

CHAPTER 4

FACTORS MODIFYING THE BEHAVIOUR OF CAPTIVE LION-TAILED MACAQUES (*Macaca silenus*)

4.1 Introduction

The behaviours an animal performs throughout the course of the day are the result of preference and choice between different behavioural options (Dawkins, 1988; McNamara & Houston, 1986). The amount of time an animal devotes to different activities (time budget) could be seen as a strategy for coping with changes taking place in the environment or variability in energy expenditure (Dawkins, 1988). The way in which an animal divides its energy across various activities is highly indicative of its needs (Menon & Poirier, 1996). Survival and reproduction will depend on an animal allocating correct amounts of time to behaviours and performing them at appropriate times (Dawkins, 1988; Defler, 1995; Watts, 1988).

Variables in the wild that affect energy expenditure and behaviour include social systems (Herbers, 1981; Watts, 1988), group size (Barton et al., 1992; Isbell & Young, 1993; Menon & Poirier, 1996; Van Schaik et al., 1983; Watts, 1988), season (Cuthill & Houston, 1993; Daan, 1981; Herbers, 1981; Isbell & Young, 1993; Lewis & Kappeler, 2005; Menon & Poirier, 1996; Santos & Martins, 2000), levels of predation (Balldelou & Henzi, 1992; Cuthill & Houston, 1993; Daan, 1981; Kappeler, 1999; Santos & Martins, 2000), food distribution (Daan, 1981; Kappeler, 1999; Lewis & Kappeler, 2005; Menon & Poirier, 1996; Santos & Martins, 2000) and the availability of mates (Kappeler, 1999; Wrangham, 1980).

The variables that affect captive animal behaviour may be different from those in the wild because in captivity many variables are controlled for

extraneously, for example, there is not the same choice of mates. Further, food is provided by caretakers (Robinson, 1998). It is likely that captive animal behaviour is affected by a number of zoo-related dependent variables (Hosey, 2005). In his review paper, Hosey (2005) discusses variables specific to the zoo environment that affect primate behaviour, for example, the presence of zoo visitors, restricted space and being managed. Captive environments are more restrictive than the wild and often include extreme restrictions on available space and resources which may prevent some species from exhibiting their full behavioural repertoire (Lukas et al., 2003). In a study on capybaras Nogueira et al (2004) found the behaviour of wild-caught individuals differed from those born in captivity. Behavioural differences have also been found in several wild-caught and captive-born primate species (Mallapur et al., 2005b).

In order to understand the needs of lion-tailed macaques, a fundamental understanding of their behaviour is required. The current study assessed the behaviour patterns of three captive groups of lion-tailed macaques and explored factors that modify their behaviour. Based on previous research discussed below it was predicted that the following variables would modify behaviour: institution, age and sex.

4.1.1 Effect of institution on behaviour

One may predict that the institution in which the animal is housed can modify its behaviour (Kerl & Rothe, 1996; Lukas et al., 2003). Primate housing can vary greatly (Honest & Marin, 2006b; Mallapur et al., 2005b) and include zoological gardens, safari parks and laboratories. In addition enclosures can vary within institutions of the same type as well as between types of institution. The current study will focus on lion-tailed macaques housed in zoological gardens where three main factors vary between institution: the presence of zoo visitors, amount of space provided and the way in which the animals are managed (Hosey, 2005). The three institutions included in this study varied in average visitor numbers, enclosure size, group size (table 4.1), and management protocol (refer to chapter 2 section 2.1). There is

controversy surrounding the effect of visitors on primate behaviour (Hosey, 2005). The effect of visitors on lion-tailed macaque behaviour will be assessed separately in chapter seven.

