Zoo visitors influence behaviour and enclosure use in lion-tailed macaques (*Macaca silenus*)

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ABSTRACT

In order to assess the impact that zoo visitors had on captive lion-tailed macaque behaviour, an observational study was conducted on five individual macaques housed at Chester Zoo. From the literature review it was established that zoo visitors may have an effect on the behaviour of captive primates. However, too few studies had been conducted on the effect zoo visitors may have on lion-tailed macaques. As the species is endangered, any research that can shed light on how they are coping in captivity was considered vital. The behaviour of the macaques, and their vertical location within the enclosure was observed during times of high, medium and low visitor presence. Also, both visitor numbers and visitor coverage of the macaque enclosure were recorded. It was found that visitors did not affect the macaques' social behaviour, but they did affect non-social behaviour. Visitors also had an impact on the vertical location of the macaques within the enclosure. The present study was one of the first to indentify a visitor effect on lion-tailed macaques in an enriched enclosure. From the study it was suggested that zoo visitor effects may be alleviated by the use of a retreat space within the macaque enclosure. Future research may consider not only the vertical location of the macaques, but also whether they spend more time near the front or back of the enclosure in relation to visitor numbers.

KEY WORDS:	**CAPTIVE WELFARE**	**SELF-DIRECTED BEHAVIOURS**	**ZOO RESEARCH**	**ANXIETY**	**ENRICHED ENCLOSURE**

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Table of Contents

List of Tables

List of Figures

Zoo visitors influence behaviour and enclosure use in lion-tailed macaques (*Macaca silenus*)

Stress in captive animals

When considering animals in captivity, stress may play an important role. Broom and Johnson (1993) suggested that stress in captive animals is the physical and psychological state of an animal in how it copes with its environment. The greatest stressor in populations of captive animals stems from being unable to escape from situations, whereas wild animals have the opportunity to avoid unpleasant or stressful situations (Morgan & Tromborg, 2006). For example, altercations involving another animal or contact with humans are avoidable by wild animals, whereas animals in captivity are forced to face them. Indeed, Broom and Johnson (1993) reported that abnormal behaviours seen in zoo animals may be formed due to an inability to escape from unpleasant situations. Thus, it seems unavoidable that when faced with such inescapable situations, many captive animals potentially become stressed.

Such stress may have a deleterious effect upon captive animals (Mallapur, Qureshi & Chellam, 2002; Clubb & Mason, 2003). For example, stress may be manifested in impaired reproduction. Dobson and Smith (2000) found strong evidence to suggest that dairy cows (*Bos taurus*) subjected to stress have reduced reproductive activity. Also, Turner, Hemsworth and Tilbrook (2005) found that sustained levels of elevated cortisol in female pigs (*Sus scrofa domestica*) led to impaired reproduction. As one of the main aims of zoos is to promote captive breeding (Ballantyne, Packer, Hughes & Dierking, 2007), the level of stress experienced by zoo-housed animals is an important factor to consider. In addition, animals in captivity experiencing stress will often retreat to a preferred area of the enclosure. For example, when threatened, captive rats (*Rattus norvegicus*) consistently fled to a preferred area of their enclosure (de Oca, Minor & Fanselow, 2007). Similarly, Ross. Schapiro, Hau and Lukas (2009) established that when presented with unfamiliar stimuli, captive gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*) showed a preference for corners. These corners were thought to be associated with natural barriers, such as trees or rocks, which may provide protection in the wild.

Enclosure complexity may also play a role on the activity budgets of captive animals. Mallapur, Qureshi and Chellam (2002) found that captive Indian leopards housed in barren environments used the edge zone nearest to the visitors more than those housed in enriched enclosures. Such findings are supported by those of Reinhardt, Liss and Stevens (1996) and Hosey (2004), who established that enclosure design has an influence on the behaviour of non-human primates. Indeed, one of the best predictors of species-specific behaviours in captive primates was the presence of objects within the enclosure, such as poles or ropes for climbing (Wilson, 1982). Furthermore, Herbert and Bard (2000) found that orang-utans (*Pongo pygmaeus*) housed in enriched enclosures with high structures resembling trees spent significantly more time higher up in the 'trees'. The authors argued that including such structures in the enclosure encouraged this arboreal animal to engage in species-specific behaviour.

There has been particular concern about the welfare of primates housed in zoo settings. Hosey (2004) states that although the welfare of animals in the zoo environment is considered important, captive environments can cause abnormal behaviours that are unseen in the wild, and this is especially true in the case of primates. The International Primatological Society (2007) states that primates need a complex and stimulating environment for their psychological well-being. A poor environment may be reflected in behaviours such as stereotypes, restricted behavioural repertoires and abnormal activity budgets (Glatson, Soeteman, Pecek & Hooff, 1984; Lambeth, Bloomsmith, & Alford, 1997; Chang, Forthman & Maple, 1999). For example, abnormal behaviours may develop in primates such as gorillas and mandrills (*Mandrillus spinx*) that naturally live in large groups. These primates often exhibit abnormal behaviours when housed alone or in small groups. Captive breeding of these animals was significantly improved when they were housed in large groups (Price & Stoinski, 2000). The authors argued that group size is a stress mediator, thus by housing primates in a more naturalistic social environment any stress resulting from captivity is reduced.

Zoo visitors and animal stress

Arguably, one of the most important aspects of a captive zoo animal's daily life is zoo visitors. In order for zoos to increase awareness regarding the importance of conservation, increased visitor-animal contact is unavoidable. The importance of educating zoo visitors may be evidenced in the findings of Barney, Mintzes and Yen (2005), who established that a poor understanding of captive bottlenose dolphins (*Tursiops truncates*) led to a higher risk of zoo visitors behaving poorly towards them. Further studies demonstrate that zoo visitors exhibit fewer negative attitudes towards captive animals once they have been educated about them in a zoo environment (Tofield, Coll, Vyle & Bolstad, 2003; Lukas & Ross, 2005). Such studies show that visitor contact may be a necessity in zoos in order to promote conservation and public awareness.

In the case of captive primates, the presence of zoo visitors may be enriching, alleviating some of the monotony they experience in captivity (Morris, 1964; Hosey, 2000). However, zoo visitors may have a negative effect on the behaviour of captive primates. Chamove, Hosey and Schaetzel (1988) found that during high visitor numbers captive primates tended to increase agonistic behaviour and decrease their levels of inactivity and grooming. Zoo visitors may also be a source of anxiety for captive primates, having an effect on behaviour. Barros and Tomaz (2002) proposed the human threat/confrontation model to test fear and anxiety in non-human primates within captive settings. This model is based on previous research that suggests that the mere presence of a human observer is capable of eliciting defensive attacks and anxiety related behaviours in captive primates. By way of example, several studies indicate that the presence of human observers in zoos is stressful for primates (bonnet macaques, *M. Radiata*, Singh & Vinathe, 1990; chimpanzees, Lambeth, Bloomsmith & Alford, 1997; orang-utans, Birke, 2002; spider monkeys, *Ateles geoffroyi*, Davis, Schaffner & Smith, 2005; diana monkeys, *Cercopithecus diana,* Todd et al, 2007; gorillas, Carder & Semple, 2008). This stress may be evidenced in elevated scratching (Schino et al 1996; Castles, Whiten & Aureli, 1999; Wells, 2005; Carder & Semple, 2008), increased cortisol levels (Davis et al., 2005), and in increased rates of yawning (Hadidian, 1980; Mallapur, Waran & Sinha, 2005a). A further indicator of stress in primates may be in increased levels of monitoring. Maestripieri (1993) found that rhesus macaque (*M. mulatta*) mothers spent more time monitoring their surroundings when they had young infants who may engage in dangerous activities. As the infants grew older the level of monitoring by the mother decreased. These findings may be linked to those of Cooke and Schillaci (2007), who found that the monitoring of visitors by captive white handed gibbons (*Hylobates lar*), was linked to a perceived threat from them.

Visitor impact in lion-tailed macaques

Although many studies have been conducted on the effects that visitors have upon captive primates, very few have specifically been conducted upon lion-tailed macaques (*M. silenus*). As the lion-tailed macaque is one of the most shy and least vocal of primates, it is also one of the least studied (Easa et al., 1994). Kumar and Karup (1993) found that the lion-tailed macaque has a low capability for coping with rapid changes in resources and recovering from population fluctuations. Therefore, any research that can illustrate how lion-tailed macaques are coping in captivity is vital, as reintroduction from captive breeding may soon be the only way the wild population of macaques can survive. As the lion-tailed macaque is considered endangered (IUCN, 2009, http://www.iucnredlist.org), any hindrance to captive breeding will have a negative impact upon the survival of the species. This was found by Mallapur, Waran and Sinha (2006), as many Indian zoos that housed their lion-tailed macaques alone or in poor conditions experienced difficulties with captive breeding; only one zoo out of 18 in India, which maintained lion-tailed macaques, managed to breed them. Conversely, Lindberg et al. (1997, as cited in Mallapur et al., 2006) argues that the intensified effort and advanced management techniques carried out at a small number of American zoos in the 1980s caused the captive lion-tailed macaque population to double in size.

