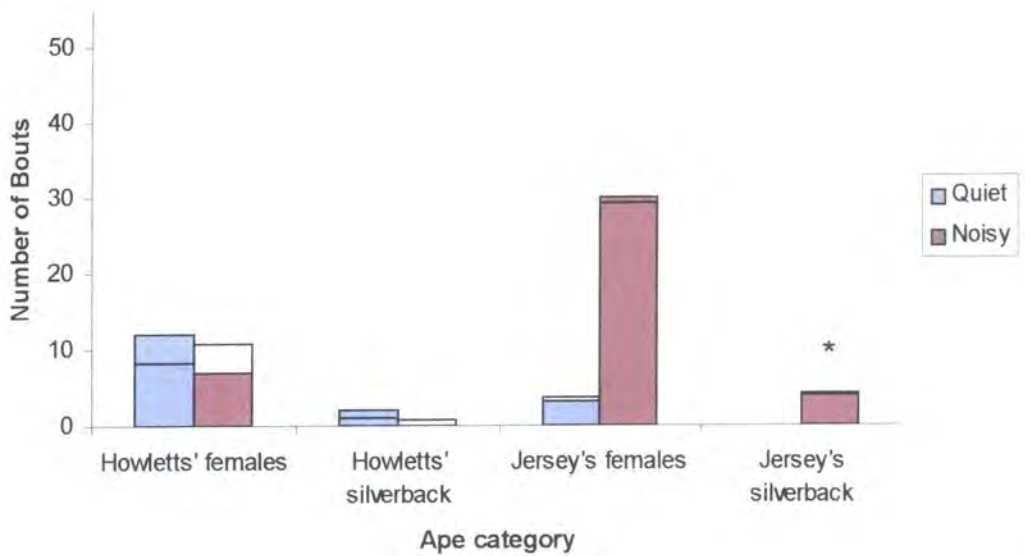


Figure 4.24

The effect of visitor noisiness on self-grooming in captive gorillas



Chimpanzees

All chimpanzees were observed in some bouts of self-grooming (see Figures 4.25 and 4.26). A statistically significant chi-squared result was obtained for Colchester Zoo's non-dominant male, in relation to the visitor crowd size variable. There is an association between the presence of large crowds of zoo visitors and more self-grooming bouts than expected in this chimpanzee ($\chi^2=8.41$, $df=1$, $p<0.01$). The results of the Kendall partial correlation tests show that time of day was not a factor in this case. Therefore Prediction 1.6.b (that there is an association between the presence of large crowds of visitors and more self-grooming bouts) is supported by the data for this chimpanzee category.

The numbers of self-grooming bouts among chimpanzees were not significantly affected by visitor noisiness, and so Predictions 1.6.a and 1.6.c are not supported by the data.

Figure 4.25

The effect of visitor crowd size on self-grooming in captive chimpanzees

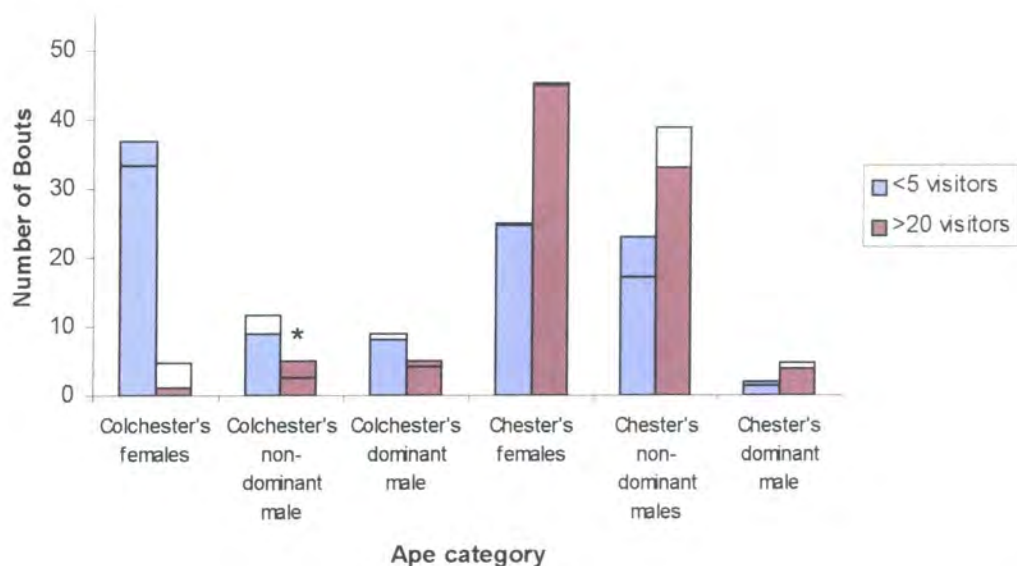
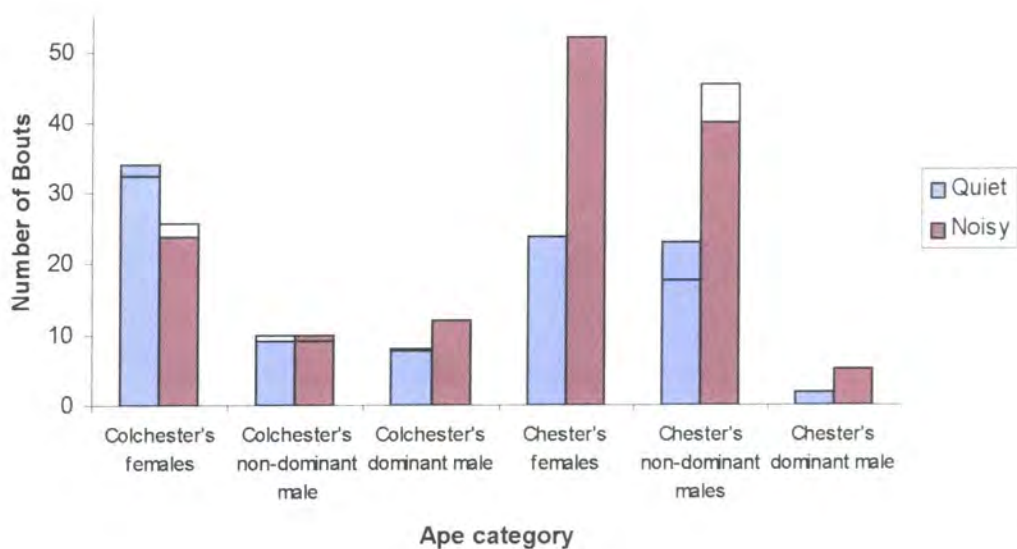


Figure 4.26

The effect of visitor noisiness on self-grooming in captive chimpanzees



Changes in the number of behavioural bouts observed at the front of the enclosure (i.e. nearest to the visitors' viewing area)

Gorillas

Gorillas at both Howletts and Jersey zoos were observed for more bouts at the front of the enclosure than they were at the back of the enclosure (see Figures 4.27 and 4.28). This means that they performed more of their daily activities in the areas of the enclosure nearest to the visitors' viewing areas, i.e. in relatively close proximity to the zoo visitors. The data for Jersey Zoo's gorillas and Howletts' silverback do not demonstrate a significant link between the visitor conditions and the number of bouts observed at the front of the enclosure. Therefore the data for these three gorilla categories do not support Predictions 2.1.a-d (i.e. there is no association between the presence of large or noisy crowds of visitors and a significant change in the number of bouts observed at the front of the enclosure).

In contrast, the chi-squared results for Howletts' female gorillas were statistically significant. When noisy zoo visitors were present, these females were observed for fewer bouts than expected at the front of the enclosure ($\chi^2=4.27$, $df=1$, $p<0.05$). Likewise, these females performed fewer bouts at the front of the enclosure than expected in the presence of a large group of visitors ($\chi^2=8.75$, $df=1$, $p<0.01$). These results are independent of the time of day, so Predictions 2.1.a and 2.1.b are supported (i.e. the presence of noisy or large groups of visitors is associated with fewer than expected bouts at the front of the enclosure).

Figure 4.27

The effect of visitor crowd size on behavioural bouts observed at the front of the enclosure in captive gorillas

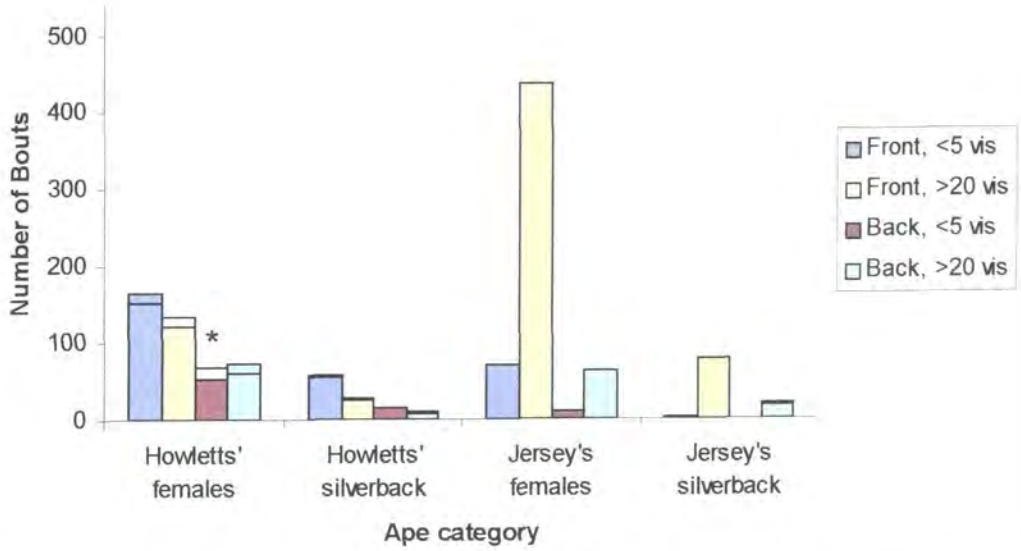
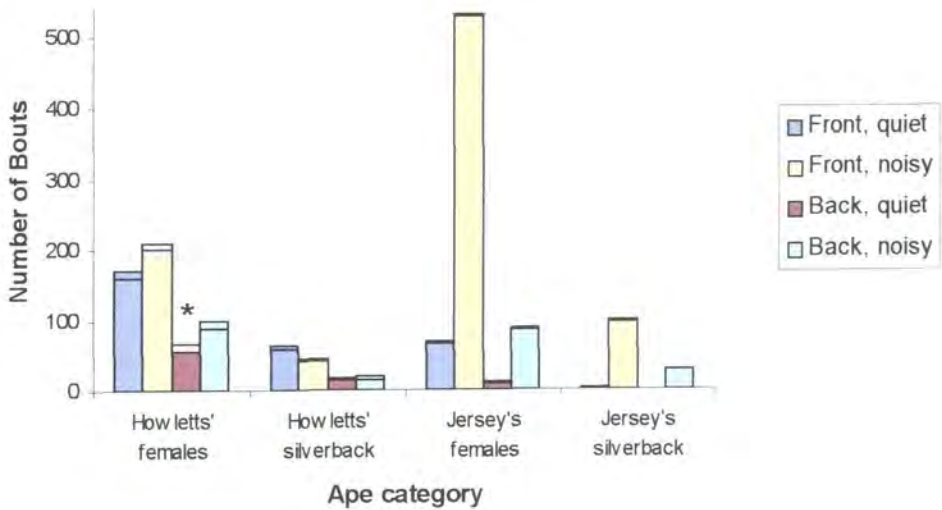


Figure 4.28

The effect of visitor noisiness on behavioural bouts observed at the front of the enclosure in captive gorillas



Chimpanzees

On the whole, Colchester Zoo's chimpanzees were observed in more bouts at the front of the enclosure in relation to visitor crowd size, but more bouts at the back of the enclosure in relation to visitor noisiness (see Figures 4.29 and 4.30).

Chester Zoo's chimpanzees were generally observed in more bouts at the back of the enclosure, under both of the visitor variables.

The only statistically significant chi-squared results obtained were for Chester Zoo's non-dominant male chimpanzees. When visitors were being noisy or were in large groups these apes were observed for fewer bouts at the front of the enclosure than was expected (noisiness, $\chi^2=34.00$, $df=1$, $p<0.001$; crowd size, $\chi^2=21.80$, $df=1$, $p<0.001$). These data are independent of time of day, so Predictions 2.1.a and 2.1.b are supported for this chimpanzee category (that noisy or large groups of visitors are associated with fewer than expected bouts at the front of the enclosure).

The data for the other five chimpanzee categories do not show an association between the visitor conditions and proximity to visitors.