There is disagreement regarding the effects of enclosure size and complexity on animal well-being (Kitchen & Martin, 1996). Some studies have shown alterations in the physical dimensions and complexity of the captive environment produce significant changes in the range and frequency of primate behaviour (Draper & Bernstein, 1963; Kerl & Rothe, 1996; Lukas et al., 2003; Paulk et al., 1977). In contrast, cage size has also been shown to be insignificant in modifying animal behaviour (Bantin & Sanders, 1989; Crockett & Bowden, 1994; Kreeger *et al.*, 1996; Line *et al.*, 1989). A barren enclosure may cause animals to show stereotypy or display abnormal behaviours (Mallapur et al., 2005b) whereas a highly enriched enclosure may encourage animals to be more naturalistic in their display of behaviours (Carlstead & Shepherdson, 2000; Mallapur et al., 2005b). Enclosure complexity is therefore important for psychological well-being and behaviour choice. Research has shown that behaviour in the same species can differ between institutions indicating the influence of different types of enclosure and management protocol (Frezard & Le Pape, 2003; Melfi & Feistner, 2002; Montaudouin & Le Pape, 2004, 2005; Perrin & Sibley, 2003; Spendrup & Larsson, 1998).

In the current study it was predicted that the institution in which the subjects were housed would modify behaviour patterns exhibited by lion-tailed macaques.

Table 4.1 – The differences in enclosure size and visitor numbers between institutions. **Note:** Chester outside and San Diego Wild Animal Park corral were open air and therefore area could only be provided.

Institution	Chester Zoo	Bristol Zoo	Assiniboine Park Zoo	San Diego Wild Animal Park
Group size	7	6	16	12
Approximate enclosure size	Inside = 1092 m ³ Outside = 792.54 m ²	Inside = 134.20 m ³ Outside = 457.38 m ³	Inside = 19.2 m ³ Outside = 360 m ³	Corral = 1590 m ² Enclosures = 195.64 m ³
Average visitor numbers over study period	3994	1266	1646	Enclosure not on public view

4.1.2 Effect of age on behaviour

The allocation of energy to behaviour can change with age (Perrin & Sibley, 2003) as animals at different ages have different needs and priorities. Age may affect the length of time behaviour is performed. For example Johnson and Bock (2004) found juvenile baboons (*Papio hamadryas ursinus*) to be significantly less efficient at foraging than adults due to their small size, lower level of knowledge and skill. Juvenile baboons as a result spent more time foraging than adults and thus had different time budgets. Similar results were found in rhesus macaques, *Macaca mulatta* (Wells & Turnquist, 2001).

In general, infant animals spend significantly more time playing than adults (De Oliveira et al., 2003). Performing play behaviour has costs: energy expenditure and the risks of injury or predation (Bekoff & Byers, 1992; De Oliveira et al., 2003). Infant animals perform play behaviours despite these costs. It can therefore be assumed from this research that play is an important behaviour for young animals to perform. Defler (1995) found juvenile and infant woolly monkeys (*Lagothrix lagotricha*) played significantly more than adults.

There is minimal research assessing the effect of age on lion-tailed macaque behaviour. Johnson (1985) observed differences in allo-grooming and vocalisations in captive lion-tailed macaques in relation to age. Infants were never seen to groom and the clucking vocalisation was only displayed by infants and juveniles.

Based on the previous research, it was predicted that age would modify time spent performing behaviours by lion-tailed macaques in the three institutions studied.

4.1.3 Effect of sex on behaviour

Male and female animals have different reproductive strategies, with different roles in breeding and the raising of infants. This has implications for energy allocation and activity budgets (Lynch Alfaro, 2005; Watts, 1988; Wrangham, 1980). Reproductive demands such as gestation and lactation require increased energy. Females cope with these reproductive demands by modifying their behaviour. Behaviour can be modified by increasing food intake, using energy reserves, reducing activity levels and investing in relationships with group members who may be required to assist with the raising of offspring (Gittleman & Thompson, 1988; Kenagy et al., 1990; Lewis & Kappeler, 2005; Pekins et al., 1998; Rogowitz, 1996; Rose, 1994; Santos & Martins, 2000). Males ensure reproduction is successful by finding a mate, monopolising females, guarding females and defending territory (Kappeler, 1999; Setchell et al., 2005; Wrangham, 1980). Differences in male and female reproductive strategies result in energy being allocated for different behaviours. In addition sexual body size dimorphism (seen in lion-tailed macaques) results in sex differences in energy requirements (Ginnett & Demment, 1997).