Lion-tailed macaques may experience difficulty in coping with the captive environment. For example, abnormal behaviours such as floating limb, stereotypes and self-harm were only seen in captive lion-tailed macaques and never in their wild counterparts (Mallapur, Waran & Sinha, 2004). Abnormal behaviours may be attributed to a barren and unstimulating environment (Mallapur et al. 2006), and in lion-tailed macaques the level of abnormal behaviour was linked to the complexity of the enclosure. Furthermore, lion-tailed macaques housed in Indian zoos are occasionally housed individually or with only one other macaque. Mallapur et al. (2006) found that lion-tailed macaques housed alone were likely to develop abnormal behaviours when compared with macaques housed in social groups.

As omnivores, feeding on a wide range of fauna including fruit and insects (Mallapur et al. 2004), lion-tailed macaques may be especially affected by the quality of their environment. Kumar and Kurup (1993) established that lion-tailed macaques living in undisturbed, protected forests spent almost half their time foraging and feeding, whereas macaques in disturbed forest fragments spent less time foraging and resting, and more time in locomotion (Menon & Poirier, 1996). Such findings suggest that when lion-tailed macaques are disturbed by people their activity budget changes. Thus, when considering the behaviour of lion-tailed macaques within a captive setting, changes to their activity budget may be of importance. Mallapur, Waran & Sinha (2005b) stated that omnivorous primates in captivity are more likely to exhibit abnormal behaviours as in the wild they spend a considerable amount of time foraging. If they are housed in environments that do not afford them the opportunity to forage, then abnormal behaviours may develop out of frustration. It has also been established that lion-tailed macaques housed in small, barren enclosures spent much of their time in the area of the enclosure that was closest to the visitors, the edge zone; presumably to break the monotony they experienced (Mallapur et al. 2005b). In contrast, lion-tailed macaques housed in enriched enclosures spend most of their time performing social behaviours and spent more time higher up in the enclosure away from visitors (Mallapur et al. 2005b). As the lion-tailed macaque is primarily an arboreal species, preferring the upper canopy of tropical rainforests (Kumar, Singh & Molur, 2008), it may be expected that captive macaques housed in enriched enclosures should prefer the upper areas of their enclosure. This was the case in research by Skyner (2006), who found that captive lion-tailed macaques generally preferred the upper areas of their enclosures. However, when visitors were present lion-tailed macaques preferred the bottom areas of their enclosure when visitor numbers were high and positioned themselves as far away from visitors as possible (Skyner, 2006).

Zoo visitors may also exacerbate the effects of a barren zoo environment on lion-tailed macaques. This was certainly the case in the study by Mallapur et al. (2005a), who considered the effects of visitor presence upon the behaviour of captive lion-tailed macaques housed in Indian zoos. It was found that higher concentrations of zoo visitors elicited a greater number of abnormal behaviours from the macaques, and also had an impact on their behaviour in general, affecting social, aggressive and mating behaviours.

A further explanation for why lion-tailed macaques often have difficulty in coping in a captive environment may be because they naturally have large home ranges (Umpathy & Kumar, 2000). Thus, the confines of the zoo enclosure may increase the chances of abnormal behaviour developing due to the restriction of natural roaming behaviour. Mallapur et al. (2005b) stated that the captive environment imposes a setting that differs vastly from that in which lion-tailed macaques have evolved to live in. To thrive in captivity the monkeys must accommodate these differences, and how well their enclosure resembles their natural environment can help them to cope in captivity. Therefore, in order to encourage captive lion-tailed macaques to engage in natural, species-specific behaviours, environmental enrichment is required. Carlstead and Shepardson (1994) state that providing enriched environments will afford captive animals more of the behavioural opportunities they would find in the wild, a concept which has been supported by many studies (Reinhardt et al., 1996; Mallapur et al., 2005a; Honess & Marin, 2006; Clubb & Mason, 2007).

As previous studies have shown, the behaviour of primates that are kept in captivity can become abnormal (Novak & Suomi, 1988; Crockett et al., 1995; Mallapur & Choudhury, 2003). Such behavioural abnormalities may be exacerbated if primates are maintained in a suboptimal facility (Mallapur et al., 2004; Mallapur et al., 2005a; Mallapur et al., 2005b). Thus, as visitors have already been established as a potential stressor for captive primates (Singh & Vinathe, 1990; Lambeth et al., 1997, Wood, 1998; Birke, 2002; Davis et al., 2005; Wells, 2005; Todd et al., 2007; Carder & Semple, 2008), it seems apparent that a poor captive environment coupled with stressful visitor interactions may have a negative impact upon the behaviour of the animal.

In the current study, the previous investigation by Mallapur et al. (2005a) was used as a basis for research. Although a negative visitor effect was found in that study, the results may not be generalised to western zoos as they only included lion-tailed macaques that were housed in Indian zoos. Animals housed in Indian zoos are often kept in sub-optimal facilities, which adversely influence the behavioural repertoires of captive non-human primates (Mallapur & Choudhury, 2003; Mallapur et al., 2004). Furthermore, visitors to these zoos often antagonised the lion-tailed macaques by throwing items at them or shouting. Such animal-visitor interactions would clearly result in increased stress experienced by the animal, and therefore result in behaviour changes. In direct contrast, most western zoos house their animals in enriched enclosures, and visitors to these zoos have little opportunity to harass the animals. This may be reflected in the research by Lindberg (1997, as cited in Mallapur et al., 2007), who found that captive lion-tailed macaques housed in India are breeding in only one of the 18 zoos nationally that house them. In contrast, lion-tailed macaques housed in western zoos have bred so successfully that such programmes have had to be controlled in order to conserve space (Skyner, 2006).

In order to generate results that are applicable to western zoos, further research into how visitors affect lion-tailed macaque behaviour in enriched enclosures is essential. Therefore, the main aim of this study was to assess whether the behaviour of captive lion-tailed macaques held at Chester Zoo was affected by visitors to the enclosure, with a view to making suggestions on how visitor impact may be reduced in order to promote the welfare of the macaques. In order to achieve this, the behaviour and location of the macaques was observed during times of high, medium and low visitor numbers. There have been few previous studies that have considered how visitors affect both the behaviour and location of captive lion-tailed macaques in enriched enclosures. This study aims to provide an insight into the complex way that zoo visitors can affect zoo animals.

The following predictions were set out for the study. Previous research has indicated that zoo visitors may cause an increase in agonistic behaviour and a decrease in foraging and resting behaviours in captive primates (Chamove et al., 1988; Mallapur et al., 2005a; Hosey, 2008). Thus, it was predicted that the behaviour of the lion-tailed macaques would be affected by increased visitor numbers and increased visitor coverage of the enclosure. Research also suggests that captive animals experiencing stress will retreat to an area of the enclosure that is considered safe (de Oca et al., 2007; Ross et al., 2009). As lion-tailed macaques are a primarily arboreal species (Kumar et al., 2008), it may be expected that when stressed they retreat to a higher part of the enclosure. Although previous research has indicated that captive lion-tailed macaques prefer the bottom area of their enclosure during periods of high visitor numbers (Skyner, 2006), no research has considered whether visitor coverage or visitor density has an effect on enclosure use. Therefore, it was expected that the vertical location of the macaques within the enclosure would differ depending on visitor density and coverage.

Method

Subjects

Subjects were five captive lion-tailed macaques (*M. silenus*) housed in a group of 21 captive lion-tailed macaques at Chester Zoological Gardens (details of subjects are shown in Table 1). Ethical approval was obtained from the Psychology Department at the University of Chester, and from Chester Zoo. The lion-tailed macaques had access to indoor and outdoor areas that were connected by three tunnels. However, for the purposes of this study the macaques were only observed when they were in the inside enclosure. The indoor enclosure ($1092m^3$) had wood bark deep litter as a floor substrate, and many poles, ropes, platforms and branches to stimulate natural behaviours. The macaques were scatter fed on various seeds, nuts and primate pellets in the morning, and were also fed a variety of fruits and vegetables at random times twice daily. Water was available from an artificial pond on an *ad libitum* basis.