Figure 4.29

The effect of visitor crowd size on behavioural bouts observed at the front of the enclosure in captive chimpanzees

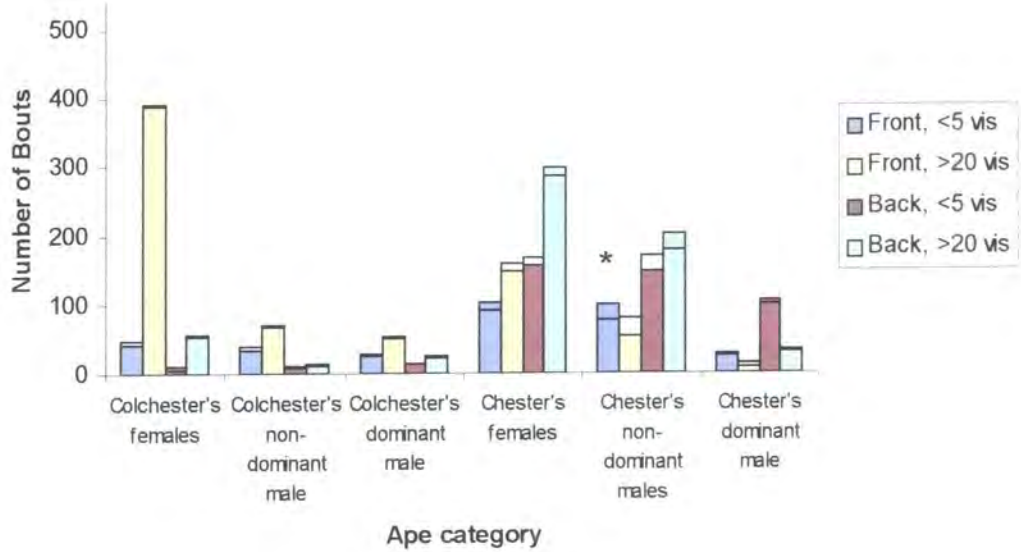
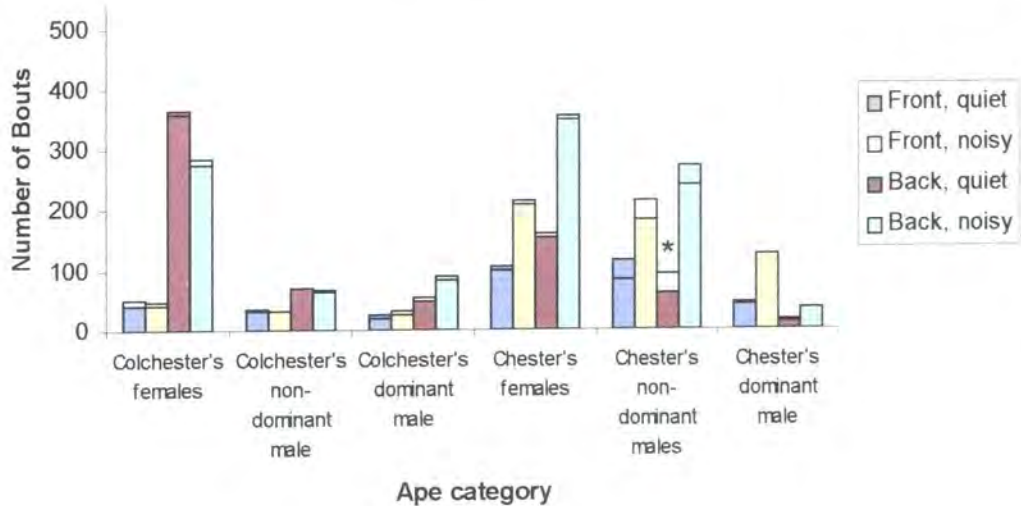


Figure 4.30

The effect of visitor noisiness on behavioural bouts observed at the front of the enclosure in captive chimpanzees



Changes in the number of behavioural bouts observed at ground level (i.e. at the same level as the visitors)

Gorillas

As the graphs in Figures 4.31 and 4.32 show, gorillas at both Howletts and Jersey zoos were observed for more bouts when located on the ground than when they were off the ground. Jersey's silverback gorilla was never observed in bouts above ground level and Jersey's females were observed above ground level only twice. Howletts' gorillas were observed above ground level more often.

None of the chi-squared results for gorillas were statistically significant, under any of the specified zoo visitor conditions. These results mean that there is no evidence of a relationship between zoo visitor conditions and the observed number of bouts when gorillas were at ground level, compared with that expected. Thus Predictions 2.2.a-d are not supported by the gorilla data.

Figure 4.31

The effect of visitor crowd size on behavioural bouts observed at ground level in captive gorillas

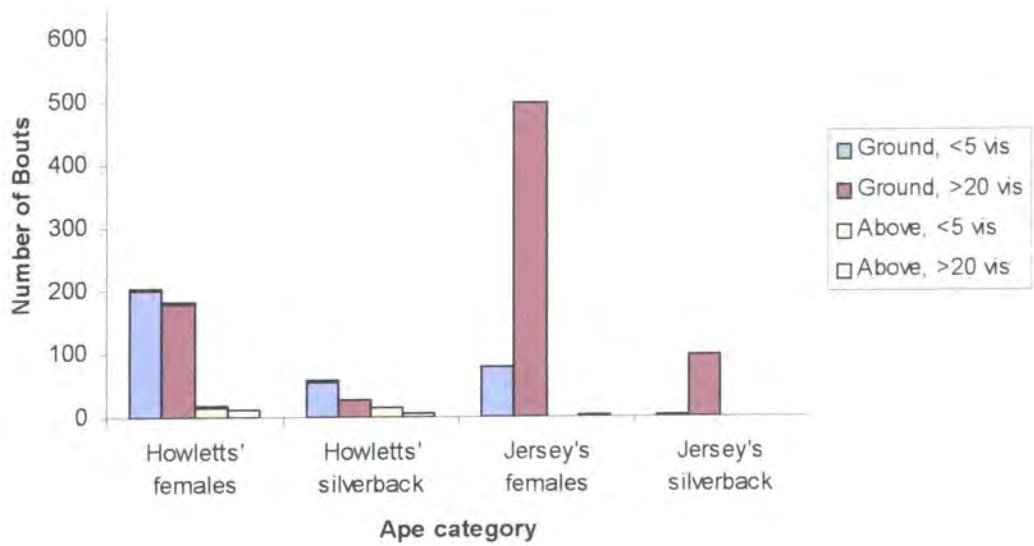
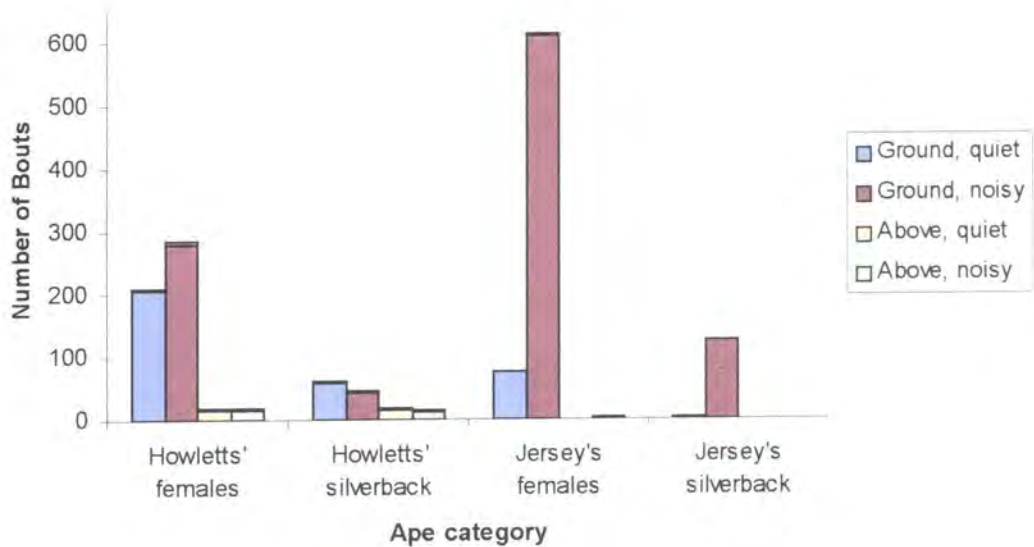


Figure 4.32

The effect of visitor noisiness on behavioural bouts observed at ground level in captive gorillas



Chimpanzees

Results obtained for chimpanzees are shown in Figures 4.33 and 4.34. Under the condition of visitor crowd size, significant chi-squared results were obtained for Colchester Zoo's non-dominant male chimpanzee, and Chester Zoo's females and non-dominant males. In the other three chimpanzee categories there is no evidence of an association between crowd size and the number of observations at ground level compared with that expected.

In Colchester Zoo's non-dominant male there is an association between the presence of a large group of visitors and an increase (over that expected) in the number of bouts observed at ground level ($\chi^2=4.49$ $df=1$, $p<0.05$). This result is independent of the time of day and thus supports Prediction 2.2.d.

Chester Zoo's female and non-dominant male chimpanzees behaved in the same way as each other. The data for these apes support Prediction 2.2.b, that there is an association between the presence of a large crowd of visitors and fewer than expected observations at ground level (females, $\chi^2=20.35$, $df=1$, $p<0.001$; non-dominant males, $\chi^2=42.03$, $df=1$, $p<0.001$). The data for these two ape classes support Prediction 2.2.a, that there is an association between the presence of noisy zoo visitors and fewer than expected observations at ground level (females, $\chi^2=12.95$, $df=1$, $p<0.001$; non-dominant males, $\chi^2=50.37$, $df=1$, $p<0.001$). The results discussed above are independent of the time of day.

Figure 4.33

The effect of visitor crowd size on behavioural bouts observed at ground level in captive chimpanzees

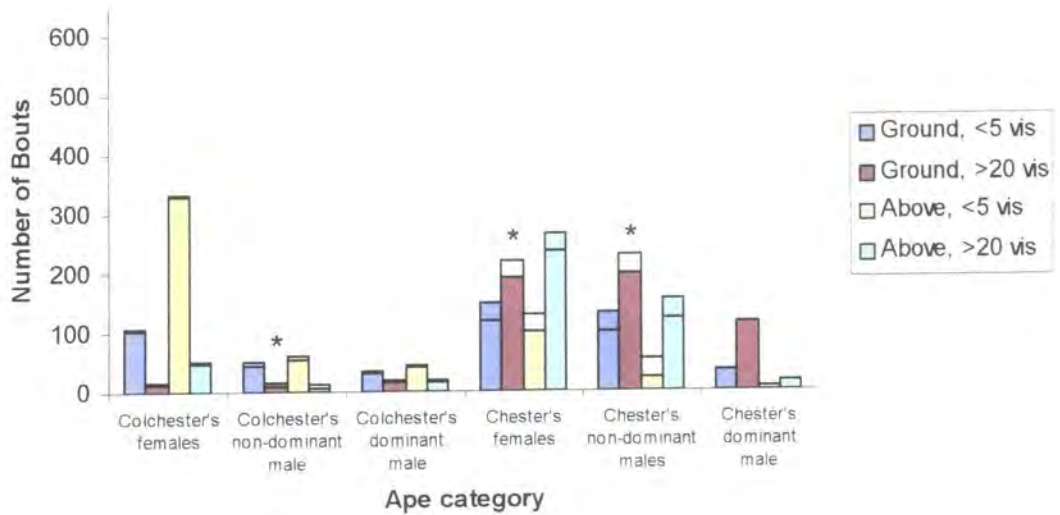
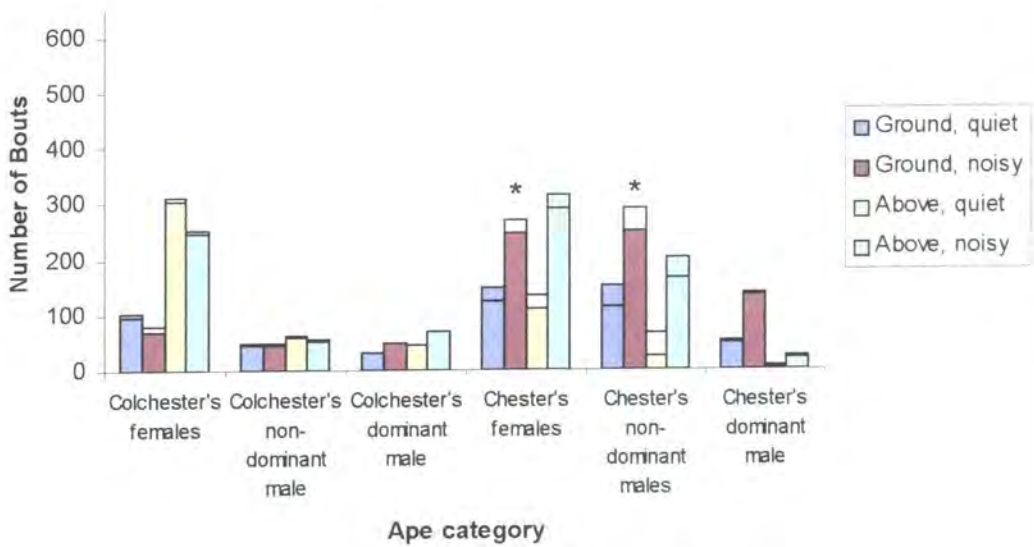


Figure 4.34

The effect of visitor noisiness on behavioural bouts observed at ground level in captive chimpanzees



Summary of results

A summary of the results for each ape category is given in Tables 4.1-4.3 below. In each of these tables, the predictions that I have tested in this study are listed, along with information as to whether or not the data support these predictions. It can be seen that the presence of noisy or large groups of zoo visitors affects ape behaviour differently than quiet or small groups, as was hypothesised in Hypothesis 1. It can also be seen that the apes' spatial use of their enclosures is affected by the zoo visitor conditions, as hypothesised in Hypothesis 2. The results indicate that apes show various responses to visitors, with certain types of behaviour being affected in some species, age and sex classes, and not in others.

Table 4.1. A summary of the data obtained for gorillas at Howletts and Jersey zoos.

PREDICTION		Howletts' females	Howletts' silverback	Jersey's females	Jersey's silverback
There is an association between the:					
Presence of noisy visitors and fewer than expected bouts of SOAF (1.1.a)		0	0	0	0
Presence of large groups of visitors and fewer than expected bouts of SOAF (1.1.b)		0	-	0	0
Presence of noisy visitors and more than expected bouts of SOAF (1.1.c)		Y	Y	0	Y
Presence of large groups of visitors and more than expected bouts of SOAF (1.1.d)		0	-	Y	Y
Presence of noisy visitors and more than expected bouts of SOAG (1.2.a)		-	-	-	-
Presence of large groups of visitors and more than expected bouts of SOAG (1.2.b)		-	-	-	-
Presence of noisy visitors and fewer than expected bouts of SOAG (1.2.c)		-	-	-	-
Presence of large groups of visitors and fewer than expected bouts of SOAG (1.2.d)		-	-	-	-
Presence of noisy visitors and more than expected bouts of TRAV (1.3.a)		0	0	0	Y
Presence of large groups of visitors and more than expected bouts of TRAV (1.3.b)		0	0	0	Y
Presence of noisy visitors and fewer than expected bouts of TRAV (1.3.c)		0	0	0	0
Presence of large groups of visitors and fewer than expected bouts of TRAV (1.3.d)		0	0	0	0
Presence of noisy visitors and fewer than expected bouts of REST (1.3.a)		Y	0	0	0
Presence of large groups of visitors and fewer than expected bouts of REST (1.3.b)		Y	0	Y	Y
Presence of noisy visitors and more than expected bouts of REST (1.3.c)		0	0	0	0
Presence of large groups of visitors and more than expected bouts of REST (1.3.d)		0	0	0	0

- = no data available, 0 = prediction not supported by data, Y = prediction supported by data

Table 4.1 (continued). A summary of the data obtained for gorillas at Howletts and Jersey zoos.