Sex differences exist in the amount of activity and play behaviour exhibited by juvenile rhesus macaques. Males perform more high-energy and rough and tumble play than females (Coelho & Bramblett, 1982; Lovejoy & Wallen, 1988). Sex differences in behaviour have been studied in wild groups of lion-tailed macaques but not captive groups. Males will migrate from the group upon reaching sexual maturity whereas females will remain in their natal group for life (Kumar et al., 2001). Adult male lion-tailed macaques also have a low rate of interaction with members of the group, often standing on the periphery of the group (Lindburg & Harvey, 1994). When exploring the ethogram of lion-tailed macaque behaviours, females have been seen to lipsmack (a behaviour that has threat, appeasement and reassurance functions) and head toss (a behaviour seen during greeting sequences) more frequently than males (Johnson, 1985). On the whole there are very few sex differences observed in wild lion-tailed macaques.

Based on the above research male and female lion-tailed macaques are expected to allocate their energy in different ways, resulting in different behaviour patterns.

4.1.4 Aims

The aims of this chapter were to determine whether the variables institution, age and sex modify captive lion-tailed macaque behaviour. This is the first study to examine these factors in lion-tailed macaques.

4.2 Methods

Behavioural data (188 hours) were collected from 29 lion-tailed macaques (12 male, 17 female) housed in three institutions (Chester Zoo, Bristol Zoo and Assiniboine Park Zoo). Details on subjects, institutions and behavioural observations are outlined in chapter 2 sections 2.1 and 2.2.1.

4.2.1 Data analysis

For each animal, the mean proportion of instantaneous, one zero and all occurrence time periods in which the behaviour occurred was calculated. Data were corrected for time spent out of sight. Data were not normally distributed so instantaneous and one-zero behavioural data was arcsine transformed while all occurrence behaviour was log transformed following the addition of 1 (Sokal & Rohlf, 1995).

A 3-Factor MANOVA was used to explore the variables that modify lion-tailed macaque behaviour. Only a selection of the behaviours recorded were included in the MANOVA. Behaviours were only included if they were mutually exclusive. Behaviours were not included if the specific function of the behaviour was unknown. The independent variables were sex, age and institution and the dependent variables were 11 behaviours (agonistic, allo-grooming, appeasement, auto-grooming, foraging, locomotion, social, social play, threat, mate and sexual inspection). Definitions for these behaviours

are shown in chapter 2 section 2.2.1. Tukey post hoc analysis was performed on significant results. An alpha level of $p < 0.05$ was used for the MANOVA and a significance level of $p < 0.01$ was used for subsequent univariate analysis to minimise type 1 errors.

4.3 Results

The results from the main MANOVA demonstrate the variables institution and age significantly modified the behaviour variables of lion-tailed macaques ($F [22, 8] = 5.86, p < 0.01$, $F [22, 8] = 13.6, p < 0.001$, respectively). There was no significant effect of sex in modifying behaviour and there were no interaction effects (table 4.2).

Table 4.2 - Table showing the results from a 3-Factor MANOVA exploring the variables (institution, age and sex) on all behaviours. * indicates a significant result.

Independent variables	Behaviour (Dependent variable)
Institution	$F (22, 8) = 5.86, p < 0.01^*$
Age	$F (22, 8) = 13.6, p < 0.001^*$
Sex	$F (11, 3) = 1.39, NS$
Institution * Age	$F (44, 24) = 1.53, NS$
Institution * Sex	$F (22, 8) = 1.74, NS$
Age * Sex	$F (22, 8) = 0.78, NS$
Institution * Age * Sex	$F (22, 8) = 1.71, NS$