Table 1
Characteristics of focal subjects

Focal ID	Sex	Age
Jimmy	M	7
Kitty	F	5
Tia	F	8
Tina	F	14
Reme	F	16

Measures

In order to accurately observe the behaviour of the macaques, an ethogram was constructed. Existing data from previous studies on lion-tailed macaques (Mallapur et al., 2005a; Skyner, 2006) were used to construct the ethogram, alongside preliminary observations of the macaques by the researcher using *ad libitum* sampling (Martin & Bateson, 2007).

In order to accurately report the location of each focal animal, a plan of the lion-tailed macaque enclosure was obtained. The enclosure was divided vertically into three sections; 1, 2 and 3 (figure 1). The animal's vertical location within the enclosure could therefore be accurately reported. Observed behaviours, locations and visitor densities were recorded on tables constructed on Microsoft Excel 2007, and a stopwatch was used to accurately report time.

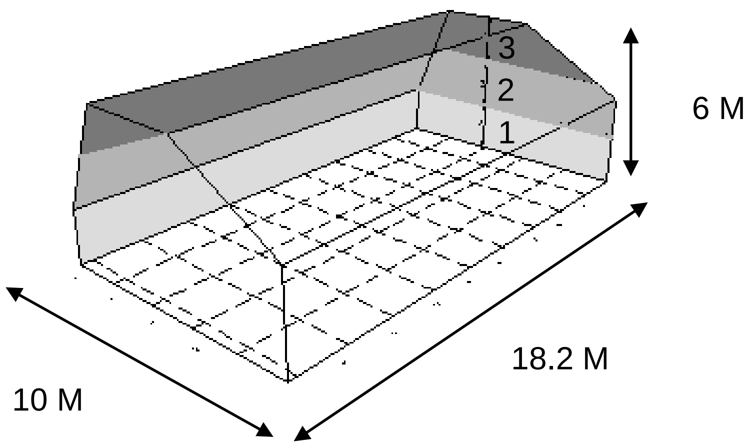

Figure 1: Levels 1, 2 and 3 of the macaque enclosure

Procedure

The macaques were observed for a total of 14 hours on days when a low number of visitors were expected, and 14 hours on days when a high number of visitors were expected, resulting in 28 hours of data. The lion-tailed macaques were available for observation from 10.00 to 17.00 hours, either inside the monkey house or in the outside enclosure.

At the beginning of each period of data gathering, visitor presence around the enclosure was determined. Visitor numbers were monitored in two ways: an absolute count of visitor numbers and the percentage of enclosure window covered by visitors were recorded at the start of every scan, and also recorded each time the focal animal changed its location or behaviour. Two measures of visitor presence were chosen because they would provide a clearer picture of exactly which aspects of visitor presence the macaques would be most affected by, either visitor density or coverage.

To obtain data, the macaques were observed using continuous recording (Martin & Bateson, 2007). This was used as all occurrences of behaviour that each focal animal exhibited over 10 minutes would be recorded, and so an accurate representation of that particular macaque's activity budget would be recorded. The order of focal animals in each observation period was randomised before each session began, and it was ensured that each animal received equal amounts of observation for each time slot. Therefore, each of the five macaques chosen was studied equally and no bias occurred.

The behaviour of a focal animal was observed for 10 minutes using continuous recording (Martin & Bateson, 2007), totalling 50 minutes to observe all five focal animals. The location of the current focal animal was observed, and then recorded as a number, such as '1', depending on their location within the enclosure. Within the 10 minute period, each time the focal animal changed its location or behaviour it was recorded.

In order to assess the amount of visitor coverage, the six windows spanning the front of the enclosure were divided into a percentage, for example three windows equalled 50%. When visitors were present, the approximate amount of the windows they covered was recorded as a percentage. Approximate visitor numbers for each focal sample were determined by a count at the beginning of each period of data collection.

Design & Analysis

Data were maintained using Microsoft Excel 2007, and data management, reduction and extraction was conducted using the Pivot Tables function in Microsoft Excel 2007. Instances in which the focal animal was out of sight were not included in the analysis and behavioural rates were corrected for these time differences in view.

Due to the small number of subjects used in the study, a randomisation test approach was employed. Although visual inspection has been described as an appropriate way to analyse data gathered from small samples (Saudergas & Drummer, 1996), it is now considered prudent to use statistical tests (Edgington, 1982, cited in Saudergas & Drummer, 1996), such as randomisation tests. Such tests are useful when a small sample size has been used because they do not discard information in the data by reducing them to ranks (Todman & Dugard, 2001). A randomisation test works by re-ordering given data according to a set number of arrangements, in this case 2,000. The amount of generated data arrangements that are as large as the obtained value are used to derive the probability that such a value could have occurred by chance (Todman & Dugard, 2001). In the present case, whenever the generated arrangements obtained results that were at least as large as the observed scores fewer than 100 times, a significant result was obtained. An alpha level of $p \leq 0.05$ was used in the analyses, and a macro developed for use with SPSS was employed to generate the statistical tests and was analogous to one-way repeated measures analysis of variance (macro provided, Todman & Dugard, 2001). The statistical test 'residual sum of squares' (referred to from this point on as RSS) test statistic is obtained from the actual sums of squares for a given dataset, and therefore do not systematically correspond to the *p* value as would be the case with more conventional statistical tests (Todman & Dugard, 2001). Finally, each statistical test performed is derived from the shuffling of obtained data and therefore can vary each time. As a result, each test was performed three times on the same data, and was only deemed significant if at least two of the three iterations yielded significant results (Todman & Dugard, 2001). Only one result from the three generated is presented in the Results section. Finally, to determine where significance lay among different treatment conditions a visual inspection of the data was used following the recommendation of Todman and Dugard (2001).

Results

Social Behaviour

Across different visitor categories, there were no significant differences in social behaviour (see Table 2 for descriptive statistics). For aggression, out of the 2000 randomly sampled data divisions, 511 were as least as large as the obtained data ($RSS = 0.004$, $p = 0.26$). For allogroom, the number of arrangements that were at least as large as the obtained data was 723 ($RSS = 0.003$, $p = 0.36$). For contact, 200 of the data arrangements were at least as large as the obtained data ($RSS = 0.0002$, $p = 0.10$). Clasping was also not affected by visitor numbers, as out of 2000 randomly sampled data divisions, 205 were at least as large as the obtained data ($RSS = 0.001$, $p = 0.103$). For social play, out of the 2000 randomly sampled data divisions, 1289 were at least as large as the obtained data ($RSS = 0.0002$, $p = 0.65$).

Table 2
Means (±SEMs) for social behaviours per 50 minutes across visitor categories

Social Behaviour	Category A	Category B	Category C
Aggression	.001 (.001)	.004 (.004)	.03 (.01)
Allogroom	.06 (.02)	.07 (0.02)	.07 (0.01)
Contact	.002 (.002)	.004 (.004)	.002 (.002)
Clasping	.005 (0.003)	.004 (.004)	.02 (.006)
Social Play	.005 (0.003)	0 (0)	.006 (.003)

Across different visitor coverage levels, there were also no significant differences in social behaviour (see Table 3). For aggression, out of the 2000 randomly sampled data divisions, 510 were as least as large as the obtained data (*RSS* = 0.008, *p* = 0.27). Levels of allogrooming were not affected by visitor coverage, as 291arrangements were as least as large as the obtained data, (*RSS* = 0.02, *p* = 0.15). Contact between macaques was also not affected by visitor coverage. Out of the 2000 randomly sampled data divisions, 200 were as least as large as the obtained data (*RSS* = 0.0004, *p* = 0.10). For clasping, out of the 2000 randomly sampled data divisions, 442 were as least as large as the obtained data, (*RSS* = 0.005, *p* = 0.22). Finally, social play was not affected by visitor coverage, as out of the 2000 randomly sampled data divisions, 200 were as least as large as the obtained data (*RSS* = 0.002, *p* = 0.10).

Table 3
Means (±SEMs) for social behaviours per 50 minutes across visitor coverage

Social Behaviour	Coverage 0-20%	Coverage 20-50%	Coverage 50-70%	Coverage 50-70%
Aggression	0 (0)	.01 (.006)	.02 (.01)	.03 (.02)
Allogroom	.06 (.03)	.06 (.03)	.10 (.03)	.12 (.04)
Contact	.002 (.002)	.003 (.003)	.003 (.003)	.007 (.007)
Clasping	.005 (.003)	.007 (.005)	.009 (.005)	.03 (.0002)
Social Play	.005 (.003)	.005 (.003)	.003 (.003)	.01 (.01)

Non-Social Behaviour

Across different visitor categories there were no significant differences in non-social behaviours (see Table 4 for descriptive statistics). Autogrooming behaviour was not significantly affected by visitor numbers. The number of arrangements that were at least as large as the obtained data was 1078 (*RSS* = 0.006, *p* = 0.54). For foraging, out of the 2000 randomly sampled data divisions, 1364 were as least as large as the obtained data, (*RSS* = 0.02, *p* = 0.68). Fleeing was also not affected by visitor numbers, as 1353 arrangements were as least as large as the obtained data (*RSS* = 0.002, *p* = 0.68). For inactivity, out of the 2000 randomly sampled data divisions, 1116 were as least as large as the obtained data (*RSS* = 0.02, *p* = 0.56). Finally, for self-scratching out of the 2000 randomly sampled data divisions, 160 were as least as large as the obtained data, and therefore the test statistic approached significance (*RSS* = 0.007, *p* = 0.08).