PREDICTION		Howletts' females	Howletts' silverback	Jersey's females	Jersey's silverback
There is an association between the:					
Presence of noisy visitors and more than expected bouts of VISD (1.4.a)		Y	0	Y	Y
Presence of large groups of visitors and more than expected bouts of VISD (1.4.b)		Y	0	Y	Y
Presence of noisy visitors and more than expected bouts of ABNL (1.5.a)		0	-	0	-
Presence of large groups of visitors and more than expected bouts of ABNL (1.5.b)		0	-	0	-
Presence of quiet visitors and more than expected bouts of ABNL (1.5.c)		0	-	0	-
Presence of small groups of visitors and more than expected bouts of ABNL (1.5.d)		0	-	0	-
Presence of noisy visitors and more than expected bouts of SGRO (1.6.a)		0	0	0	Y
Presence of large groups of visitors and more than expected bouts of SGRO (1.6.b)		0	0	0	Y
Presence of quiet visitors and more than expected bouts of SGRO (1.6.c)		0	0	0	0
Presence of small groups of visitors and more than expected bouts of SGRO (1.6.d)		Y	0	0	0
Presence of noisy visitors and fewer than expected bouts observed at front of enclosure (2.1.a)		Y	0	0	0
Presence of large groups of visitors and fewer than expected bouts observed at front of enclosure (2.1.b)		Y	0	0	0
Presence of noisy visitors and more than expected bouts observed at front of enclosure (2.1.c)		0	0	0	0
Presence of large groups of visitors and more than expected bouts observed at front of enclosure (2.1.d)		0	0	0	0
Presence of noisy visitors and fewer than expected bouts observed at ground level (2.2.a)		0	0	0	-
Presence of large groups of visitors and fewer than expected bouts observed at ground level (2.2.b)		0	0	0	-
Presence of noisy visitors and more than expected bouts observed at ground level (2.2.c)		0	0	0	-
Presence of large groups of visitors and more than expected bouts observed at ground level (2.2.d)		0	0	0	-

- = no data available, 0 = prediction not supported by data, Y = prediction supported by data

Table 4.2. A summary of the data obtained for Chester Zoo's chimpanzees.

PREDICTION	Chester's		
	females	non-dominant males	dominant male
There is an association between the:			
Presence of noisy visitors and fewer than expected bouts of SOAF (1.1.a)	0	0	0
Presence of large groups of visitors and fewer than expected bouts of SOAF (1.1.b)	0	0	0
Presence of noisy visitors and more than expected bouts of SOAF (1.1.c)	0	0	0
Presence of large groups of visitors and more than expected bouts of SOAF (1.1.d)	0	0	0
Presence of noisy visitors and more than expected bouts of SOAG (1.2.a)	0	0	0
Presence of large groups of visitors and more than expected bouts of SOAG (1.2.b)	0	0	0
Presence of noisy visitors and fewer than expected bouts of SOAG (1.2.c)	0	0	0
Presence of large groups of visitors and fewer than expected bouts of SOAG (1.2.d)	0	0	0
Presence of noisy visitors and more than expected bouts of TRAV (1.3.a)	0	0	0
Presence of large groups of visitors and more than expected bouts of TRAV (1.3.b)	0	0	0
Presence of noisy visitors and fewer than expected bouts of TRAV (1.3.c)	0	0	0
Presence of large groups of visitors and fewer than expected bouts of TRAV (1.3.d)	Y	0	0
Presence of noisy visitors and fewer than expected bouts of REST (1.3.a)	Y	0	0
Presence of large groups of visitors and fewer than expected bouts of REST (1.3.b)	Y	0	0
Presence of noisy visitors and more than expected bouts of REST (1.3.c)	0	0	0
Presence of large groups of visitors and more than expected bouts of REST (1.3.d)	0	0	0
Presence of noisy visitors and more than expected bouts of VISD (1.4.a)	Y	0	0
Presence of large groups of visitors and more than expected bouts of VISD (1.4.b)	Y	0	0

- = no data available, 0 = prediction not supported by data, Y = prediction supported by data

Table 4.2 (continued). A summary of the data obtained for Chester Zoo's chimpanzees.

PREDICTION	Chester's		
	females	non-dominant males	dominant male
There is an association between the:			
Presence of noisy visitors and more than expected bouts of ABNL (1.5.a)	0	0	0
Presence of large groups of visitors and more than expected bouts of ABNL (1.5.b)	0	0	0
Presence of quiet visitors and more than expected bouts of ABNL (1.5.c)	0	0	0
Presence of small groups of visitors and more than expected bouts of ABNL (1.5.d)	0	0	Y
Presence of noisy visitors and more than expected bouts of SGRO (1.6.a)	0	0	0
Presence of large groups of visitors and more than expected bouts of SGRO (1.6.b)	0	0	0
Presence of quiet visitors and more than expected bouts of SGRO (1.6.c)	0	0	0
Presence of small groups of visitors and more than expected bouts of SGRO (1.6.d)	0	0	0
Presence of noisy visitors and fewer than expected bouts observed at front of enclosure (2.1.a)	0	Y	0
Presence of large groups of visitors and fewer than expected bouts observed at front of enclosure (2.1.b)	0	Y	0
Presence of noisy visitors and more than expected bouts observed at front of enclosure (2.1.c)	0	0	0
Presence of large groups of visitors and more than expected bouts observed at front of enclosure (2.1.d)	0	0	0
Presence of noisy visitors and fewer than expected bouts observed at ground level (2.2.a)	Y	Y	0
Presence of large groups of visitors and fewer than expected bouts observed at ground level (2.2.b)	Y	Y	0
Presence of noisy visitors and more than expected bouts observed at ground level (2.2.c)	0	0	0
Presence of large groups of visitors and more than expected bouts observed at ground level (2.2.d)	0	0	0

- = no data available, 0 = prediction not supported by data, Y = prediction supported by data

Table 4.3. A summary of the data obtained for Colchester Zoo's chimpanzees.

PREDICTION	Colchester's females	Colchester's non-dominant male	Colchester's dominant male
There is an association between the:			
Presence of noisy visitors and fewer than expected bouts of SOAF (1.1.a)	0	0	0
Presence of large groups of visitors and fewer than expected bouts of SOAF (1.1.b)	0	0	0
Presence of noisy visitors and more than expected bouts of SOAF (1.1.c)	Y	0	0
Presence of large groups of visitors and more than expected bouts of SOAF (1.1.d)	Y	0	0
Presence of noisy visitors and more than expected bouts of SOAG (1.2.a)	0	-	-
Presence of large groups of visitors and more than expected bouts of SOAG (1.2.b)	0	-	-
Presence of noisy visitors and fewer than expected bouts of SOAG (1.2.c)	0	-	-
Presence of large groups of visitors and fewer than expected bouts of SOAG (1.2.d)	0	-	-
Presence of noisy visitors and more than expected bouts of TRAV (1.3.a)	0	0	0
Presence of large groups of visitors and more than expected bouts of TRAV (1.3.b)	0	0	0
Presence of noisy visitors and fewer than expected bouts of TRAV (1.3.c)	0	0	0
Presence of large groups of visitors and fewer than expected bouts of TRAV (1.3.d)	0	0	0
Presence of noisy visitors and fewer than expected bouts of REST (1.3.a)	Y	0	0
Presence of large groups of visitors and fewer than expected bouts of REST (1.3.b)	Y	0	0
Presence of noisy visitors and more than expected bouts of REST (1.3.c)	0	0	0
Presence of large groups of visitors and more than expected bouts of REST (1.3.d)	0	0	0
Presence of noisy visitors and more than expected bouts of VISD (1.4.a)	Y	0	0
Presence of large groups of visitors and more than expected bouts of VISD (1.4.b)	0	0	0

- = no data available, 0 = prediction not supported by data, Y = prediction supported by data

Table 4.3 (continued). A summary of the data obtained for Colchester Zoo's chimpanzees.

PREDICTION		Colchester's females	Colchester's non-dominant male	Colchester's dominant male
There is an association between the:				
Presence of noisy visitors and more than expected bouts of ABNL (1.5.a)		0	Y	0
Presence of large groups of visitors and more than expected bouts of ABNL (1.5.b)		0	Y	0
Presence of quiet visitors and more than expected bouts of ABNL (1.5.c)		0	0	0
Presence of small groups of visitors and more than expected bouts of ABNL (1.5.d)		0	0	0
Presence of noisy visitors and more than expected bouts of SGRO (1.6.a)		0	0	0
Presence of large groups of visitors and more than expected bouts of SGRO (1.6.b)		0	Y	0
Presence of quiet visitors and more than expected bouts of SGRO (1.6.c)		0	0	0
Presence of small groups of visitors and more than expected bouts of SGRO (1.6.d)		0	0	0
Presence of noisy visitors and fewer than expected bouts observed at front of enclosure (2.1.a)		0	0	0
Presence of large groups of visitors and fewer than expected bouts observed at front of enclosure (2.1.b)		0	0	0
Presence of noisy visitors and more than expected bouts observed at front of enclosure (2.1.c)		0	0	0
Presence of large groups of visitors and more than expected bouts observed at front of enclosure (2.1.d)		0	0	0
Presence of noisy visitors and fewer than expected bouts observed at ground level (2.2.a)		0	0	0
Presence of large groups of visitors and fewer than expected bouts observed at ground level (2.2.b)		0	0	0
Presence of noisy visitors and more than expected bouts observed at ground level (2.2.c)		0	0	0
Presence of large groups of visitors and more than expected bouts observed at ground level (2.2.d)		0	Y	0

- = no data available, 0 = prediction not supported by data, Y = prediction supported by data

Chapter 5 - Discussion

Interpretation of results

The data presented in this thesis address two hypotheses based on the notion that zoo visitors affect captive ape behaviour. However, one should not expect all apes to react in the same way. Each zoo's keepers have different regimes, such as those involving feeding times, ways of giving food to the animals and different levels of personal relationship with the apes (personal observation). In addition, the composition of the social groups at each zoo varies, including the age and sex ratios and the number of animals. Alpha males are likely to have different priorities than subordinate males and females, for example protecting the group from outsiders, and so the hierarchical system might affect behaviour. Each zoo enclosure is of a different design with a variety of enrichment items, which may promote certain ape behaviours over others, or preoccupy the apes so that their daily behaviour is relatively undisturbed by zoo visitors. Factors such as these may well influence the ways in which animals will respond to the zoo visitors. Therefore, in this study the results obtained in each zoo have not been statistically compared with one another, rather I have looked at within-group patterns.

Species-differences should also be expected between chimpanzees and gorillas. Although both species are very closely related, their wild conspecifics have adapted to live in different niches. Chimpanzees, for example, are highly sociable and are terrestrial as well as arboreal; conversely, gorillas are not very sociable and are not as arboreal as chimpanzees are. Chimpanzees are more extroverted than gorillas and, therefore, might be more interested in the presence of zoo visitors than gorillas. It may be the case that zoo visitors are more of an "enrichment" device (or conversely, more stressful) for chimpanzees than for gorillas. Alternatively both species may have become habituated to the presence of zoo visitors and not show any behavioural responses to the various audience conditions, as discussed in Chapter 2 (Snyder, 1975).

Hosey (1997) has brought to light the lack of research that has been conducted in the zoo setting in comparison with studies undertaken in the wild. He argues that possible reasons for this might include the difficulty in incorporating evolutionary theory into studies on zoo animals, or practical constraints such as small sample sizes and different keeper regimes. As mentioned above, I have not directly compared the results from each zoo in this study, rather I have looked at patterns that have emerged in relation to each of the ten ape groups (based on sex, zoo and dominance), under the different audience conditions. By doing this, the confounding factors that are associated with undertaking fieldwork in several different zoos are reduced.

Adams and Babladelis (1977) have discussed some of the problems that they faced when undertaking zoo-based research, including a lack of co-operation from zoo management and the difficulty in obtaining basic information on the animals. Unfortunately, I experienced some initial difficulties with one of the zoos involved in this study. The main difficulty was in obtaining details about the animals prior to the data collection. I tried to gather information from the four zoos regarding the age and sex of their apes so that I could plan which age/sex groups to study. Unfortunately, one of the zoos would not give me any information in advance, in spite of my reasons for wanting it. Another zoo involved in my study very kindly contacted that zoo to try to obtain the information on my behalf, but they were also denied this request.

As discussed in Chapter 2, information regarding the effects of zoo visitors on the typical daily behaviour of chimpanzees and gorillas was previously lacking in the field of zoo biology and other related disciplines. This study has contributed to filling the gap in our knowledge by comparing the number of bouts of certain ape behaviours in the presence of small versus large crowds, and quiet versus noisy crowds. In this way, it has been possible to determine whether or not there is a universal visitor effect on these apes, if a visitor effect only applies to some ape categories or some behaviours, or if apes are completely habituated to zoo visitors as Snyder (1975) has argued.

In comparing the behavioural profiles of captive apes under these different audience conditions, some statistically significant results have been obtained, as were detailed in Chapter 4. These associations were not correlated with the time of day (using the Kendall partial rank-order correlation) except in one instance, which is dealt with in the section on visitor-directed behaviour later in this chapter. However, one must bear in mind a possible pitfall associated with multiple statistical analyses. I have tested my hypotheses and predictions for each of the 10 ape classes, totalling over 300 statistical tests. This sort of “fishing expedition” can be misleading: despite the fact that each individual test has a confidence level of $p < 0.05$, this probability cannot be applied to the collection of tests (Rice, 1995).

As an illustration, out of my 334 chi-squared tests one would expect 5% (17) of them to yield “significant” results just by chance (based on $p < 0.05$). Multiple hypothesis testing is more likely to have an impact on data that are at lower levels of significance, such as those between $p = 0.03$ and $p = 0.05$ (Argyle, J. and de Ruiter, J., personal communication, this study). Out of the 43 statistically significant results in this study, 12 results are at levels below $p < 0.01$ and 15 results are at confidence levels below $p < 0.001$. Therefore, one may conclude that the problems associated with the “fishing expedition” paradigm may not be cause for too much concern here.