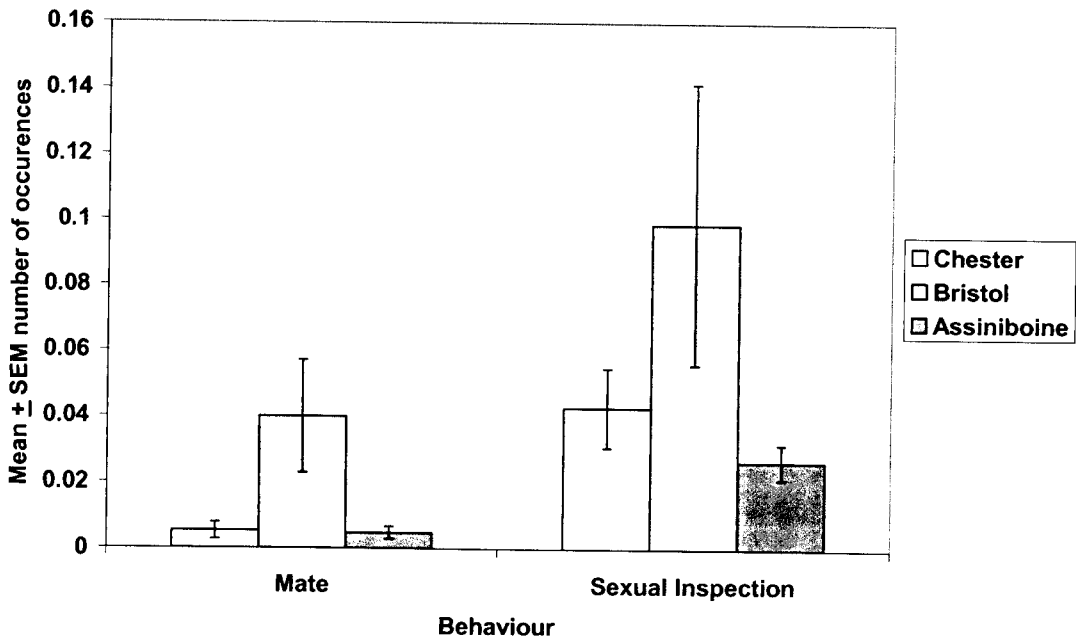
Univariate analysis for institution and age were conducted following significant results in main effects. Institution (table 4.2 and figure 4.1) modified levels of sexual inspection and mating. The institution did not modify levels of agonistic, allo-grooming, appeasement, auto-grooming, foraging, locomotion, social, social play and threat behaviours.

Age (table 4.2 and figure 4.2) modified levels of allo-grooming, auto-grooming, locomotion, social play, sexual inspection and mating. Levels of agonistic, appeasement, auto-grooming, foraging, social and threat behaviours were not modified by age.

Table 4.3 – Table showing the results of univariate analysis exploring the effect of the variables (institution and age) on behaviour, *indicates significant results.

Dependent variables	Independent variables	
	Institution	Age
Agonistic	F (15, 13) = 0.26, NS	F (15, 13) = 2.0, NS
Allo-grooming	F (15, 13) = 2.50, NS	F (15, 13) = 23.06, p<0.001*
Appeasement	F (15, 13) = 4.35, NS	F (15, 13) = 4.21, NS
Auto-grooming	F (15, 13) = 4.63, NS	F (15, 13) = 13.84, NS
Foraging	F (15, 13) = 0.27, NS	F (15, 13) = 3.52, NS
Locomotion	F (15, 13) = 3.25, NS	F (15, 13) = 25.22, p<0.001*
Social	F (15, 13) = 0.50, NS	F (15, 13) = 1.52, NS
Social Play	F (15, 13) = 1.69, NS	F (15, 13) = 19.10, p<0.001*
Threat	F (15, 13) = 1.80, NS	F (15, 13) = 3.02, NS
Mate	F (15, 13) = 20.44, p<0.001*	F (15, 13) = 21.82, p<0.001*
Sexual Inspection	F (15, 13) = 8.82, p<0.01*	F (15, 13) = 20.47, p<0.001*