Table 4
Means (±SEMs) for non-social behaviours per 50 minutes across visitor categories

Non-social Behaviour	Category A	Category B	Category C
Autogroom	.02 (.00)	.04 (.02)	.04 (.009)
Foraging	.10 (.02)	.12 (.03)	.11 (.02)
Fleeing	.001 (.001)	.01 (.007)	.009 (.008)
Inactivity	.11 (.03)	.10 (.02)	.06 (.03)
Self-scratching	.02 (.008)	.03 (.007)	.08 (.02)

Some non-social behaviour was affected by visitor numbers. The macaques performed more monitoring behaviour when more visitors were present (Figure 2). Out of the 2000 randomly sampled data divisions, only 9 were at least as large as the obtained data, therefore the statistic was significant (*RSS* = 0.04, *p* = 0.005). Visual inspection of Figure 1 indicates that the high visitor category was significantly different from the other visitor categories. Yawning was also significant across visitor categories; the macaques yawned more when more visitors were present (Figure 3). Out of the 2000 randomly sampled data divisions, only 81 were at least as large as the obtained data, therefore the statistic was significant (*RSS* = 0.004, *p* = 0.05). Visual inspection of Figure 2 indicates that the medium and high visitor categories were significantly different from the low visitor category.

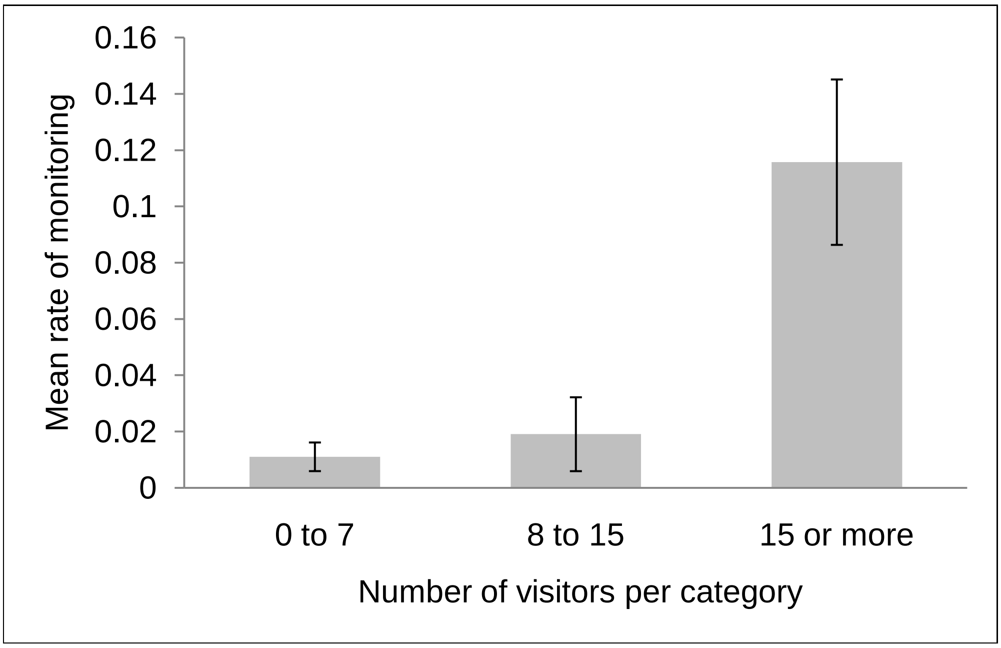

Figure 2: Mean rates of monitoring per 50 minutes are shown across the three different visitor categories

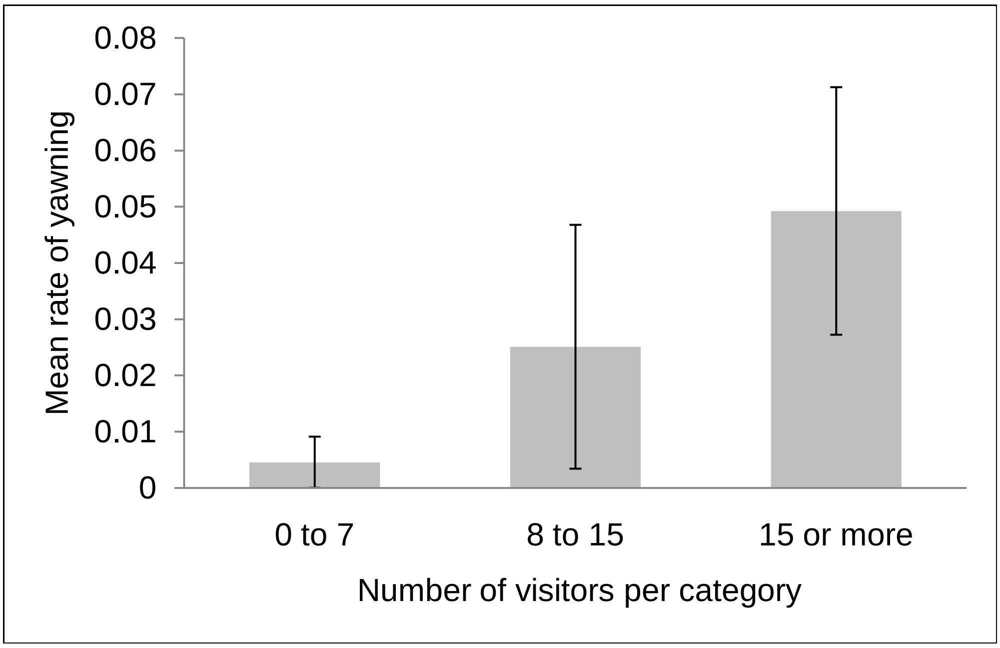

Figure 3: Mean rates of yawing per 50 minutes are shown across the three different visitor categories

Finally, although autogrooming and self-scratching were not significantly different when tested on their own, when they were collapsed together into the class of behaviours 'self-directed behaviours', they were significant across visitor categories. The macaques performed more self-directed behaviours when more visitors were present (Figure 4). Out of the 2000 randomly sampled data divisions, only 79 were at least as large as the obtained data, therefore the statistic was significant (*RSS* = 0.01, $p = 0.04$). Visual inspection of the means indicates that self-directed behaviours were highest under the category of 15 or more visitors compared to the other categories.

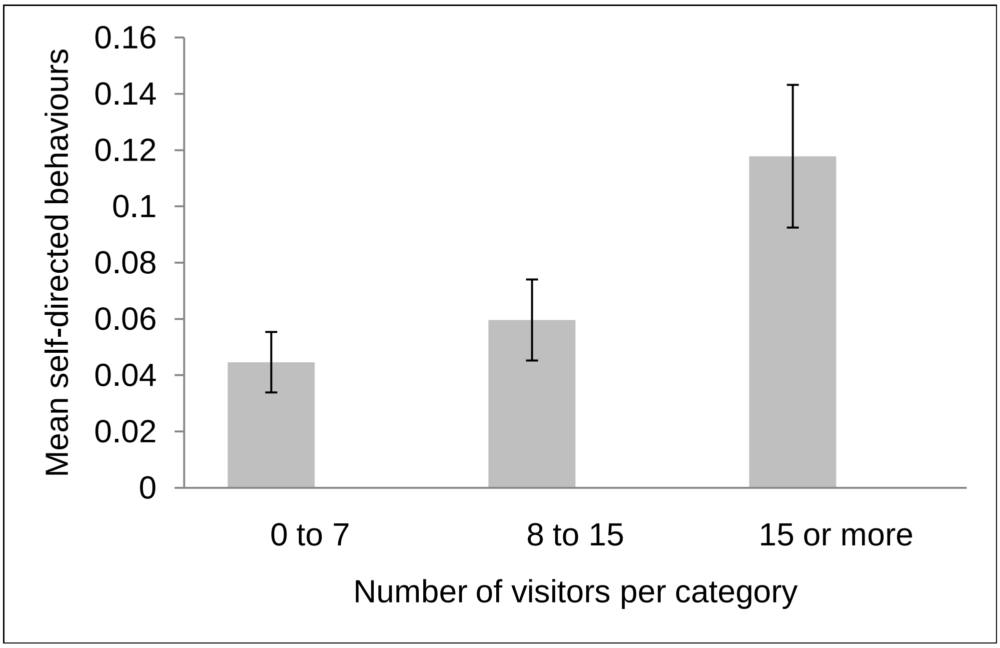

Figure 4: Averages for self-directed behaviours per 50 minutes are shown across the three different visitor categories