Of the 16 results at confidence levels between $p > 0.01$ and $p < 0.05$, 6 results had low p values (i.e. between 0.03 and 0.05). Associations between visitor crowd size and certain bouts of behaviour were as follows: social affiliation in Jersey Zoo’s female gorillas ($p = 0.049$), abnormal behaviour in Chester Zoo’s dominant male chimpanzee ($p = 0.036$), being observed on or off the ground in Colchester’s non-dominant male chimpanzee ($p = 0.034$). Associations between visitor noisiness and ape behaviour were as follows: social affiliation in Howletts Zoo’s female gorillas ($p = 0.035$), travelling in Jersey Zoo’s silverback gorilla ($p = 0.33$), being observed at the front or back of the enclosure in Howletts Zoo’s female gorillas ($p = 0.039$). Therefore, these results are more at risk of losing validity than the rest of the data. However, the overall conclusion of this study (that zoo visitors affect captive apes’ typical daily behaviour) is not affected by the

“fishing expedition” problem, because an abundance of other data show visitor effects at higher confidence levels.

As Tables 4.1-4.3 show (Chapter 4), the ape groups demonstrated differing responses under the specified zoo visitor conditions. In addition, members of some ape categories were never observed performing bouts of certain types of behaviour. Gorillas, for example, were never observed in social aggressive interactions, and nor were male chimpanzees at Colchester Zoo. Data for one ape category provided no evidence to suggest that visitors affect behaviour. In Chapter 1 of this thesis, I proposed four models regarding the type of influence that zoo visitors might have on apes. I discuss the results for each type of behaviour in turn, and interpret the results based upon these models. To remind the reader, the models were as follows:

- ◆ Model 1: Noisy visitors as aversive
- ◆ Model 2: Noisy visitors as enrichment
- ◆ Model 3: Large groups of visitors as aversive
- ◆ Model 4: Large groups of visitors as enrichment

Social affiliative behaviour

Jersey Zoo’s gorillas performed more social affiliative bouts (SOAF) than expected when zoo visitors were being noisy or were present in large numbers (see Chapter 4). One explanation for this could be attributed to a two-year old male in the group. This infant seemed to play (“show off”) more often when there was an obvious visitor presence (i.e. large or noisy groups), and other

members of his group would often join in and play with him. Indirectly, zoo visitors might be an enriching presence in this case, supporting Models 2 and 4.

Noisy visitors were associated with more bouts of social affiliation than expected in Howletts' gorillas. These apes tended to hug one another when visitors were being noisy (especially mothers hugging their older female offspring, or females touching the silverback). The apes' sex is probably relevant here: it is the silverback male gorilla's role to protect his group, and so the females might require more reassurance from each other and from him (by touching). The increase in social affiliation in Howletts' gorillas could indicate that they were threatened or annoyed by noise from zoo visitors, suggesting that noisy visitors are an aversive presence (Model 1).

It is also possible that noisy or large groups of zoo visitors were an aversive presence to Colchester Zoo's female chimpanzees. These females performed more bouts of social affiliation than expected (mainly allo-grooming) under these visitor conditions, which could indicate that these females were trying to reassure one another by engaging in affiliative physical contact (Models 1 and 3). Male chimpanzees were unaffected, perhaps because they are dominant over the females and would be expected to protect them in the case of an outside threat to the group.

From what is understood about the behaviour of gorillas and chimpanzees in the wild, we know that chimpanzees engage in more affiliative interactions with one another than do gorillas (e.g., Goodall, 1986; Sabater Pi, 1993). My data show the same general pattern, with an overall greater number of social affiliative bouts being observed among chimps compared with gorillas (however, see comments below about sample sizes). We also know that females of both species engage in more such interactions than do males in the wild. This same pattern has been observed in this study, with females engaging in social affiliative bouts more often than the males overall. However, these similarities are more likely to be a consequence of biases in the sample sizes of apes (more females were involved in this study than males, and more chimpanzees than gorillas). This could have been overcome by looking at the mean or median bout frequencies in

apes, rather than the actual numbers of observations. However, the chi-squared test for two independent samples, which was used to analyse data in this study, requires the use of the observed values. Therefore, I used the latter in the graphical representations of my data, so that my descriptions of the analyses were reflected in the graphs.

Howletts' gorillas live in a larger social group (n=14) than those at Jersey (n=7) and, therefore, have more opportunity to engage in affiliative interactions. However, Howletts' females were observed engaging in fewer such bouts than Jersey's females overall. Chester's chimpanzees were observed in more social affiliative interactions with one another than were Colchester's chimpanzees. This might be the result of Chester's chimpanzees living in a larger group (Chester, n=28; Colchester, n=9) and therefore having more opportunity to engage in this kind of behaviour (although Howletts' female gorillas did not follow this pattern).

It is unlikely that the amount of time that the apes have spent together is a factor in determining the amount of social affiliation that takes place. All of the apes in this study have been housed with their fellow group members for at least several years, so each group is a well-established social unit. It may be the case that the observed differences in the number of bouts of social affiliation are due to the type of enclosure in which the animals live. In each species, island-inhabiting apes were observed for a greater number of social affiliative bouts than were their caged conspecifics overall. This is a possible area for future investigation.

Social aggressive behaviour

As mentioned above, none of the gorillas were observed in bouts of social aggression (SOAG), and nor were male chimpanzees at Colchester Zoo. Where bouts of social aggression did occur in chimpanzees, these were not associated with the specified visitor conditions. Therefore, the data in relation to social aggressive bouts do not fit any of the proposed models.

From data collected in the wild, it is known that gorillas are not usually aggressive towards other group members and so the results obtained in my study are not very surprising. Wild chimpanzees are much more aggressive than gorillas because they must compete for dominance, whereas gorillas have an age-graded hierarchy (Napier and Napier, 1985). Aggression is necessary in the wild from the viewpoint of survival, particularly in times of food shortage, for protection from predators and for the protection of territory and mating rights. These issues are not particularly relevant in the captive setting, because food and mates are provided, and the enclosure's boundaries mark the animals' territory.

Most zoos do not allow their staff to enter enclosures while the animals are in there. Zoos such as Howletts, that do encourage close bonds between keepers and animals, build the human-animal relationship up slowly so that the keepers can enter the enclosure without normally experiencing physical confrontation from the animals. Zoos also provide enough food for each individual animal, thereby eliminating aggression that might erupt during times of shortage, for example. In addition, the structure of the captive social group is relatively static, in the sense that animals cannot simply come and go as they please as they might in the wild. Aggression over mating access is thus reduced in zoos because males do not have to face competition for mates to the same extent that they would in the wild.

Therefore, the lack of aggression in the zoo-housed chimpanzees and gorillas in my study is likely to be a product of captivity. Perhaps the gorillas and chimpanzees in this study were typical of their species with regards to the effect of zoo visitors on social aggressive behaviour. Conversely, it is possible that these particular animals were not affected whereas gorillas and chimpanzees in other zoos might have been. I suggest that further research into the effects of zoo visitors on the behaviour of captive chimpanzees and gorillas should not omit the examination of social aggressive behaviour.

The captive setting does not eliminate all opportunities for aggression, in spite of the provision of food and so forth. As mentioned in Chapter 2, a study on the aggressive facial displays in golden-bellied mangabeys demonstrates that these monkeys were regularly engaged in aggression towards zoo visitors, intra-group

members and primates of other species located in nearby enclosures (Mitchell *et al.*, 1992). The results of that study show that there was a positive correlation between the number of zoo visitors and the amount of public-oriented aggressive facial displays in this species. Likewise, when a higher number of visitors were present these monkeys were more aggressive to other members of their social group. In this case, the presence of larger groups of zoo visitors increased the amount of intra-group aggression.

Travelling

Overall, bouts of travelling (TRAV) in apes were not associated with zoo visitor crowd size or noisiness. There were a few exceptions, which will be discussed here. Jersey Zoo's silverback gorilla travelled more frequently than expected in the presence of noisy and large groups of visitors, a possible explanation being that he was patrolling his territory as a consequence of the potentially threatening zoo visitors (large and noisy groups) at the enclosure. In contrast, the increase in travelling over that expected could have alleviated boredom, thus being enriching. Therefore there are insufficient data to suggest whether or not the zoo visitors were perceived as an aversive or enriching presence in this case.

However, the data for other types of behaviour (such as self-grooming) by this silverback suggest that he finds large and noisy groups of visitors stressful (e.g. Maple, 1980; Castles and Whiten, 1998).

The results show an association between the presence of a large group of zoo visitors and fewer than expected bouts of travelling in Chester Zoo's female chimpanzees. It is unclear why this should be so (these females were not occupied in more "reassurance behaviours" (e.g. social affiliation, see above) than expected in the presence of large groups of visitors, which might have indicated that these visitor conditions were aversive).

Resting

As the results show, female apes generally rested more frequently than expected when visitors were being quiet or were present in a small number. Noisy or large

groups of visitors are therefore likely to be more obtrusive (aversive) or entertaining (enriching) to female apes, although there is insufficient data to suggest which is the most likely.

Data on other types of behaviour in these females suggest that noisy or large visitor groups are an aversive presence (Models 1 and 3 respectively). One such example of this is in Howlett's female gorillas. These females were observed in more bouts of social affiliation than expected, and were observed in fewer than expected bouts at the front of the enclosure, in the presence of noisy visitors, both of which could indicate that this visitor condition is an aversive one. Another such example is that Chester's female chimpanzees were observed in fewer than expected bouts at ground level, in the presence of noisy and large groups of visitors. Furthermore, Colchester Zoo's female chimpanzees were observed in more bouts of social affiliation than expected in the presence of large and noisy visitor groups. Because fewer resting bouts were observed in female apes than expected when visitors were being noisy or were in large groups, these visitor conditions are unlikely to be enriching.

To what extent is a reduction in resting in the presence of large or noisy groups of visitors likely to be aversive? One would not expect wild apes to rest a lot in the presence of a large or noisy group of conspecifics: a large intergroup encounter in the wild would most probably be exciting and/or stressful (e.g. Goodall, 1986). In this sense, one might view a reduction in resting among captive apes to be a "species-typical" response. However, Chamove and Moodie's study (1990) of stress in cotton-topped tamarins (see Chapter 2) has shown that primates seem to respond to brief, low intensity arousal as they would to environmental enrichment, because they have evolved to deal with short-term stressors in the wild. In contrast, that study also showed that the effect of zoo visitors was the same as the effect of long-term stressors, which did not benefit the primates.

Therefore, I argue that the presence of large or noisy groups of zoo visitors is a long-term stressor, which Chamove and Moodie (1990) have shown to be aversive. As I have already mentioned in Chapter 2, life in the wild is far from

stress free but wild animals are not normally subjected to a stressful stimulus over a long, continuous period of time. Whilst a certain amount of stress is probably beneficial to animals in the wild (because they have adapted to cope with it), I argue that if zoo animals experience constant long-term stress then this is probably aversive. In contrast, if the apes have become completely habituated to zoo visitors, then this is not an issue.

As discussed in Chapter 2, wild western lowland gorillas and chimpanzees spend a great deal of the day resting (e.g. Sabater Pi, 1993), and so one would also expect captive apes to rest frequently if zoos are succeeding in promoting species-typical behaviour. My data show that zoo-housed gorillas and chimpanzees do rest for a large part of the day. During the period of data collection for this study, I often overheard zoo visitors commenting on how bored or lazy the apes looked because they were just lying or sitting around doing very little. It may be the case that some zoo apes are indeed bored, especially as in most cases food is provided at a designated time, removing the need to forage throughout the day. Nevertheless, zoos might benefit from indicating to their zoo visitors that it is normal for animals to rest during the day. In doing so, zoos would reduce the likelihood that visitors would gain a negative impression of the zoo (that it does not provide a stimulating environment for its animals) or of the species (being lazy).

Visitor-directed behaviour

Regarding bouts of visitor-directed behaviour (VISD) apes demonstrated differential responses to the variables of crowd size and noisiness, as revealed in Chapter 4. Gorillas generally behaved as predicted, performing more bouts of visitor-directed behaviour than expected in the presence of a large or noisy crowd of visitors. Female chimpanzees at Chester Zoo were similarly affected. Howletts' silverback gorilla and all categories of male chimpanzee were unaffected by the visitors, perhaps because they were disinterested in the zoo visitors and were sufficiently occupied with what their enclosures had to offer them.

In the majority of cases, visitor-directed bouts by apes actually comprised visitor-directed vigilance. Begging and aggressive behaviours directed at the public were infrequent. Visitor-directed vigilance would probably not be beneficial to apes if this was one of their main occupations throughout the day, because they would be forfeiting the opportunity to engage in species-typical behaviour such as social interactions with other group members. In such a case, zoos would have to renew their efforts to provide suitable enrichment for the apes in order to divert their attention away from the zoo visitors and back into their social group and enclosure.

Zoo visitors would probably learn very little accurate information about a species that spends most of its day engaging in visitor-directed behaviour. Begging is one of the ways in which apes can direct their behaviour towards zoo visitors. Cook and Hosey (1995) studied the interaction sequences between chimpanzees and human zoo visitors at Chester Zoo and found that chimpanzees primarily initiated interactions with zoo visitors in an attempt to gain food or social interaction. These authors argue that the animals were possibly seeking social stimulation as a result of deprivation associated with captivity, thus visitors were being used as an enrichment "device." At Arnhem Zoo, in the Netherlands, visitor-directed begging does not occur because zoo visitors are kept at a greater distance from the chimpanzees. The exhibit at Arnhem Zoo was designed to present the chimpanzees for research rather than for interaction with zoo visitors (de Waal, 1991).

Begging for food does, of course, happen frequently among chimpanzees in the wild, with subordinate chimpanzees begging to those who are dominant over them (e.g. Goodall, 1986). Goodall describes how wild chimpanzees usually beg to conspecifics by reaching out to touch the food item while glancing at the face of the possessor, or by holding out a hand with the palm facing upwards, or by reaching to the mouth if the possessor is chewing. Members of the Arnhem Zoo chimpanzee colony beg to one another in a similar way (de Waal, 1991).

Begging to human zoo visitors could therefore be an extension of this behaviour. Chimpanzees might perceive their human visitors as they would conspecifics,

begging to them in the genuine hope of getting some of their food. Wild chimpanzees at Gombe have even begged to Jane Goodall at the feeding station, presumably for bananas (even though bananas are no longer kept there) (personal observation, July 1998). However, I would argue that the main difference between “natural” begging and visitor-directed begging is the apparently excessive way in which the apes beg, which I believe should be a cause for concern. Zoo apes act more like spoilt humans, engaging in loud, “childish” tantrums, even among adult apes (personal observation, 1998, this study). I have often overheard zoo visitors making such comments when apes are begging to them, and this presumably has negative repercussions for the conservation education role of the zoo. From the visitors’ comments that I have overheard with regards to begging, it seems highly unlikely that they would be encouraged to consider that this is a species worth saving.