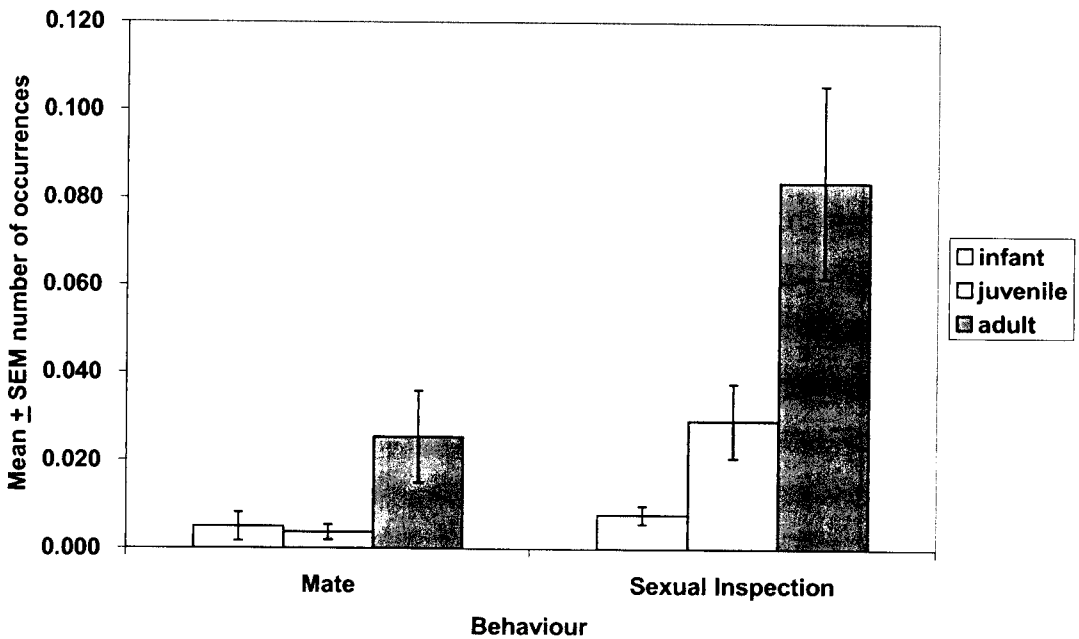
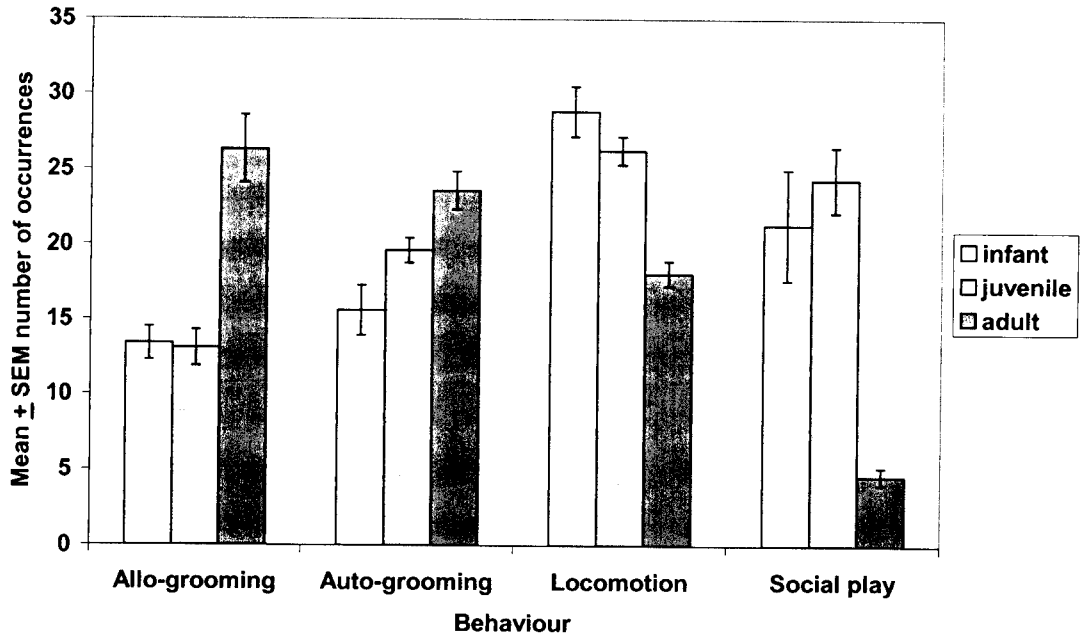
Figure 4.1 – Mean \pm SEM rate of behaviour modified by institution.