Across different visitor coverage levels, the majority of non-social behaviours were not affected by the presence of visitors (Table 5). Autogrooming levels were not significantly affected by visitor numbers. Out of the 2000 randomly sampled data divisions, 1681 were as least as large as the obtained data (*RSS* = 0.01, $p = 0.84$). For foraging, out of the 2000 randomly sampled data divisions, 1555 were as least as large as the obtained data (*RSS* = 0.01, $p = 0.78$). Fleeing was also not affected by visitor numbers. Out of 2000 randomly sampled data divisions, 1543 were as least as large as the obtained data (*RSS* = 0.02, $p = 0.77$). For inactivity, out of the 2000 randomly sampled data divisions, 111 were as least as large as the obtained data, and therefore the test statistic only approached significance (*RSS* = 0.01, $p = 0.07$). For self-scratching, out of the 2000 randomly sampled data divisions, 1138 were as least as large as the obtained data (*RSS* = 0.06, $p = 0.57$). For yawning, out of the 2000 randomly sampled data divisions, 374 were as least as large as the obtained data (*RSS* = 0.01, $p = 0.19$). For self-directed behaviour, out of the 2000 randomly sampled data divisions, 809 were as least as large as the obtained data (*RSS* = 0.05, $p = 0.41$).

Table 5
Means (±SEMs) for non-social behaviours per 50 minutes across visitor coverage

Non-social behaviour	Coverage 0-20%	Coverage 20-50%	Coverage 50-70%	Coverage 70-100%
Autogroom	.02 (.01)	.04 (.02)	.03 (.02)	.03 (.02)
Foraging	.10 (.02)	.11 (.02)	.10 (.02)	.12 (.01)
Fleeing	.001 (.001)	.01 (.004)	.003 (.003)	.04 (.03)
Inactivity	.10 (.03)	.11 (.03)	.09 (.03)	.03 (.07)
Self-scratch	.02 (.01)	.04 (.01)	.03 (.02)	.09 (.06)
Self-directed	.005 (.005)	.02 (.01)	.03 (.01)	.04 (.04)

Across differing visitor coverage levels, only monitoring was significantly affected by the level of visitor coverage; the macaques performed more monitoring behaviour when a greater percentage of the glass was covered by visitors (Figure 5). Out of the 2000 randomly sampled data divisions, only 4 were at least as large as the obtained data, therefore the statistics were significant ($RSS = 0.01$, $p = 0.003$). Visual inspection of the means indicates that the two higher coverage conditions led to more monitoring by the macaques compared to the lower coverage conditions.

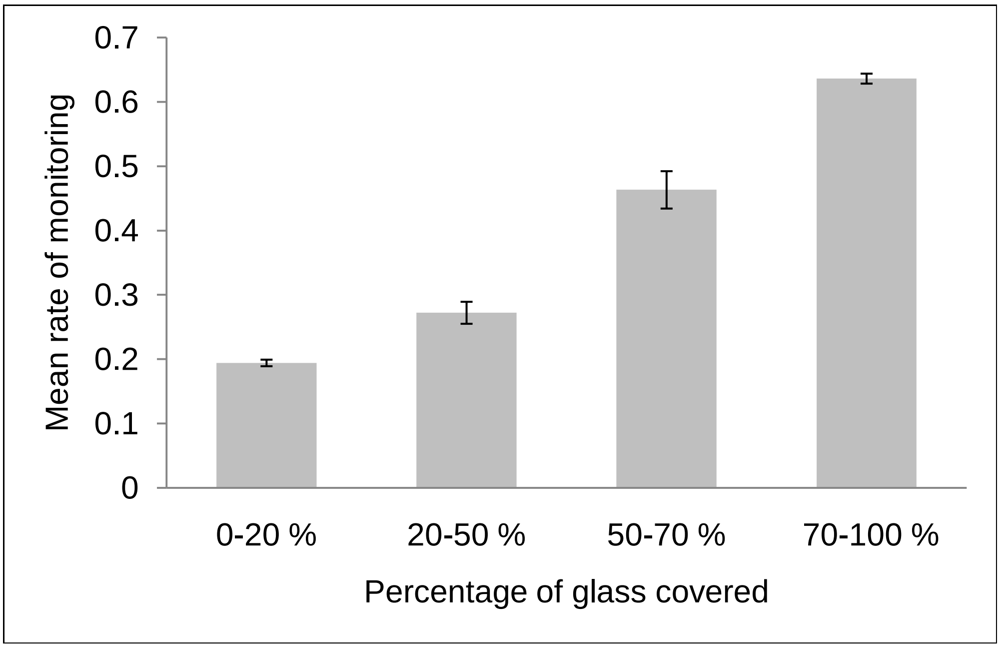

Figure 5: Averages for monitoring per 50 minutes are shown across four differing percentages of visitor coverage

Location across visitor coverage

The vertical location of the macaques within the enclosure was only partially affected by the amount of visitor coverage (Table 6). The location of the macaques on level one of the enclosure was not significantly affected by visitor coverage. Out of the 2000 randomly sampled data divisions, 1180 were as least as large as the obtained data (*RSS* = 0.10, p = 0.99). Similarly, the location of the macaques on levels two and three of the enclosure was not significantly affected by visitor coverage; 126 arrangements were as least as large as the obtained data for level two, (*RSS* = 0.55, p = 0.06) and only 158 were as least as large as the obtained data for level three (*RSS* = 0.16, p = 0.09). However, when the data for level two and three were collapsed together, a significant result was obtained as the macaques spent more time higher up in the enclosure when the level of visitor coverage was greater (Figure 6). Out of the 2000 randomly sampled data divisions, only 3 were at least as large as the obtained data, therefore the statistics were significant (*RSS* =0.49, p = 0.001). Visual inspection of the means indicates that the two higher visitor coverage conditions led to the macaques spending more time in the upper areas of the enclosure compared to the lower coverage conditions.

Table 6
Means (±SEMs) for location per 50 minutes across visitor coverage

Location (level)	Coverage 0-20%	Coverage 20-50%	Coverage 50-70%	Coverage 70-100%
1	.14 (.03)	.18 (.05)	.14 (.08)	.21 (.09)
2	.05 (.01)	.10 (.04)	.15 (.05)	.34 (.19)
3	.15 (.06)	.17 (.05)	.31(.07)	.30 (.04)

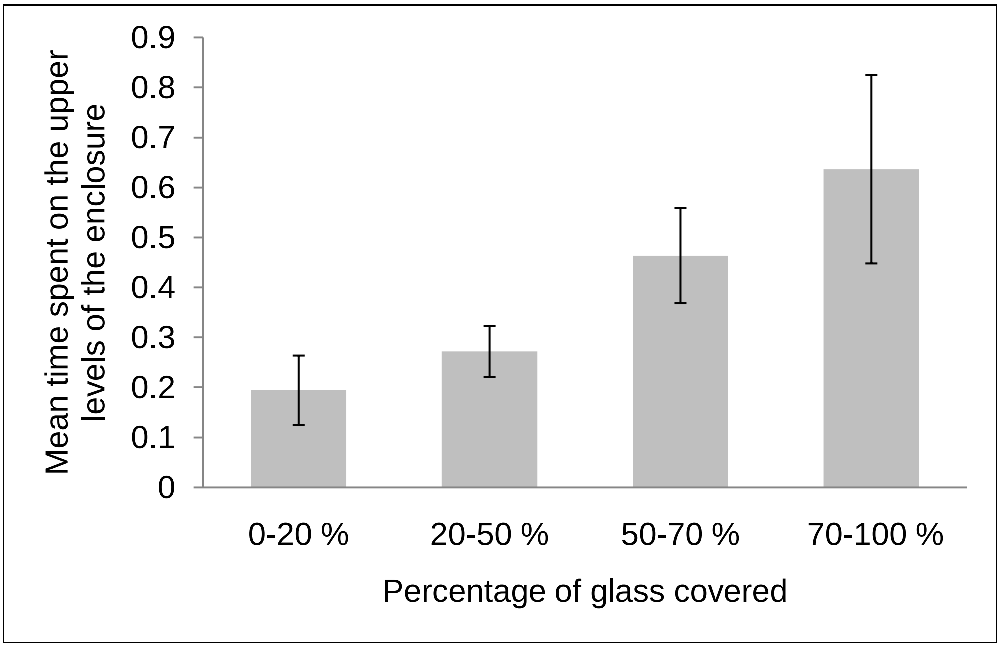

Figure 6: Averages for time spent on the upper levels of the enclosure per 50 minutes are shown across four differing percentages of visitor coverage