Other welfare issues surround the problem of visitors feeding the animals, such as giving them unsuitable food, or the animals being overfed. Zoo keepers become worried if one of their animals refuses a meal, because it may be a sign that the animal is ill. If the animal is simply full because the visitors have fed it, keepers are not to know. I give some more examples of zoo visitor misconduct later in this chapter.

Perhaps zoos should inform their visitors about the natural context of begging, explaining that even though begging is a natural behaviour in the wild, visitors should refrain from feeding the animals and should not encourage apes to beg to them. In contrast, behaviour such as visitor-directed vigilance seems to intrigue zoo visitors, who regularly make comments such as “Who’s watching whom?” or “He’s looking at you!” (personal observation, 1998, this study). Such intrigue might even help to promote a more deep-rooted interest in the animals among zoo visitors. In my study, the majority of visitor-directed behaviour at all four zoos involved simply watching the visitors, which might also be enriching for the apes in the same way that some people like to “watch the world go by.”

As discussed in Chapter 2, Hosey and Druck (1987) studied the influence of zoo visitors on the behaviour of 12 monkey species. Their research found that

significantly more behaviours were directed by monkeys towards large active visitor groups than at small active groups, whereas there was no difference in the number of behaviours directed at large passive compared with small passive groups. The methodology and ethogram in my study and in the study by Hosey and Druck differed, but nevertheless similarities have been found in that my results show that large and noisy visitor groups elicit more visitor-directed behaviour than small and quiet groups. At the species level, neither gorillas nor chimpanzees ignored the visitors totally (which would be the case if there had been no observations of visitor-directed behaviour whatsoever), and none of the subjects in Hosey and Druck's study did either. Research by Mitchell *et al.* (1992) also provides evidence that zoo visitors affect primate behaviour. As discussed in Chapter 2, these authors found that golden-bellied mangabeys at the Sacramento Zoo engaged in more visitor-directed aggressive facial displays when larger groups of visitors were present (ranges of visitor crowd sizes are not given).

I have discussed above some of the issues that zoos would have to deal with if their animals spent a great deal of the day in visitor-directed bouts. In my study, there is no evidence to suggest that apes spend too much of their time in such bouts (hence these data might provide some support for Models 2 and 4, that visitors are an enriching presence) but further research could be undertaken in this matter.

There is the possibility that the type of enclosure influences the amount of visitor-directed bouts performed by apes. Overall, my data show that such bouts were observed more often in apes on island enclosures (Jersey Zoo's gorillas and Chester Zoo's chimpanzees) than in apes in cages (Howletts' gorillas and Colchester's chimpanzees), as can be seen in Figures 4.15–4.18. This could be a consequence of the type of enclosure. Apes in caged enclosures are perhaps more aware of the physical barrier between them and the zoo visitors (cage mesh and so forth), whereas island enclosures are open and the only obvious barrier is air. Therefore it is possible that island-inhabiting apes engage in a greater number of visitor-directed bouts than their caged conspecifics, because they are more aware of the presence of the zoo visitors. In addition, although bouts of visitor-directed

begging were infrequent, they only occurred in apes on island enclosures (Jersey and Chester zoos) presumably because the lack of a physical barrier makes it easier for apes to receive food from the visitors.

Wild apes are obviously not watched on a daily basis by the equivalent of zoo visitors (potentially large and noisy groups of people whose composition is constantly changing) as is the case for zoo-housed apes. Even if wild apes are followed by a group of tourists or fieldworkers, for example, the apes can at least move off to another area if the presence of people bothers them, which is an option that the majority of zoo animals do not have.

I have mentioned above that the type of enclosure seems to influence the amount of visitor-directed behaviour that occurs. As discussed in Chapter 2, zoo visitors seem to appreciate zoo animals to a greater extent if the animals are viewed in enclosures with no bars (Hediger, 1959; Coe, 1985). However, the animals might be more aware of the presence of visitors when an “invisible” barrier separates them. The woodland in Jersey Zoo’s tamarin exhibit (see Chapter 2) conceals the visitors far more than Jersey’s gorilla island does by providing vegetation cover (personal observation, 1998, this study). However, further research would have to be conducted in a greater number of zoos to test the hypothesis that apes on open, island-type enclosures will respond differently to zoo visitors than will apes in caged or glass-fronted enclosures. This is an area that requires further investigation.

Visitor-directed vigilance might be akin to vigilance directed by wild apes to any other species (or conspecifics) that might be deemed as threatening or interesting. As zoo visitors are a dynamic part of a captive animal’s otherwise static environment, it is not surprising that visitor-directed behaviours occur. If anything, it is perhaps surprising that the apes were observed in so few bouts of visitor-directed vigilance. It is probable that the apes’ cognitive ability enables them to comprehend that the visitors do not pose a threat, because they are outside the enclosure (visitors might still be annoying, though, if they invade the apes’ privacy or cause a lot of noise).

Abnormal behaviour

Fortunately, bouts of abnormal behaviour (ABNL) were not very common in apes in this study. Therefore it is unlikely that the visitors' perceptions of these animals (or of zoos) will have been tainted as a result of this type of behaviour occurring. I have explained in Chapter 2 that abnormal behaviour (i.e. activities that are not usually observed in the wild such as stereotypic rocking) is usually associated with a lack of certain stimuli in the animal's environment (e.g. Poole, 1988; Meyer-Holzapfel, 1968). However, finding the cause of such behaviour can be problematic – animals often continue to perform abnormal behaviour as if by habit, even when the captive conditions are greatly improved.

In this study, the absence of data regarding abnormal behaviour in silverback gorillas mean that one can assume that these two apes do not lack certain stimuli needed in the promotion of well-being. In addition, the data suggest that these apes have not experienced (or been affected by) impoverished environments earlier in life (Meyer-Holzapfel, 1968). Female gorillas exhibited a very small and non-significant number of abnormal bouts. Overall, Howletts' female gorillas performed more abnormal bouts in the presence of small or quiet groups of zoo visitors, mainly the regurgitation and reingestion (R/R) of food. During such bouts, visitors were overheard commenting on R/R along the lines of “disgusting,” “vomit” and other such unpleasant descriptions.

Conversely, Jersey's female gorillas were never observed performing R/R; in the presence of a large and noisy group of zoo visitors, one of these females was observed engaging in an abnormal bout (masturbation) only once. This female (as with two of the other three females at Jersey Zoo) showed no sexual interest in the silverback male. Masturbation by apes is not regarded as “normal,” because it is rarely observed in the wild. Fossey (1988) observed only one occurrence of masturbation, by an eight-year-old mountain gorilla following disciplinary action by the silverback (a potentially stressful experience). Goodall (1986) also notes that for masturbation to occur among the Gombe chimpanzees, it usually follows a frustrating or stressful experience. In addition, Goodall

reports that masturbators are usually wild orphaned chimpanzees or human-reared captive chimpanzees.

Among captive western lowland gorillas, the regurgitation and reingestion of food is a relatively common behaviour. While this behaviour may be “normal” for zoo gorillas, it is “abnormal” in that it has not been observed in the wild (Akers and Schildkraut, 1985). It should come as no great surprise that zoo visitors are not willing observers of this behaviour: they think that the animals are vomiting and as a result they find it unappealing – even disgusting - to watch (personal observation, 1998, this study). Various reasons for the prevalence of R/R in captivity have been put forward, including the use of R/R to extend the feeding time (Akers and Schildkraut, 1985). As mentioned previously, gorillas in the wild spend a great deal of time feeding and so if they are presented with several daily meals at regulated times in captivity, there is a lot of “slack” time left during the day. This is potentially stressful if the animals become bored and disinterested in their captive environment. Stress and boredom seem to increase the frequency of R/R, mainly because food is too readily available.

However, as mentioned above, Howletts’ female gorillas engaged in R/R even though they had to forage for food daily (the whole of their enclosure is covered in a thick straw “carpet” into which the keepers throw food items, to encourage foraging). Therefore it seems unlikely that the apes were not stimulated by feeding-related activities in this case. Perhaps these females performed R/R with their favourite foodstuffs, as has also been reported in the paper by Akers and Schildkraut (1985). It may also be a result of the high fruit diet that the Howletts gorilla bands are given (Furley, C., personal communication).

If visitors are to be accurately educated about the behaviour of gorillas, zoos may well want to try eliminating R/R from their animals, especially as visitors find it so off-putting (a repercussion of which might be lost sympathy or disinterest with the gorilla’s plight in the wild). Even though the frequency of R/R was quite small in this study, I have seen other gorillas at Howletts engaging in this behaviour quite often (personal observation, 1998, this study). R/R could be

studied in greater detail at Howletts to try to determine the stimuli.

As the results show, Colchester's non-dominant male chimpanzee performed more bouts of abnormal behaviour than expected when visitors were in large or noisy groups (mainly coprophagy, which is not a normal part of the behavioural repertoire in wild chimpanzees (Goodall, J., personal communication)). Perhaps noisy and large crowds of visitors affected this male because he felt threatened or annoyed by them (under Models 1 and 3 respectively), or maybe he enjoyed the visitors' reactions to his coprophagic acts (Models 2 and 4). I have seen some chimpanzees at other zoos engaging in coprophagy that was seemingly "aimed" at the particular visitors who were showing the most disgust, almost as though the ape was doing it "on purpose" to get attention or to be entertained by the visitors' reaction. This study does not provide enough data to determine the cause of Colchester's non-dominant male's coprophagic acts but it is an area for further research at this and other zoos.

In contrast, Chester Zoo's dominant male chimpanzee was observed in more bouts of abnormal behaviour than expected (namely hair plucking, coprophagy and masturbation) in the presence of small visitor groups. A possible explanation for this is that the dominant male might prefer to be surrounded by people. As a youngster, this male was kept as a pet in a New York flat prior to being donated to Chester Zoo, and so his humanised upbringing might predispose him to being happier (less stressed) when there are more people around. Again, further investigation could be carried out in this matter, but these data might provide some support for Model 4 (large crowds as enrichment).

One of Colchester Zoo's female chimpanzees (Billy Jo) was occasionally observed performing stereotypic rocking against a wall while clutching a pile of straw, under a variety of visitor conditions (the results were non-significant in terms of visitor effect). One of the keepers suggested that there is a pattern to Billy Jo's stereotypy: she tends to sit holding the straw and watching zoo visitors, then as soon as she "catches eyes" with the visitors, she will start to rock against a wall. The keeper suggested that if this individual were a human then one would think that she was purposefully waiting until she got some attention before she

would start rocking, rather than rocking as a result of getting the attention. However, as this is anecdotal evidence one would have to investigate this matter further to try to ascertain the trigger of her stereotypy.

Although there was not enough data to state a firm conclusion during this study, Billy Jo seemed to commence rocking following a possible stimulus from visitors. To exemplify this, one of her bouts of rocking followed an aggressive display at the visitors (before the observation session began), and another bout began following a period when most of the visitor group had comprised very loud children. Some bouts of rocking occurred in the presence of large or noisy groups of visitors, and others when there were five or fewer visitors (sometimes only the observer was present). At this stage, therefore, one cannot put forward a particular visitor condition that might increase the frequency of such behaviour.

This issue highlights a potential problem: Billy Jo (and potentially other apes) might react to a stimulus from the visitors after the event itself – for example, a large or noisy group of zoo visitors may cause abnormal behaviour to manifest itself even after the visitors have left the enclosure. It would perhaps be better for future visitor effect studies to take this problem into account, perhaps by trying to observe one focal animal per day rather than all of the animals for a relatively short observation session per day. This problem might of course apply to all types of behaviours, not just abnormal activities, but the issue has been highlighted by this particular case.

Self-grooming

Excessive self-grooming (SGRO) is widely accepted as being associated with stress. Castles and Whiten (1998) have investigated post-conflict behaviour in a large group of wild olive baboons. Their research has found that levels of self-directed behaviour, including self-grooming, increased among both the victims and the initiators of aggression during a 10-minute post-conflict period. During that period, they report that the baboons were more likely to receive further aggression, and so this would obviously be a stressful time. An increase in self-grooming can therefore be associated with stress.

It was predicted in this thesis that if large or noisy crowds of visitors are more stressful to apes, then these characteristics would encourage apes to engage in more self-grooming bouts than small or quiet groups would. In fact, as the results show the frequencies of self-grooming bouts in most of the ape categories were unaffected by the specified visitor variables.

As shown in Chapter 4, Colchester Zoo's non-dominant male chimpanzee was observed in more bouts of self-grooming than expected when large crowds were present. Therefore, he might find large crowds of visitors more stressful than smaller groups (Model 3). Jersey's silverback gorilla also performed more self-grooming bouts than expected in front of large or noisy crowds, again perhaps indicating that these conditions are more stressful (Models 1 and 3).

In contrast, Howletts' female gorillas seemed to be more stressed when a small number of visitors were present, as this is when they performed more self-grooming than one would expect. Perhaps these females find the lack of "enrichment" provided by a small group of visitors more stressful than the presence of a large crowd, which would provide some support for Model 4. Alternatively, these females might have spent more time doing something else in the presence of large groups of visitors that would have eliminated the time available for self-grooming (for example, these females were observed in more visitor-directed behaviour bouts than expected in the presence of large crowds).

Time spent at or above ground level

Regarding the apes' vertical use of the enclosures (i.e. whether they were observed on or above the ground) under the specified visitor conditions, some significant results were obtained. Obviously, potential opportunities for the use of height within a zoo enclosure are entirely dependent upon what the animals are provided with. In the caged enclosures of Howletts and Colchester zoos, the apes live within three-dimensional climbing frames (the cages), providing ample opportunity to get above ground level. On the island enclosures of Jersey and Chester zoos, apes are provided with trees or metal/wooden climbing frames of various heights. However, due to the obvious danger that animals on islands

could escape if too many or badly positioned climbing structures are provided, the climbing opportunities within island enclosures are not as great as in cages. As the graphs in Figures 4.31 and 4.32 show, Howlett's gorillas (cage) did spend more time above ground than Jersey's gorillas (island) did overall, but this pattern was not so marked in chimpanzees (see Figures 4.33 and 4.34).