Higher levels of sexual inspection and mating were performed at Bristol Zoo than Chester Zoo and Assiniboine Park Zoo. Levels of sexual inspection and

mating at Bristol were significantly higher than at Assiniboine Park Zoo ($p < 0.001$, $p < 0.001$, respectively). Levels of sexual inspection and mating at Chester Zoo were significantly different to levels at Bristol ($p < 0.01$, $p < 0.001$, respectively) but not Assiniboine Park Zoo.

Figure 4.2 – Mean \pm SEM rate of behaviours exhibited by three different age groups. **Note:** Results are displayed in two graphs due to difference in axis scales.



Adult levels of allo-grooming were significantly higher than infant ($p < 0.001$) and juvenile ($p < 0.001$) levels. Infant levels of auto-grooming were significantly lower than juvenile ($p < 0.05$) and adult ($p < 0.001$) levels. Adult levels of locomotion were significantly lower than infant ($p < 0.001$) and juvenile ($p < 0.001$) levels. Adult levels of social play were significantly lower than infant ($p < 0.01$) and juvenile ($p < 0.001$) levels. Adult levels of sexual inspection and mating were significantly higher than infant ($p < 0.001$, $p < 0.01$) and juvenile levels ($p < 0.01$, $p < 0.001$).

4.3.1 Results Summary

- The institution in which the lion-tailed macaques were housed had a significant effect on the behaviour they performed.
- The age of the individual had a significant effect on the behaviour it performed.
- The sex of the individual did not affect the behaviour it performed.

4.4 Discussion

As predicted the behaviour of lion-tailed macaques was significantly modified by the institution in which the animal was housed and the age group it belonged to. The sex of the animal however did not significantly modify its behaviour. This latter result was surprising in light of the different strategies employed by the two sexes.

4.4.1 Effect of institution on lion-tailed macaque behaviour

The institution modified the behaviour of lion-tailed macaques therefore showing the environment an animal is housed in modifies its behaviour. Similar results have been found in other studies (Kerl & Rothe, 1996; Lukas et al., 2003). Specifically the institution had a significant effect on levels of sexual behaviours. Sexual inspection and mating were performed the most at Bristol Zoo and the least at Assiniboine Park Zoo. One explanation for the difference in sexual behaviour may be group size. There was an inverse

relationship between group size and levels of sexual behaviour. The zoo with the smallest group (Bristol $n=6$) performed the most sexual behaviours and the zoo with the largest group size (Assiniboine Park Zoo, $n=16$) performed the least sexual behaviours. These results were not expected since in the largest group individuals have more opportunities for sexual partners and therefore sexual behaviours. Levels of sexual inspection and mating may have been higher in Bristol Zoo due to more adult females being in oestrus at the time of the study, despite there being only two adult females in the Bristol group, in comparison with the four adult females in the Assiniboine group. It was also noticed that the male at Bristol masturbated at higher levels than males in other groups (Skyner, personal observation), so this particular male may have a higher "libido" than the other males studied (however the adult male sample size was small, $n=3$). Masturbation is thought to increase the quality of sperm competition of subsequent ejaculations (Baker & Bellis, 1995). The time of the year that the different groups were studied may have resulted in different sexual behaviours being displayed (Chester = June to October, Bristol = January to April and Assiniboine = April to July). However in lion-tailed macaques mating and birth seasonality does not tend to be observed in captivity (Lindburg & Harvey, 1996) so this is not likely.

It is interesting that the zoo with the highest breeding success and highest number of adult females (Assiniboine Park Zoo) had the least number of occurrences of sexual inspection and mating. It could be suggested that this is a result of the male being more successful at ejaculation. Lion-tailed macaques are multi-mount ejaculators (Kumar, 2001; Lindburg et al., 1985) and the average number of mounts to ejaculation is 9.1 (Lindburg & Harvey, 1996). It has been shown that when exposure to females is limited to an hour a day a male can sometimes ejaculate on the first mount (Lindburg et al., 1985). It may be possible that the male at Assiniboine Park Zoo had to mount less on average to ejaculate, in comparison to the males at the other zoos.