Location across visitor categories

The location of the macaques within the enclosure was mostly not influenced by visitor category (Table 7). The location of the macaques on level one of the enclosure was not significantly affected by visitor category. Out of the 2000 randomly sampled data divisions, 1492 were as least as large as the obtained data (*RSS* = 0.06, *p* = 0.75). The location of the macaques on level two of the enclosure was also not significantly affected by visitor category; 646 arrangements were as least as large as the obtained data (*RSS* = 0.04, *p* = 0.32). However, the macaques spent more time on level three when more visitors were present (Figure 7). Out of the 2000 randomly sampled data divisions, only 70 were at least as large as the obtained data, therefore the statistic was significant (*RSS* =0.10, *p* = 0.04). Visual inspection of the means indicates that the macaques spent more time higher up in the enclosure when 15 or more visitors were present than when 8-15 visitors were present, but not when 0-7 visitors were present. Finally, when the data for level 2 and 3 were collapsed together, no significant result was found. Out of the 2000 randomly sampled data divisions, 111 were as least as large as the obtained data (*RSS* = 0.03, *p* = 0.06).

Table 7
Means (±SEMs) per 50 minutes for the location of the macaques across visitor categories

Location (level)	Category A	Category B	Category C
1	.12 (.08)	.04 (.01)	.20 (.07)
2	.05 (.01)	.06 (.03)	.11 (.04)
3	.21 (.08)	.15 (.05)	.41 (.06)

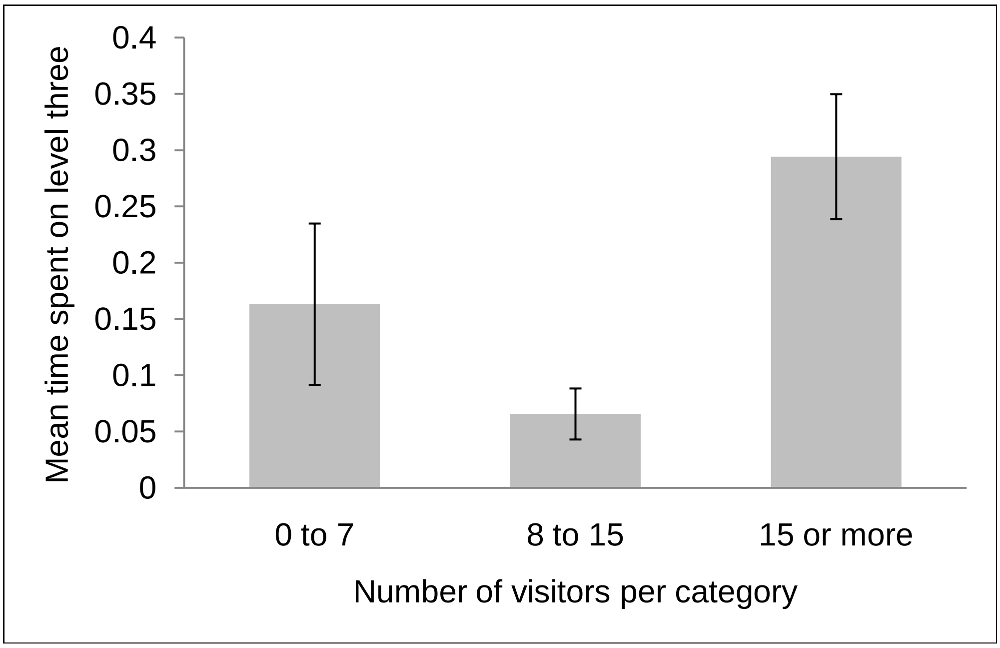

Figure 7: Averages for amount of time spent per 50 minutes on level three across visitor categories

Discussion

One aim of the present study was to understand the effects zoo visitors had on captive lion-tailed macaque behaviour. Previous research indicated that zoo visitors had a deleterious effect on macaque behaviour; however such research was conducted in zoos which maintained their macaques in suboptimal facilities. Therefore, it was predicted that increased visitor numbers and coverage would have an effect on the behaviour of the lion-tailed macaques, although the enriched enclosure at Chester Zoo may have a mediating effect on this. It was also predicted that the macaques, as an arboreal species, would retreat higher in the enclosure if they felt threatened by visitors.

Social behaviour was not affected by increased visitor numbers or coverage. Levels of aggression, allogrooming, contact, clasping, and social play were not changed by the presence of visitors. This is in contradiction with previous research on visitors and captive primates. Research indicates that zoo visitors have a deleterious effect on primate behaviour, increasing levels of aggression and decreasing levels of allogrooming and social play (Chamove et al., 1988; Barros & Tomaz, 2002; Hosey, 2004; Wells, 2005; Todd, Macdonald & Coleman, 2007). This effect was also found in captive lion-tailed macaques housed in Indian zoos. Mallapur et al. (2005a) found that social and aggressive behaviours were affected by increased visitor numbers. In the current study, many of the macaques' non-social behaviours were not affected by increased visitor numbers or coverage. Levels of foraging, fleeing, self-scratching, autogrooming and inactivity were not affected by visitors. The findings are not in perfect agreement with previous research, as several studies have established a link between increased visitor presence and the disruption of behaviours such as foraging (Birke, 2002), inactivity (Chamove et al.,1988) and autogrooming (Wells, 2005).

The fact that visitor numbers or coverage did not modify much of the behaviour of the macaques may be a testament to the success of the naturalistic environment provided for the lion-tailed macaques at Chester Zoo. Although Mallapur et al. (2005a) found that increased visitor numbers had an effect on the behaviour of captive lion-tailed macaques; such results were gathered from Indian zoos which housed their animals in sub-optimal facilities. Recent research has established that the provision of enrichment within the captive environment may offset some of the impact zoo visitors may have on zoo animals (Honess & Marin, 2006; Carder & Semple, 2008). It is argued that environmental enrichment affords captive animals more of the behavioural opportunities found in the wild (Carlstead & Shepardson, 1994), and so such opportunities may detract from any negative influence that visitors may have on captive primates. In this case, the lion-tailed macaque enclosure at Chester Zoo closely mimics their natural environment; providing climbing opportunities and feeding enrichment. Also, the macaques are maintained in a large group of 21 animals; the largest group in Britain (Skyner, 2006). In the wild, lion-tailed macaques normally live in groups of up to 40 individuals (Ramachandran & Joseph, 2000). Previous research has established that a large group size can mediate stress experienced in captivity (Price & Stoinsk, 2007). Thus, by maintaining the macaques at Chester Zoo in such a large group the animals may experience less stress than captive macaques held in smaller groups. Indeed, it was shown by Skyner (2006) that the behaviour of lion-tailed macaques in response to visitors varied significantly between different zoos; those zoos that provided a more naturalistic enclosure managed to reduce visitor impact on their lion-tailed macaques.

However, some lion-tailed macaque behaviour was affected by increased visitor presence. Monitoring behaviour was increased by larger numbers of visitors; when 15 or more visitors were present the macaques observed for this study spent approximately 20% of their time monitoring their surroundings. A similar result was also achieved when visitor coverage was considered; a greater percentage of the enclosure covered by visitors elicited more monitoring behaviour by the macaques. Such findings are in agreement with previous research, which indicated that when threatened by aversive stimuli, such as zoo visitors, primates increase their levels of monitoring (Maestripieri, 1993; Cooke & Schillaci, 2007). This may be due to zoo visitors being perceived by captive primates as a threat. The fact that the macaques increased their level of monitoring when visitor numbers increased indicates that visitors may have been seen as a threat.

The macaques also increased their rate of yawning when visitor numbers increased. In several species of old world monkey, yawning is used as a form of threat display, intimidating others by displaying the canines (Hadidian, 1980). This is consistent with research by Mallapur et al. (2005a), who found that captive lion-tailed macaques yawned more in the presence of visitors. Also, Hadidian (1980) found that Sulawesi crested black macaques (*M. nigra*) yawned as a form of threat display towards an aversive stimulus, such as zoo visitors. The fact that the lion-tailed macaques yawned more in the presence of zoo visitors supports the idea that zoo visitors were viewed as a potential threat by the macaques.