Chester Zoo's female and non-dominant male chimpanzees spent more time located above ground level (i.e. above the visitors) than expected when noisy or large groups were present, which could indicate that these visitor conditions are more stressful to these apes (Models 1 and 3). As discussed in Chapter 2, Coe (1985) has argued that zoo animals that elevate themselves above the visitors will probably adopt a sense of dominance or protection (the notion of "the safety of the trees"). Therefore, the presence of zoo visitors exhibiting threatening characteristics is likely to be associated with an increase in the amount of time that apes spend "in the trees". In the case of Chester's females and non-dominant males described above, large or noisy crowds of visitors seem to be an aversive presence thus supporting Coe's theory that "threatening" groups of visitors encourage zoo animals to seek height. In contrast, Colchester Zoo's non-dominant male chimpanzee spent more time on the ground than one would expect when large crowds were present, and might therefore be more interested in large crowds, whose presence could be felt to a greater extent at ground level (through large viewing windows). There is no evidence to suggest that this male was positioning himself on the ground to protect the females from the threat of a large visitor crowd (and he is not the dominant male).

On the whole, chimpanzees were observed above the ground more frequently than gorillas were. This situation is similar to what one would expect in the wild. We know that both species are arboreal and terrestrial, although gorillas spend a great deal of time on the ground probably because of their sheer size and body weight (e.g., Sabater Pi, 1993). In my study, no association was found between the visitor conditions and the number of observations when gorillas were located on or above the ground. Overall, the captive gorillas did seem to perform more behavioural bouts while located on the ground, as would be expected in the wild and probably for the same reasons (i.e. body size and weight).

Time spent at the front or back of the enclosure

It was predicted that the presence of large or noisy crowds of zoo visitors would discourage apes from spending time at the front of the enclosure, nearest to the visitors' viewing areas. Apes were therefore expected to put a greater distance between themselves and a potentially annoying or threatening crowd. Chester Zoo's non-dominant male chimpanzees and Howletts' female gorillas did behave in this way, spending less time at the front of the enclosure than one would expect when visitors were being noisy or were in large numbers. One can therefore assume that these two ape categories did not like those visitor conditions (Models 1 and 3). The presence of large or noisy crowds seems to have driven these two ape groups towards the back of the enclosure. There is no obvious reason why these apes should have been affected and not the other ape groups (no association was found between the visitor variables and other apes' proximity to the visitors).

One might assume that bouts of visitor-directed behaviours would be more likely to take place at the front of the enclosure. On the few occasions that apes at Chester and Jersey zoos begged to visitors the apes were always at the front of the enclosure, presumably because of the obvious practicalities of this. Likewise, aggressive displays at visitors took place at the front of the enclosure (although again these bouts were infrequent). Visitor-directed vigilance seemed to take place at the front of the enclosure slightly more frequently than at the back.

Differences between zoos and between species

As discussed at the beginning of this chapter, it was not the intention to contrast the data from the four zoos in this study. However, I will make some general comparisons here in the light of some differences that one might expect between species and between zoos, and I will attempt to interpret the results in this vein. The majority of these comparisons have been made in earlier sections of this chapter when interpreting particular results, and they are summarised here for clarity.

We know that gorillas and chimpanzees are different to one another in terms of behaviour and physiology, in spite of their close evolutionary relationship, as detailed earlier. We expect, therefore, some species-typical results to emerge in this study, and this appears to be the case. Firstly, my data show that the effect of zoo visitors on visitor-directed behaviour is generally more pronounced in gorillas than in chimpanzees. This could result from a difference in experimental set up, as may be the case for some examples mentioned below. Alternatively the inter-specific variance that has been observed in this study could be explained by a difference in disposition and sensitivity to disturbance.

Gorillas naturally live in a more stable social environment than chimpanzees, with a steady dominance hierarchy and relatively few agonistic interactions within the group (e.g. Napier and Napier, 1985; Tutin, 1997). Conversely, chimpanzees live in fission-fusion societies and are more accustomed to social change and disturbances within the community (e.g. Goodall, 1986). It could be argued, therefore, that one could expect chimpanzees to be less sensitive to social turbulence and perhaps also to varying human interaction patterns. Furthermore, my data suggest that zoo-housed chimpanzees seek height in the presence of large or noisy groups of visitors to a greater extent than gorillas do. This is surely the species-typical response – wild chimpanzees are far more arboreal than gorillas are, and use the height of the trees in the presence of a perceived threat, and so the differences shown in my data may therefore not come as a surprise.

Behaviours associated with social aggression and affiliation should also differ between these two ape species. As my data show, zoo chimpanzees generally engage in more social affiliation than gorillas do, as would be expected from data on wild gorillas. However, my data show that zoo visitors have a stronger effect on social affiliation in gorillas rather than chimpanzees, perhaps because gorillas seek more reassurance from one another in the presence of “threatening” visitor groups (large and noisy groups) whereas the more gregarious chimpanzees are not affected in this way. This study’s data show that social aggression differs between the two species as well. No observations of social aggression were made in gorillas, whereas there were a small number of such bouts in chimpanzees. Again, these data correspond with what we know about the behaviour of the two

species in the wild (e.g. Goodall, 1986; Sabater Pi, 1993; Tutin, 1997), as a consequence of social structure and resource competition as discussed earlier.

Also within species, differences between apes at different zoos might be expected. None of the zoos are directly comparable with each other, due to different enclosure designs, group composition, etc. As discussed earlier, the type of enclosure seems to affect ape behaviour (island apes were more strongly affected by zoo visitors than were caged apes). For example, more bouts of social affiliation (for reassurance?) and more visitor-directed behaviour were observed in island apes than in caged ones, probably because cage bars provide apes with a greater sense of distance and security from the visitors. Visitor-directed begging was only observed in island apes, facilitated by the absence of a physical barrier. In addition, island-dwelling chimpanzees were generally more socially aggressive than were caged chimpanzees.

The type of enclosure might also influence the apes' use of space within the enclosure. Caged gorillas spent more time above the ground than did their island-dwelling conspecifics, most likely because there are more climbing opportunities within cages). Chimpanzees on islands spent more time at the back of the enclosure than at the front when large or noisy crowds were present, with the opposite being seen in caged chimpanzees. Perhaps chimpanzees in island enclosures distance themselves from zoo visitors by spending more time away from the front of the enclosure, thus compensating for the lack of physical barrier between them.

Some differences relating to group composition are apparent, and some examples are given here. Female chimpanzees at Colchester Zoo rested more frequently than their female conspecifics at Chester Zoo, perhaps because more focal females at Colchester were nursing infants than at Chester. Jersey Zoo's gorillas were more socially affiliative than Howletts' gorillas when large or noisy visitor groups were present. An alternative explanation to the one given above (relating to enclosure type) is that Jersey's gorillas were interacting with a 2-year-old male, who seemed to "show off" to large crowds of people. Another observed difference between zoos involves abnormal behaviour. Howletts Zoo's female

gorillas were observed regurgitating and reingesting (R/R), which was not seen in Jersey Zoo's gorillas. A possible explanation for this intra-specific difference is the high fruit diet of Howletts' gorillas, often attributed with the occurrence of R/R (Furley, C., personal communication, this study). Chester Zoo's dominant male chimpanzee, a former pet, was observed in more bouts of abnormal behaviour than expected when small or quiet groups were present, perhaps because he is more relaxed in the presence of human groups. Because of such idiosyncrasies in the composition of these four groups of apes we should be wary of extrapolating too much from inter-zoo comparisons in this study.

Zoo visitors: an overview

Zoo visitors pay their entry fee to a zoo but zoo management should try to enforce certain ground rules for the sakes of both animals and visitors, much in the same way that museums have rules of conduct for their visitors. Zoo visitors must be made aware that their role as spectators does not guarantee them the privilege of viewing animals who are sitting right at the front of the enclosure, or who are at their most active. I have heard many zoo visitors complaining – some even voicing their complaints to zoo management – that they have paid their money and have “not seen much” in return. These people presumably visit the zoo for the sole purpose of entertainment, in the same way that they might visit a circus.

With zoo visitors contributing crucial finances, zoo management must endeavour to reach a compromise between the demands of the visitors and the needs of the animals. One can sympathise with zoo officials who are somewhat reluctant to create more naturalistic enclosures for their animals in case zoo visitors are not impressed with having to actively seek out animals to observe. However, studies such as that done by Price *et al.* (1994, see Chapter 2) positively reinforce the ability of zoos to satisfy their visitors by keeping the animals in enclosures that simulate the natural habitats that zoo visitors will perhaps have seen in nature documentaries and magazines. Even though visitors would have to spend more time searching for the animals in a naturalistic enclosure, it is presumably rewarding in itself to view them in a habitat more closely resembling their natural one than in a traditional, comparatively barren cage.

Regarding zoo visitor conduct, the feeding of animals is usually prohibited in zoos but it seems to occur quite frequently nevertheless (personal observation, 1998, this study). As mentioned earlier in this chapter, apes in this study did not beg to zoo visitors very often but such behaviour can be a problem. Zoo visitors can pose a sinister risk to animals, stemming from a combination of their lack of knowledge and understanding, and the (hopefully unintentional) failure of zoo management to provide suitable information to visitors regarding appropriate conduct at the zoo.

Some visitors throw items (not only food) into zoo exhibits, even though this is normally forbidden. This problem can be highlighted by several cases. Cigarettes and a cigarette lighter were discovered by keepers on a zoo's orang-utan island, thrown over there by an undetected visitor who presumably wanted to see whether or not the orang-utans could smoke (personal observation, 1997, prior to this study). At Jersey Zoo, a visitor threw an entire pack of biscuits, including the plastic wrapping, into the gorilla enclosure; a two-year-old male gorilla ate the

wrapping but fortunately it passed through him without causing any obvious damage (personal observation, August 1998, this study).

A posting to the University of Wisconsin's e-mail list "Primate-Talk" in 1998 reported the case of Khartiko, an eight-year-old male orang-utan at the Toronto Zoo. He died as a result of zoo visitors who disobeyed the zoo's "no feeding" signs. Khartiko was at the back of the enclosure when visitors threw a cookie into the enclosure, which landed near the moat. As he rushed to the moat to get the cookie, he slipped and fell into the water and died later that night in the animal hospital. As so often happens in these sorts of situations, the visitors who had thrown the cookies were not caught. This case highlights the terrible consequences that the inappropriate behaviour of zoo visitors can have.

When apes beg to visitors who are eating, a frequently observed misconception that zoo visitors have is that the apes are "hungry" and by implication are not well looked after by the zoo (personal observation, 1999, not this study). Visitors that respond to this begging by offering the apes some food probably think that they are being helpful and doing the animals a favour, and if they have noticed the "no feeding" signs at all, may think the signs are there because the zoo management are killjoys. Whatever the reason, the effect of zoo visitors on the animals can obviously be a very serious problem.

Another case of zoo visitor misconduct can be highlighted here. The areas surrounding Howletts Wild Animal Park's gorilla enclosures contain many signs publicising the areas as "no smoking" zones, because of the large quantities of straw in the enclosures being an obvious fire hazard. Regardless of the signs, there are always some visitors who read them aloud and then continue to smoke. One such visitor was heard laughing that the reason for the "no smoking" signs was that gorillas do not like cigarette smoke, while he was standing only a few feet away from what is effectively a huge flammable carpet (personal observation, 1998, this study). This visitor continued to smoke, thus demonstrating not only a lack of common sense and a blatant disregard for an official zoo sign, but also disrespect for the animals. Even if the reason was that gorillas do not like to smell cigarette smoke, this visitor did not care.

Some zoos try to overcome such problems by using trained volunteer docent^{5.1}. Docents wear zoo uniforms and are on hand at the enclosures to try to keep an eye on the visitors' behaviour and to answer questions (personal observation, 1998, this study). These docents can act as a deterrent to visitors who are knowingly doing something wrong, or they can explain to visitors why they should not behave in a particular way. In addition, they can educate the visitors as to the problems that these species face in the wild.

Docents seem to be appreciated by zoo visitors because docents can answer more in-depth questions that zoo signs cannot effectively deliver, perhaps due to space limitations (personal observation, 1998, this study). Hence docents can help zoos to reach their education and conservation goals, and also possibly contribute to the animals' welfare by being on-hand to check any irresponsible visitor behaviour. Sabater Pi (1993) discusses the misconceptions that many people seem to have about gorillas and chimpanzees as a result of popular films such as King Kong, in which gorillas are depicted as aggressively sexual monsters. Zoo docents could help to re-educate visitors whose opinions (and only experience of) apes may be from negative media, or bad experiences of visiting older zoos in the past.

Future research

Previous investigations by other workers in this field have concentrated on areas such as human-ape interactions (e.g. Cook and Hosey, 1995) and the effects of zoo visitors on general types of behaviour rather than more specific daily behaviour (e.g. Chamove *et al.*, 1988). While those studies argue that primates do not become habituated to the presence of zoo visitors, there was a gap in the literature addressing the issue of more specific effects of zoo visitors on ape behaviour. The data presented in this thesis have contributed towards filling that gap by making a preliminary assessment of the effect of zoo visitors on the typical daily behaviour of gorillas and chimpanzees. The results of my study do

^{5.1}. A docent is a person involved in educating others.

not support Snyder's argument that zoo animals become completely habituated to zoo visitors (Snyder, 1975).

From the data presented in this thesis, one cannot draw strong conclusions about whether these effects are enriching or aversive to the apes, although I have made tentative inferences throughout this chapter based upon the direction of the changes in behaviour, and summarise these in Chapter 6. If noisy or large groups of zoo visitors are an aversive presence, there are a number of ways to deal with this problem. Firstly, zoo management could try to encourage their visitors to visit the enclosure in small or quiet groups, perhaps by using tour guides to take visitors around the zoo (as happens in some museums). If this is not a practical solution, the number of enrichment items in the enclosure could be increased, or rotated, so that the apes are more stimulated by the environment within the enclosure rather than adversely affected by what is going on outside it. In addition, zoos could change the ways in which they present food to the animals. As discussed in Chapter 2, animals in the wild must spend a large part of the day engaged in feeding-related activities such as foraging. If zoo animals also had to forage for food, they would probably be made less aware of the presence of zoo visitors because they would have less "slack" time during the day.