Self-directed behaviours were also affected by increased visitor numbers, but not by increased visitor coverage of the enclosure. The results for 'self-scratching' and 'autogroom' were collapsed together to produce the category 'self-directed behaviours'. When visitor numbers were high, the macaques performed more self-directed behaviours. Previous research suggests that elevated scratching is an established indicator of stress in primates (Schino et al., 1996; Castles et al., 1999; Wells, 2005; Carder & Semple, 2008). The difference in why self-directed behaviour was only affected by increased visitor numbers and not increased visitor coverage may be due to a difference in visitor behaviours. Large crowds of visitors to the lion-tailed macaque enclosure were often noisy, and many such visitors attempted to interact with the macaques by banging on the glass. Conversely, the size of the enclosure meant that even when the glass was covered by visitors, the total number of visitors present would often be much less than the highest category of visitor numbers. Thus, the macaques appeared to be more affected by visitor numbers rather than how much of the enclosure visitors covered. In addition, this difference in patterning of responses by the macaques to absolute visitor numbers and the extent of coverage suggest that in future, studies measuring only visitor numbers are sufficiently sensitive to assess the impact of zoo visitors for this species.

When the location of the macaques within the enclosure was considered in relation to visitors, a significant result was found. In terms of both visitor numbers and coverage, the macaques spent more time in the higher levels of the enclosure when visitor presence was increased. Such findings are in contradiction with some previous research on lion-tailed macaques. Skyner (2006) found that increased visitor numbers resulted in the macaques spending more time on the lower levels of the enclosure. However, the findings from the current study are supported by research into how captive animals use their enclosure. de Oca et al. (2007) found that when threatened captive rats consistently fled to a preferred area of their enclosure. As lion-tailed macaques are an arboreal species, it is not surprising that they preferred the higher areas of their enclosure. Research by Ross et al. (2009) established that when threatened, captive gorillas and chimpanzees showed a preference for areas of their enclosure that resembled 'safe' areas in the wild.

Because the macaques chose the higher areas of their enclosure during periods of high visitor numbers, particularly taken together with the increases in yawning and self-directed behaviours, it may be stated that visitors were seen as a threat by the macaques. Therefore, the increase in the anxiety-related behaviours monitoring and yawning, as well as self-directed behaviours indicates that the lion-tailed macaques potentially perceived large numbers of zoo visitors as a threat. This is further indicated by the macaques retreating to the higher parts of their enclosure when visitor numbers were greater than 15.

One limitation with the present study may be the sample size. As only five macaques out of a group comprising 21 individuals were used in the study, the results may not be generalised to the rest of the group. However, due to the preliminary nature and time constraints of the study, the amount of focal animals that could be observed was restricted. Therefore, five focal animals were considered a satisfactory number to provide sufficient data for the study. A further limitation of the study may be that only one group of macaques was considered. If more than one group of macaques were observed, the reliability of the findings from this study could be ensured, as animals from differing levels of enclosure enrichment would be included. Thus, the findings from such research would be applicable to more of the captive population of lion-tailed macaques.

The implications from this study may have far reaching consequences in that some aspects of the captive environment may be altered. Because the macaques retreated to the higher areas of their enclosure during periods of high visitor presence, it is apparent that the macaques felt threatened by zoo visitors. Previous research has indicated that captive animals that frequently feel threatened by human visitors benefit from an area within their enclosure that they can use to retreat from visitors. Anderson, Benne, Bloomsmith and Maple (2002) found that petting zoo animals that performed abnormal behaviours in the presence of zoo visitors reduced such behaviours dramatically given the option of a retreat space. The macaques at Chester Zoo do not currently have the option of a retreat space from visitors when access to the outside closure is not available, although they do retreat to higher places in their enclosure. It may therefore benefit the macaques if such an area was created. As the macaques clearly preferred the upper areas of their enclosure when stressed, a retreat space may be placed in the upper areas of the enclosure. Previous research by Weiss (1968) found that rats which could perform a coping response to avoid or escape an unpleasant stimulus suffered less stress than rats that had no control. Thus, if the macaques had the opportunity to avoid visitors, any effects that visitors have on the macaques may be lessened.

In terms of future research, more of the behavioural repertoire of the macaques could be considered in terms of visitor impact. For example, visitor impact on abnormal and mating behaviours could be assessed. Also, the location of the macaques within the enclosure with respect to the distance from zoo visitors could be investigated, resulting in a more detailed picture of exactly how much influence zoo visitors have on how the macaque use their enclosure. Finally, visitor effects on the lion-tailed macaques could be investigated over the summer holiday period, where the number of daily zoo visitors can exceed 10,000. Consequentially, the macaques would be confronted with many more than 15 visitors at one time, particularly as the monkey house is located close to the main entrance of the zoo. Thus, the effect visitors have on the macaques may be greatly increased.

Conclusions

Overall, the present study identified the impact that zoo visitors had on lion–tailed macaque behaviour in an enriched enclosure, and was one of the first to do so. It was found that behaviours related to anxiety and the macaques' vertical location within the enclosure were affected by increased visitor numbers and coverage of the enclosure windows. Although the small sample size may effect on how well the results can be generalised to the whole macaque population at Chester Zoo, it nonetheless provided insight on how macaques can still be affected by visitors even in an enriched enclosure. Finally, the addition of a retreat space for the macaques to escape from visitors in the upper area of their enclosure may serve to mediate future visitor effects on the macaques.

References

Anderson, U.S., Benne, M., Bloomsmith, M.A., & Maple, T.L. (2002). Retreat space and human visitor density moderate undesirable behaviour in petting zoo animals. *Applied Animal Welfare Science, 5 (2),* 125-137.

Ballantyne, R., Packer, J., Hughes, K., & Dierking, L. (2007). Conservation learning in wildlife tourism settings: lessons from research in zoos and aquariums. *Environmental Education Research, 13 (3)*, 367-383.

Barney, E.C., Mintzes, J.J., & Yen, C. (2005). Assessing knowledge, attitudes, and behaviour toward charismatic megafauna: The case of dolphins. *Journal of Environmental Education, 36,* 41-55.

Barros, M., & Tomaz, C. (2002). Non-human primate models for investigating fear and anxiety. *Neuroscience and Biobehavioural Reviews, 26,* 187-201.

Birke, L. (2002). Effects of browse, human visitors and noise on the behaviour of captive orang-utans. *Animal Welfare*, *11*, 189-202.

Blaney, E.C., & Wells, D.L. (2004). The influence of a camouflage net barrier on the behaviour, welfare and public perceptions of zoo housed gorillas. *Animal Welfare*, *13*, 111-118.

Boccia, M.L., Reite, M., & Laudenslager, M. (1989). On the physiology of grooming in the pigtail macaque. *Physiology of Behaviour, 45,* 667-670.

Broom, D.M., & Johnson, K.G. (1993). *Stress and animal welfare.* London: Chapman and Hall.

Carder, G., & Semple, S. (2008). Visitor effects on anxiety in two captive groups of western lowland gorillas. *Applied Animal Behaviour Science*, *115*, 211-220.

Carlstead, K., & Shepardson, D. (1994). Effects of environmental enrichment on reproduction. *Zoo Biology*, *13 (5)*, 447-459.

Castles, D.L., Whiten, A., & Aureli, F. (1999). Social anxiety, relationships and self–directed behaviour among wild female olive baboons. *Animal Behaviour*, *58*, 1207-1215.

Chamove, A.S., Hosey, G.R., & Schaetzel, P. (1988). Visitors excite primates in zoos. *Zoo Biology, 7,* 359-369.

Chang, T.R., Forthman, D.L., & Maple, T.L. (1999). Comparison of confined mandrill (*Mandrillus spinx*) behaviour in traditional and “ecologically representative” exhibits. *Zoo Biology, 18,* 163-176.

Clubb, R., & Mason, G.J. (2003). Captivity effects on wide-ranging carnivores. *Nature, 425 (6957),* 473-474.

Clubb, R., & Mason, G.J. (2007). Natural behavioural biology as a risk factor in carnivore welfare: how analysing species differences could help zoos improve enclosures. *Applied Animal Behaviour Science, 102 (3-4),* 303-328*.*

Cooke, C.M., & Shillaci, M.A. (2007). Behavioural responses to the zoo environment by white handed gibbons. *Applied Animal Behaviour Science*, *106*, 125-133.

Crockett, C.M., Bowers, C.L., Shimoji, M., Leu, M., Bowden, D.M., & Sackett, G.P. (1995). Behavioural responses of longtailed macaques to different cage sizes and common laboratory experiences. *Journal of Comparative Psychology, 109 (4),* 368-383.

Davis, N., Schaffner, C.M., & Smith, T.E. (2005). Evidence that zoo visitors influence HPA activity in spider monkeys (*Ateles geoffroyii rufiventos*). *Applied Animal Behaviour Science*, *90*, 131-141.

Dobson, H., & Smith, R.F. (2000). What is stress, and how does it affect reproduction? *Animal Reproductive Science*, *60-61*, 743-752.