Another way of making the visitors' presence less obvious would be to make the enclosures more naturalistic, with vegetation partially covering the boundaries of the enclosure separating apes from visitors. Apes would still be visible to visitors and vice versa, but visitors would be better hidden from the animals should the animals not want the sensation of their privacy being invaded. From the work by Price *et al.* (1994), visitors would prefer to see animals in more naturalistic enclosures and would be more inclined to support *in situ* conservation efforts.

There is also insufficient evidence from my study to suggest whether or not there are species differences in the responses, and whether the type of enclosure plays a role in determining the strength of the visitor effects. The confounding factors that present themselves when trying to compare several different zoos and species were too great to try to compare the results directly. However, some possible links have emerged such as the inference that visitor-directed behaviour

occurs more frequently in apes on island enclosures than it does in apes housed in cages (see above). Thus there is a great potential to investigate further the effects of zoo visitors on specific behaviours of captive gorillas and chimpanzees.

The chi-squared test for two independent samples, which was used to analyse my data, requires that expected values should not be fewer than 5. Therefore, I have sometimes had to use Yates' Correction for Continuity (Siegel and Castellan, 1988). Although not likely to be particularly robust, this test has yielded some statistically significant results. However, it would be preferable to have a larger amount of data upon which the analyses can be based, rather than having to rely upon a statistical correction.

What is not clear from this study is who is influencing whom? Do apes perform a certain behaviour that then attracts a large (or noisy) crowd of visitors, or is it the visitors who elicit a certain behavioural response from the apes? From my data, it is only possible to determine whether or not there is an association between the specified visitor variables and changes in the frequency of ape behaviour; no causal inferences can be made at this stage. Future research should incorporate the influence of captive apes upon the visitors, and I will discuss some alternative means for addressing this issue towards the end of this chapter.

My data show that zoo visitors affect the apes in different ways, and so there is no evidence of a universal visitor effect on ape behaviour. With this in mind, I would like to extend my study to investigate the effects of visitors on individual animals, rather than grouping ape categories together. Because of the differential responses exhibited by each ape category, it may be the case that greater differences are observed between individuals. For example, hand-reared animals are likely to be more humanised and their behaviour may therefore be affected by the presence of human visitors to a greater or lesser extent than group-reared animals.

Likewise, the past experiences of individual animals might play a role in determining their responses to zoo visitors. To exemplify this, Djala (one of the

silverback gorillas at Howletts Wild Animal Park, not involved in this study) was rescued from poachers in Africa and has suffered a great deal at the hands of humans (Furley, C., personal communication). The behaviour of this particular male seems to change dramatically when large or noisy crowds of visitors are present, perhaps because of his past experience of humans. Were data collected on this male instead of the silverback that I chose, then the results of my study could have been very different^{5.2}.

Based on my experiences during this study, I have some suggestions as to how this study could be done in future, addressing some of the issues that the present study could not answer. Future research should incorporate a recording method where the data points are already independent, such as continuous recording. As mentioned in Chapter 3, I collected my data using instantaneous time sampling of a focal animal. The data then had to be re-organised to ensure that the data points in each observation session were statistically independent of one another. Continuous recording would eliminate the need to reorganise the data (although it may be difficult to collect all of the data accurately if the type of behaviour changes very quickly, and if a lot of different information is required). If continuous recording could be used reliably, it would be time-saving (the data would not have to be re-organised) and would mean that no data would be lost.

Continuous recording would also be useful in trying to determine who influences whom (i.e. do the apes affect the visitors' behaviour or is it the other way around?). The collection of sequential data benefits from a continuous recording method (Martin and Bateman, 1994; Bakeman and Quera, 1995). I suggest that it would be worth trying to use interval sequences. Data would be collected on a focal ape, recording the observations onto a lined check sheet (each line representing a short time period, perhaps 10 seconds). Coded data regarding the ape's behaviour and the visitor characteristics would be written on the line, in the order in which they occur. On the stopwatch's "beep" the observer would move to the next line and continue to record data for the next time period (Bakeman and Quera, 1995). This would enable the observer to determine the order in

^{5.2} It was not possible to collect data on Djala and his group because construction work was going on in that part of the gorilla house at the time.

which things happened and it may become apparent as to who is influencing whom. This could also help to eliminate the potential problem that I discussed in relation to Colchester Zoo's female chimpanzee Billy Jo. This female seemed to be affected by visitors even though the stimulus was no longer there.

As mentioned above regarding Howletts' silverback, Djala, I believe that it would be worthwhile analysing the data for each individual animal separately. It is my opinion that in species as complex as the great apes, differences in individual personalities and previous experiences are likely to affect the ways in which the individual animal will behave in response to zoo visitors. In addition, I suggest that where background information is known, data should be compared for hand-reared and group-reared animals, to see if any patterns in behavioural responses to visitors emerge.

I have discussed earlier in this chapter that one has to be careful when trying to label visitor effects as "enriching" or "aversive." Behavioural responses that are beneficial to apes in the wild might not be beneficial in captivity, perhaps because of the extent to which it occurs, with behaviours varying in degree rather than kind (such as exposure to short- and long-term stressors, as discussed previously). Behaviour patterns in captivity may be suppressed, enhanced (elevated in frequency or duration) or distorted (Patterson, 1992). It is possible, therefore, that behaviour *per se* is not a reliable welfare indicator. In a future study of visitor effects, it would be useful to measure cortisol levels in urine or stool samples (stool samples would probably be easier to collect) from the focal apes. It may be that the apes' behaviour suggests that zoo visitors cause them stress, but cortisol levels remain unchanged, or vice versa (ape behaviour remains unchanged but cortisol levels rise). Physiological data would probably make it clearer for us to determine whether zoo visitors have an enrichment potential or whether they can be aversive.

Another approach to the investigation of zoo visitors would be to interview a large sample of them to determine their perceptions of apes in zoos. This would help zoos to assess the extent to which they are succeeding in their conservation education role. It is imperative that, in addition to understanding more fully the

effects of zoo visitors on ape behaviour, more is learnt about the effects of a zoo visit on human attitudes towards wildlife; there is the danger that zoos might unwittingly instil negative impressions in their visitors. Visitors might leave the zoo with the notion that animals restrained in captivity deserve to be “in prison,” or that the apes resemble circus clowns. It might never even cross a zoo visitor’s mind that zoo animals can suffer, or that their wild conspecifics are threatened with extinction.

It may be the case that visitors affect animals in other zoos to a greater or lesser extent than in my study. Further research needs to be undertaken in this area, and the findings might encourage zoos to design or provision their enclosures taking into account the ways in which visitors affect ape behaviour. It cannot be accepted that animals become completely habituated to the daily and unavoidable influx of human zoo visitors.

A different angle to studying the effects of humans on ape behaviour would be to conduct research in national parks, when tourists are present. I present some anecdotal evidence from the Gombe Stream National Park in Tanzania. On one occasion, Jane Goodall was at the feeding station along with a large group of tourists. The tourists were sitting in a line watching the female chimpanzee, Fifi, with her new baby. A male chimpanzee, Goblin, was also present. Goblin got up, walked through the line of tourists, turned around and sat down between them in the line to watch Fifi, almost as though he was trying to determine what these tourists were looking at by seeing it from their perspective (Goodall, J., personal communication).

Another example of the Gombe chimpanzees interacting with tourists involves the alpha male, Frodo, who has become infamous for hitting tourists or knocking them over like dominoes, apparently for fun (Goodall, J., personal communication). In addition, Tutin and Fernandez (1987) have reported some of the responses (such as intimidation displays) by wild unhabituated gorillas and chimpanzees to primatologists in the Lopé Reserve, Gabon. It would therefore seem that the change in the behaviour of wild gorillas and chimpanzees in the

presence of humans is another potential area for future research, and could help us to further our knowledge on the behavioural flexibility of animals.

Chapter 6 – Conclusions

The purpose of this study was to investigate some of the ways in which the zoo environment can influence the typical daily behaviour of captive chimpanzees and western lowland gorillas. The primary focus of this study dealt with the possibility that there is an association between certain zoo visitor conditions and particular behavioural bouts in apes. Given that the zoo animals in my study (as in the majority of zoos) are “on exhibit” for the whole of the zoo day and are unable to retire completely from the public’s view, it is extremely important that we are aware of the implications of this.

My study addressed several issues. I wanted to know whether these zoo apes have become so habituated to their captive environment that they ignore the zoo visitors entirely. If the answer to this question were found to be “yes”, then future visitor effect studies would probably be unnecessary, at least involving the gorillas and chimpanzees at the four zoos in my investigation. Were the answer found to be “no”, that zoo apes are not completely habituated to their captive environment (associated with the presence of zoo visitors), then the subject is open for further investigation.

I have examined the effects of zoo visitor noisiness and crowd size on the number of bouts of certain behaviours in apes and have made inferences where possible as to the likely implications that this will have for the animals themselves. As discussed in Chapter 1, if ape behaviour changes in association with the specified zoo visitor variables, then it is likely to be because the visitors have either an enriching or an aversive effect on the animals. If this effect is deemed enriching for the animals, the zoos should want to know the ways in which this is going to affect the visitors themselves. The presence of zoo visitors might enrich the animals’ lives, but might not be conducive to the conservation education role of the zoos if the animals are occupied but not performing species typical behaviour (see Chapter 2 for a wider discussion of this issue). Alternatively, if zoo visitors are an enrichment “device” and do encourage species-typical behaviour in apes, then zoos would probably want to maximise

the conservation education potential by actively encouraging certain types of visitor conduct (e.g., encouraging visitors to be noisy if this was deemed enriching).

In contrast (and of greater importance from the animals' perspective), if certain types of zoo visitor characteristics mean that visitors are an aversive presence then zoos must have the accurate knowledge to enable them to address this issue and try to improve the situation. Not only will this be beneficial from the viewpoint of animal welfare, it will also help to improve the zoo's conservation education potential by exhibiting animals that are not suffering and therefore look happier to the visitors. Zoo visitors are probably less likely to be interested in the conservation of animal species that they have seen performing stereotypic behaviour, for example.

Findings from my research generally show that there is an association between the presence of particular types of zoo visitor crowd and a change in ape behaviour. Therefore, one cannot conclude that these apes are completely habituated to the zoo setting, with the exception of Colchester Zoo's dominant male chimpanzee. The data provide no evidence that this male was affected by the specified zoo visitor conditions.

The results show differential responses by the 10 ape classes to the visitor variables, and so the effects of zoo visitors are not uniform across the species, or even across animals housed within the same enclosure as one another. Some behaviours were affected in some ape classes and not in others. In addition, changes in behaviour in some groups of ape were associated with the visitor conditions but in different directions. Therefore, I have made some suggestions as to how further research into this area of zoo biology could be conducted (see Chapter 5).

My data do not provide enough evidence to conclusively state whether the effects of zoo visitors are enriching (i.e. entertaining) or aversive (i.e. annoying or threatening) to apes. However, I have made some tentative inferences based upon

the directions in which ape behaviours changed under the specified zoo visitor conditions. Overall, data from my study seem to suggest that large or noisy groups of visitors have aversive qualities in relation to certain types of ape behaviour. However, the effects do not seem to be severe, as many types of ape behaviour were unaffected by the presence of zoo visitors. The results are summarised below per ape category, regarding whether the visitor effect is probably enriching or aversive (see Chapter 5 for a more detailed account). The reader is also referred back to Models 1-4 (see Chapter 1).

1. It is possible that Chester Zoo's female chimpanzees experienced noisy and large groups of visitors as an aversive presence (these apes were observed above the ground more often than expected, and for fewer bouts of resting than expected, under these visitor conditions).
2. Chester Zoo's non-dominant male chimpanzees probably experienced noisy and large groups of zoo visitors as an aversive presence (these apes were observed at the front of the enclosure, and at ground level, for fewer bouts than expected under these visitor conditions).
3. Chester Zoo's dominant male chimpanzee might have found large groups of visitors more enriching than small ones, which is the opposite of the general proposed pattern of results (he was observed in fewer bouts of abnormal behaviour than expected in the presence of large groups of visitors).
4. Colchester Zoo's female chimpanzees possibly experienced noisy and large groups of zoo visitors as an aversive presence (they were observed for more bouts of social affiliation, and fewer resting bouts, than expected under these visitor conditions).
5. Colchester Zoo's non-dominant male chimpanzee might also have experienced noisy and large visitor groups as aversive (he was observed for more bouts of both abnormal behaviour and self-grooming than expected in

the presence of such visitors). Alternatively, he might have been entertained by the visitors' disgusted responses to his coprophagic acts.

6. Colchester Zoo's dominant male chimpanzee was the only ape category whose behaviour was entirely unaffected by the specified visitor conditions used in this study. From the data, one can therefore conclude that this male is habituated to the variations in zoo visitor crowd size and noisiness.
7. Female gorillas at Howletts Wild Animal Park might have experienced large and noisy groups of zoo visitors as either enriching or aversive (these females were observed for fewer bouts than expected at the front of the enclosure (possibly aversive), but also for fewer self-grooming bouts than expected (possibly enriching)).
8. Howletts' silverback gorilla might have experience noisy zoo visitors as aversive (he was observed for more social affiliative bouts than expected under this visitor condition).
9. Jersey Zoo's female gorillas might have experienced large groups of visitors as either enriching or aversive. These apes were observed for more bouts of social affiliation than expected under this visitor condition, which might have been an aversive effect if for reassurance, or an enriching effect if they were playing with the young male who "shows off" to visitors.
10. The data obtained for Jersey Zoo's silverback gorilla could also imply that noisy and large crowds of visitors are an aversive presence (he was observed self-grooming more often than expected under these visitor conditions).

As detailed above, the data do not enable us to make very firm conclusions regarding the effects of zoo visitors as being aversive or enriching to apes. Nonetheless it is clear that more work should be done in this field, as detailed in Chapter 5. If it can be convincingly shown that certain kinds of visitor conditions are indeed threatening or annoying to apes, no matter how low the intensity of

the effect, then zoos should make every effort to improve the zoo habitats to enable their animals to live out healthy and normal lives.

No matter how great or small the effects of zoo visitors are on ape behaviour, it is the responsibility of all those involved with the keeping of captive animals to ensure that the animals are kept in optimal conditions. Only through the continued investigation into the effects of zoo visitors on the typical daily behaviour of captive gorillas and chimpanzees (and vice versa, as mentioned in Chapter 5) can we enhance our understanding of the effects of captivity on these species. In this way we can ultimately aim to offer zoos some realistic recommendations for improving the captive setting for the sake of both the animals and the visitors. We can also increase our theoretical understanding of the relationship between human and non-human primates, and the abilities of non-human primates to adapt to captive environments.