Easa, P.S., Surendranathan, A., & Chand Basha, S. (1994). Status and distribution of the endangered lion-tailed macaque (*Macaca silenus*) in Kerala, India. *Biological Conservation*, *80*, 33-37.

Glatson, A.R., Soeteman, E.G., Pecek, E.H., & Hooff, J.A.R.A.M.V. (1984). The influence of the zoo environment on social behaviour of groups of cotton-topped tamarins (*Saguinus oedipus oedipus)*. *Zoo Biology, 3,* 241-253.

Handidian, J. (1980). Yawning in an old world monkey (*Macaca nigra)*. *Behaviour, 75,* 133-147.

Herbert, P.L., & Bard, K. (2000). Orang-utan use of vertical space in an innovative habitat. *Zoo Biology, 19,* 239-251.

Honess, P.E., & Marin, C.M. (2006). Review: enrichment and aggression in primates. *Neuroscience and Biobehavioural Reviews*, *30*, 413-436.

Hosey, G.R. (2000). Zoo animals and their human audiences: what is the visitor effect? *Animal Welfare, 9,* 343-357.

Hosey, G.R. (2004). How does the zoo environment affect the behaviour of captive primates? *Applied Animal Behaviour Science*, *90*, 107-129.

Hosey, G.R. (2008). A preliminary model of human–animal relationships in the zoo. *Applied Animal Behaviour Science, 109,* 105-127.

International Primatological Society. (2007). IPS international guidelines: IPS code of practice 1: housing and environmental enrichment. *Primate report*, *35*, 8-16.

Kumar, A., & Karup, G.U. (1993). Demography of the lion-tailed macaque (*Macaca silenus*) in the wild. *Bombay Natural History Society*, *75*, 321-340.

Kumar, A., Singh, M., & Molur, S. 2008. *Macaca silenus*. In: IUCN 2009. IUCN Red List of Threatened Species. Version 2009.2. Retrieved 06/01/2010 from www.iucnredlist.org.

Lambeth, S.P., Bloomsmith, M.A., & Alford, P.L. (1997). Effects of human activity on chimpanzee wounding. *Zoo Biology*, *16*, 327-333.

Lukas, K.E., & Ross, S.R. (2005). Zoo visitor knowledge and attitudes toward gorillas and chimpanzees. *Journal of Environmental Education, 36 (4),* 33-48.

Maestripieri, D. (1993). Maternal anxiety in rhesus macaques (*Macaca mulatta*) 1: measurement of anxiety and identification of anxiety eliciting situations. *Ethology*, *95*, 19-31.

Mallapur, A. (2005). Managing primates in zoos: lessons from animal behaviour. *Current Science, 89 (7),* 1214-1219.

Mallapur, A., Qureshi, Q., & Chellam, R. (2002). Enclosure design and space utilisation by Indian leopards (*Panthera pardus*) in four zoos in southern India. *Applied Animal Welfare Science, 5 (2),* 111-124.

Mallapur, A., & Choudhury, B.C. (2003). Behavioural abnormalities in captive non-human primates. *Applied Animal Welfare Science, 6, 275-284.*

Mallapur, A., Waran, N., & Sinha, A. (2004). Factors influencing the behaviour of captive lion-tailed macaques in Indian zoos. *Applied Animal Behaviour Science*, *91*, 337-353.

Mallapur, A., Waran, N., & Sinha, A. (2005a). Influence of visitor presence on the behaviour of captive lion-tailed macaques (*Macaca silenus*) housed in Indian zoos. *Applied Animal Behaviour Science*, *94*, 341-352.

Mallapur, A., Waran, N., & Sinha, A. (2005b). Use of enclosure space by captive lion-tailed macaques (*Macaca silenus*) housed in Indian Zoos. *Applied Animal Welfare Science, 8 (3),* 175-185.

Mallapur, A., Waran, N., & Sinha, A. (2006). A note on enrichment for captive lion-tailed macaques (*Macaca silenus*). *Applied Animal Behaviour Science*, *108*, 191-195.

Mallapur, A., Waran, N., & Sinha, A. (2008). The captive audience: the educative influence of zoos on their visitors in India. *International Zoo Yearbook, 42,* 214-224.

Martin, P., & Bateson, P. (2007). *Measuring behaviour: An introductory guide.* Cambridge University Press.

Menon, S., & Poirier, F.E. (1996). Lion-tailed macaques (*Macaca silenus*) in a disturbed forest fragment: activity patterns and time budget. *International Journal of Primatology, 17,* 969-985.

Morgan, K.N., & Tromborg, C.T. (2006). Sources of stress in captivity. *Applied Animal Behaviour Science*, *102*, 262-302.

Morriss, D. (1964). The responses of animals to a restricted environment. *Symposia of the Zoological Society of London*, *13,* 99-118.

Novak, M.A., & Suomi, S.J. (1988). Psychological wellbeing of primates in captivity. *American Psychologist, 43 (10),* 765-773.

de Oca, B., Minor, T.R., & Fanselow, M.S. (2007). Brief flight to a familiar enclosure in response to a conditional stimulus in rats. *Journal of General Psychology, 134(2),* 153-172.

Overmier, J.B., Patterson, J., & Wielkiewicz, R.M. (1980). Environmental contingencies as sources of stress in animals. In Levine, S., and Ursin, H. (eds)., Coping and Health. Plenum Press, New York, pp 1-38.

Price, E.E., & Stoinski, T.S. (2000). Group size: determinants in the wild and implications for the captive housing of wild mammals in zoos. *Applied Animal Behaviour Science, 103,* 255-264.

Ramachandran, K.K., & Joseph, G.K. (2000). Habitat utilization of lion-tailed macaques (*Macaca silenus*) in Silent Valley National Park, Kerala, India. *Primate Report, 58,* 17-25.

Reinhardt, V., Liss, C., & Stevens, C. (1996). Comparing cage space requirements for non-human primates in the United States and in Europe. *Animal Welfare Information Centre Newsletter, 7,* 12-13.

Ross, S.R., Lonsdorf, E.V., & Stoinski, T. (2007). Assessing the welfare implications of visitors in a zoo setting: a comment on. *Applied Animal Behaviour Science*, *102 (1-2)*, 130-133.

Ross, S.R., Schapiro, S.J., Hau, J., & Lukas, K.E. (2009). Space use as an indicator of enclosure appropriateness: a novel measure of captive animal welfare. *Applied Animal Behaviour Science, 121,* 42-50.

Saudergas, R.A., & Drummer, L.C. (1996). Single subject (small N) research designs and zoo research. *Zoo Biology, 15,* 173-181.

Schino, G., Perretta, G., Taglioni, A.M., Monaco, V., & Troisi, J. (1996). Primate displacement activities as an ethopharmacological model of anxiety. *Anxiety*, *2*, 186-191.

Singh, M., & Vinathe, S. (1990). Inter-population differences in the time budgets of bonnet macaques (*Macaca radiata*). *Primates*, *31*, 589-596.

Skyner, L.J. (2006). Factors modifying welfare in captive lion-tailed macaques (*Macaca silenus*). Unpublished P.H.D thesis, University of Liverpool.

Todd, P.A., Macdonald, C., & Coleman, D. (2007). Visitor associated variation in captive Diana monkey (*Cercopithecus diana diana*) behaviour. *Applied Animal Behaviour Science*, *107*, 162-165.

Todman, J.B., & Dugard, P. (2001). *Single-Case and Small-n Experimental designs.* New York: Lawrence Earlbaum Associates.

Tofield, S., Coll, R.K., Vyle, B., & Bolstad, R. (2003). Zoos as a source of free choice learning. *Research in Science and Technological Education, 21 (1),* 67-99.

Turner, A.I., Hemsworth, P.H., & Tilbrook, A.J. (2005). Susceptibility of reproduction in female pigs to impairment by stress or elevation of cortisol. *Domestic Animal Endocrinology*, *29*, 398-410.

Umpathy, G., & Kumar, A. (2000). The occurrence of arboreal mammals in the rainforest fragments in the Anamali hills, South India. *Biological Conservation, 92*, 311-319.

Weiss, J.M. (1968). Effects of coping responses on stress. *Journal of Comparative and Physiological Psychology*, *65(2)*, 251-260.

Wells, D.L. (2005). A note on the influence of visitors on the behaviour and welfare of zoo housed gorillas. *Applied Animal Behaviour Science*, *93*, 13-17.

Wilson, S.F. (1982). Environmental influences on the activity of captive apes. *Zoo Biology, 1,* 201-209.

Wood, W. (1998). Interactions among environmental enrichment, viewing crowds, and zoo chimpanzees (*Pan troglodytes*). *Zoo Biology, 17,* 211-230.