In addition, the findings of this study highlight the importance of considering the influence of zoo visitors on ape behaviour when conducting other zoo-based research in these species. Results of studies undertaken in captivity could be biased by factors associated with zoo visitor presence. Thus the results of such studies might give inaccurate representations of captive ape behaviour unless these factors are accounted for. Therefore, there is great scope for visitor effect studies to be undertaken on all captive animal species (not just chimpanzees and gorillas).

Today we face the responsibility of dealing with the legacy that previous-day menageries have left behind. Like them or loathe them, zoos are here to stay and it is essential that every effort is made to ensure that zoo animals are ambassadors for the conservation of their wild conspecifics. Recognising the role of zoos as centres for conservation and captive breeding of endangered species is to accept the inevitable; zoos may have a bad reputation as a result of history, but all this needs to change (Nardelli, 1988). It is essential that the possible effects of zoo visitors, as part of the captive environment, are taken seriously and explored in greater detail in the future.

Bibliography

- Adams, S. and Babladelis, G. 1977. "An ecological approach to animal groups in zoos: Part 1." *International Zoo News* 24/5: 14-22.
- Akers, J. S., and Schildkraut, D. S. 1985. "Regurgitation/reingestion and coprophagy in captive gorillas." *Zoo Biology* 4: 99-109.
- Altman, J. D. 1998. "Animal activity and visitor learning at the zoo." *Anthrozoös* 11(1): 12-21.
- Altmann, J. 1974. "Observational study of behavior: sampling methods." *Behaviour* 49: 227-265.
- Altmann, J. and Muruthi, P. 1988. "Differences in daily life between semiprovisioned and wild-feeding baboons." *American Journal of Primatology* 15: 213-221.
- Animals and Ethics Working Party. 1980. *Animals and Ethics – A Report of the Working Party Convened by Edward Carpenter*. Dulverton, Somerset: Watkins Publishing.
- Ape Alliance. 1998. *The African Bushmeat Trade – A Recipe for Extinction*. Cambridge: Fauna and Flora International.
- Aspinall, J. 1986. "The Howletts Gorilla Bands." *International Zoo News* 33/1: 11-19.
- Bakeman, R. and Quera, V. 1995. *Analysing Interaction: Sequential Analysis with SDIS and GSEQ*. Cambridge: Cambridge University Press.
- Baldwin, P. J. 1979. *The Natural History of the Chimpanzee (*Pan troglodytes verus*) at Mt. Assirik, Senegal*. Unpublished PhD thesis, University of Stirling (cited in Sabater Pi, 1993).
- Batten, P. 1976. *Living Trophies*. New York: Crowell (cited in Malamud, 1998).

- Bitgood, S., Benefield, A., Patterson, D., Lewis, D., and Landers, A. 1985. "Zoo visitors: Can we make them behave?" *AAZPA Annual Conference Proceedings*. Pp. 419-432.
- Bitnoff, J. A. 1996. *The Effect of Physical Environment on the Behavior of Captive Chimpanzees: A Comparison of Three Northern California Zoos*. Unpublished MA thesis, Department of Biological Sciences, San Jose State University.
- Bostock, S. St. C. 1993. *Zoos and Animal Rights: The Ethics of Keeping Animals*. London: Routledge.
- Bruner, G. and Meller, L. 1992. "Convergent evolution in design philosophy of Gorilla habitats." *International Zoo Yearbook* 31: 213-221.
- Castles, D. L. and Whiten, A. 1998. "Post-conflict behaviour of wild olive baboons. II. Stress and self-directed behaviour." *Ethology* 104(2): 148-160.
- Chamove, A. S., Hosey, G. R., Schaetzel, P. 1988. "Visitors excite primates in zoos." *Zoo Biology* 7: 359-369.
- Chamove, A. S. and Moodie, E. M. 1990. "Are alarming events good for captive monkeys?" *Applied Animal Behaviour Science* 27: 169-176.
- Cherfas, J. 1984. *Zoo 2000: A Look Behind the Bars*. London: BBC.
- Clutton-Brock, T.H. 1977. "Appendix 1: Methodology and Measurement." Pp. 585-589. In T.H. Clutton-Brock (ed.), *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes*. London: Academic Press.
- Coe, J. C. 1985. "Design and perception: Making the zoo experience real." *Zoo Biology* 4: 197-208.
- Cook, S. and Hosey, G. R. 1995. "Interaction sequences between chimpanzees and human visitors at the zoo." *Zoo Biology* 14: 431-440.
- Doran, D. M. and McNeilage, A. 1998. "Gorilla ecology and behaviour." *Evolutionary Anthropology* 6(4): 120-131.

- Fossey, D. and Harcourt, A. H. 1977. "Feeding Ecology of Free-Ranging Mountain Gorilla (*Gorilla gorilla beringei*).” In T.H. Clutton-Brock (ed.), *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes*. Pp. 415-447. London: Academic Press.
- Fossey, D. 1988. *Gorillas in the Mist*. London: Penguin Books.
- Galbraith, J. 1996. *The Effects of Varying Audience Size and Composition on Visual Interest, Position and Behaviour of Captive Chimpanzees*. Unpublished BSc thesis, Department of Biological Sciences, Napier University, Edinburgh.
- Garner, K. J. and Ryder, O. A. 1996. "Mitochondrial DNA diversity in gorillas.” *Molecular Phylogenetics and Evolution* 6 (1): 39-48.
- Glatson, A. R., Geilvoet-Soeteman, E., Hora-Pecek, E., and van Hooff, J. A. R. A. M. 1984. "The influence of the zoo environment on social behavior of groups of cotton-topped tamarins, *Sanguinus oedipus oedipus*.” *Zoo Biology* 3: 241-253.
- Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge, Mass.: Harvard University Press.
- Hahn, E. 1968. *Zoos*. London: Martin Secker and Warburg Ltd.
- Hatley, J. 1980. "The educational role of zoos.” *International Zoo News* 27/7: 4-11.
- Hediger, H. 1955. *The Psychology of Animals in Zoos and Circuses*. London: Butterworths Scientific Publications.
- Hediger, H. 1969. *Man and Animal in the Zoo*. London: Routledge and Kegan Paul Ltd.
- Hosey, G. R. 1997. "Behavioural research in zoos: Academic perspectives.” *Applied Animal Behaviour Science* 51: 199-207.

- Hosey, G. R., and Druck, P. L. 1987. "The influence of zoo visitors on the behaviour of captive primates." *Applied Animal Behaviour Science* 18: 19-29.
- Hutchings, M., Hancocks, D., Calip, T. 1978. "Behavioral engineering in the zoo: A critique." *International Zoo News* 25/7: 16-23.
- Jones, C. and Sabater Pi, J. 1971. Comparative Ecology of *Gorilla gorilla* (Savage and Wyman) and *Pan troglodytes* (Blumenbach) in Rio Muni, West Africa. *Bibliotheca Primatologica* 13: 1-96. Basel: Karger.
- Jones-Davies, K. 1996. *An Investigation into Visitor Behaviour at Edinburgh Zoo*. Unpublished BSc thesis, Department of Psychology, University of Stirling.
- Kawata, K. and Hendy, M. 1978. "Zoo-going and animal popularity." *International Zoo News* 25/7: 14-15.
- Lemmon, T. 1994. *Chimpanzees*. London: Whittet Books.
- Maier, F and Page, J. 1990. *Zoo: The Modern Ark*. New York: Facts on File, Inc.
- Malamud, R. 1998. *Reading Zoos: Representations of Animals and Captivity*. London: Macmillan Press Ltd.
- Maple, T. L. 1980. *Orang-utan Behavior*. New York: Van Nostrand Reinhold Company.
- Maple, T. L. and Hoff, M. P. 1982. *Gorilla Behavior*. New York: Van Nostrand Reinhold Company.
- Margodt, K. 1999. *The Welfare Ark: Suggestions for a Renewed Policy in Zoos*. In press.
- Markowitz, H. 1982. *Behavioural Enrichment in the Zoo*. New York: Van Nostrand Reinhold Company.

- Martin, P. and Bateson, P. 1994. *Measuring Behaviour: An Introductory Guide*. Cambridge: Cambridge University Press.
- Martin, R. 1976. "Breeding great apes in captivity." *New Scientist* 14: 100-102.
- McGrew, W. C. 1992. *Chimpanzee Material Culture: Implication for Human Evolution*. Cambridge: Cambridge University Press.
- McKenna, V. 1987. *Beyond the Bars: The Zoo Dilemma*. UK: Thorsons Publishing Group Ltd.
- Meyer-Holzapfel, M. 1968. "Abnormal behavior in zoo animals." Philadelphia: W. B. Saunders Co.
- Mitchell, G., Herring, F., Tromborg, C., Dowd, B., Steiner, S., and Obradovich, S. 1992. "Targets of aggressive facial displays by golden-bellied mangabeys (*Cercocebus galeritus chrysogaster*) at the Sacramento Zoo." *Applied Animal Behaviour Science* 33: 249-259.
- Mittermeier, R. A. 1997. "Foreword." In J. Wallis (ed.), *Primate Conservation: The Role of Zoological Parks*. Pp. xi-xiii. USA: The American Society of Primatologists.
- Mullan, B. and Marvin, G. 1987. *Zoo Culture*. London: Weidenfeld and Nicholson.
- Napier, J. R. and Napier, P. H. 1985. *The Natural History of the Primates*. Cambridge: Cambridge University Press.
- Nardelli, F. 1988. "The zoo: Last haven, last chance?" *International Zoo News* 35/1: 17-24.
- Patterson, J. D. 1992. *Primate Behavior: An Exercise Workbook*. Illinois: Waveland Press.
- Perkins, L. A. 1992. "Variables that influence the activity of captive orangutans." *Zoo Biology* 11: 177-186.

- Poole, T. B. 1988. "Normal and Abnormal Behaviour in Captive Primates." *Selected Proceedings of the XIIth IPS-Congress. Primate Report* 22: 3-12.
- Price, E. C., Ashmore, L. A., McGivern, A-M. 1994. "Reactions of zoo visitors to free-ranging monkeys." *Zoo Biology* 13: 355-373.
- Reynolds V. 1965. *Budongo: A Forest and its Chimpanzees*. London: Methuen and Co. Ltd.
- Reynolds, V. 1968. *The Apes*. London: Cassell and Company Ltd.
- Richards, A. F. 1985. *Primates in Nature*. New York: W. H. Freeman and Company.
- Rice, J. A. 1995. *Mathematical Statistics and Data Analysis*. Duxbury Press.
- Rybot, D. 1972. *It Began Before Noah*. London: Michael Joseph Ltd.
- Sabater Pi, J. 1993. *Gorilas y Chimpancés del África Occidental: Estudio Comparativo de su Conducta y Ecología en Libertad*. México: Fondo de Cultura Económica.
- Schaller, G. B. 1963. *The Mountain Gorilla: Ecology and Behavior*. Chicago: University of Chicago Press.
- Scothern, P. 1997. "I Could Watch the Animals all Day." *An Analysis of some Aspects of Zoo Visitor Behaviour*. Unpublished BA (Hons) thesis, University College Stockton.
- Siegel, S. and Castellán, N. J. 1988. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill Book Company.
- Snyder, R. L. 1975. "Behavioral stress in captive animals." Pp. 41-76. In *Research in Zoos and Aquariums*. Washington, DC: National Academy of Sciences.
- Sommer, R. 1972. "What do we learn at the zoo?" *Natural History* 81(7): 26-29 and 84-84

- Stoinski, T., Beck, B., Bowman, M., Lehnhardt, J. 1997. "The Gateway Zoo Program: A recent initiative in golden lion tamarin reintroductions." In J. Wallis (ed.), *Primate Conservation: the Role of Zoological Parks*. Pp. 113-129. USA: American Society of Primatologists.
- Tutin, C. E. G. and Fernandez, M. 1987. "Responses of wild chimpanzees and gorillas to the arrival of primatologists: Behaviour observed during habituation." *International Journal of Primatology* 8(5): 192
- Tutin, C. E. G. 1996. "Reproductive success story: Variability among chimpanzees and comparisons with gorillas. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal and P. G. Heltne (eds.), *Chimpanzee Cultures*. Pp. 181-193. Cambridge, Mass.: Harvard University Press.
- Tutin, C. E. G. 1997. "Ranging and social structure of lowland gorillas in the Lopé Reserve, Gabon." In W. C. McGrew, Marchant, L. F. and Nishida, T. (eds.), *Great Ape Societies*. Pp. 58-69. Cambridge: Cambridge University Press.
- de Waal, F. B. M. 1991. *Peacemaking Among Primates*. London: Penguin Books.
- de Waal, F. B. M. 1996. "Chimpanzee's adaptive potential." In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal and P. G. Heltne (eds.), *Chimpanzee Cultures*. Pp. 243-260. Cambridge, Mass.: Harvard University Press.
- Wallis, J. 1997. "From ancient expeditions to modern exhibitions: The evolution of primate conservation in the zoo community." In J. Wallis (ed.), *Primate Conservation: The Role of Zoological Parks*. Pp. 1-27. USA: The American Society of Primatologists.
- Wilson, S. F. 1982. "Environmental influences on the activity of captive apes." *Zoo Biology* 1: 201-209.
- Wood, W. H. 1995. *Environmental Influences upon the Relationship of Engagement in Occupation to Adaptation among Captive Chimpanzees*. Unpublished PhD thesis, Occupational Science, University of Southern California.

Wrangham, R. W., de Waal, F. B. M. and McGrew, W. C. 1996. "The challenge of behavioural diversity." In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal and P. G. Heltne (eds.), *Chimpanzee Cultures*. Pp. 1-18. Cambridge, Mass.: Harvard University Press.

Yamagiwa, J., Maruhashi, T., Yumoto, T., Mwanza, N. "Dietary and ranging overlap in sympatric gorillas and chimpanzees in Kahuzi-Biega National Park, Zaïre." In W. C. McGrew, L. F. Marchant and T. Noshida (eds.), *Great Ape Societies*. Pp. 82-98. Cambridge: Cambridge University Press.

Yerkes, R. M. 1925. *Almost Human*. New York: Century (cited in Bitnoff, 1996).