The history of the adult male in each group may have had an effect on the performance of sexual behaviours. Males had been in the group for approximately the same length of time when each study commenced but backgrounds obviously differed. The male at Chester was mother-reared at Belfast zoo and was eight years old when studied. The male at Bristol was mother-reared on St Catherine's Island and was 13 years old when studied. The male at Assiniboine was part hand-reared at Toronto Zoo and was nine years old when studied. It is interesting that the male showing more occurrences of sexual behaviours was older than the other males and therefore you could assume more experienced. The male from Bristol was also reared in a free-ranging group on St Catherine's Island, Georgia, which means the experiences for this male were probably very different to the experiences of the other males housed in zoos. The group at St Catherine's Island are provisioned daily but except for observational studies, human contact is minimised (Lindburg et al., 1997). Individuals in this group have learned to forage on naturally occurring foods and cope successfully with a variety of local fauna and predators such as raptors and alligators (Lindburg et al., 1997). It may be that individuals in this group behave more naturally than individuals housed in zoos. The male at Assiniboine was partly hand-reared and while this does not seem to affect the overall performance of sexual behaviours it may however have caused the number of occurrences of sexual inspection and mating to be less than the other groups. As this group is producing high numbers of infants this is not a concern. It is important to note that the sample size of adult males in this study was low ($n=3$) and therefore a larger sample size is required to form accurate conclusions.

It is surprising that the institution did not modify levels of agonistic, allo-grooming, appeasement, auto-grooming, foraging, locomotion, social, social play and threat behaviours, as different variables within each institution (such as enclosure size and group structure) were predicted to have an effect on the performance of behaviours. It is surprising that social play was not modified by institution as there were more infants and juveniles in the Assiniboine Park Zoo group compared to Chester and Bristol Zoos. Juvenile

lion-tailed macaques were observed to spend more time performing social play in this study as discussed below. One would expect crowded conditions (i.e. a small enclosure with a large number of individuals in it, such as that at Assiniboine Park Zoo) to modify agonistic behaviour (Baker & Aureli, 1997).

4.4.2 Effect of age on lion-tailed macaque behaviour

The age of lion-tailed macaques modified levels of allo-grooming, auto-grooming, locomotion, social play, sexual inspection and mating. Auto-grooming increased with age which may be due to infants being allo-groomed more by their mothers and family members and as a result not needing to spend time auto-grooming. Macaques and baboons show developmental changes in mother offspring grooming (Cheney, 1978; Muroyama, 1995). The time spent grooming immature offspring by their mothers decreased with offspring age (Cheney, 1978; Muroyama, 1995).

Levels of allo-grooming increased with age. Allo-grooming was performed more by adults and the least by juveniles which is similar to observations by Johnson (1985) who found that infant lion-tailed macaques were never seen to groom each other. The research by Johnson (1985) is the only other study examining the effect of age on modifying lion-tailed macaque behaviour. Allo-grooming has been shown to be a tension reduction mechanism (Boccia et al., 1995; Kutsukake & Castles, 2001; Schino et al., 1988) and heart rate and cortisol levels have been shown to decrease when primates receive grooming (Aureli et al., 1999; Boccia et al., 1989; Gust et al., 1993; Ray & Sapolsky, 1992). Adult lion-tailed macaques may therefore perform more allo-grooming than younger lion-tailed macaques to reduce tension in the group, since they are potentially exposed to more tense situations than infants and juveniles.

Sexual inspection and mating increased with age which is to be expected as animals will start to perform sexual related behaviours upon reaching reproductive age. Male lion-tailed macaques reach sexual maturity at approximately eight years old (Green & Minkowski, 1977) although in

captivity males can be fertile from six years of age (Krebs & Kaumanns, 2001, 2002). Sub-adult male rhesus macaques have been observed to mate significantly less than adults (McMillan, 1989) which is consistent with this research. Sub-adult macaques have low dominance rank (McMillan, 1989). Mating success has been found to correlate with dominance rank in rhesus macaques when sub-adult males were included in the analysis (McMillan, 1989) so low dominance may result in less mating. The higher levels of sexual inspection and mating by adult lion-tailed macaques in this study could therefore be related to dominance. The sub-adult males in all three groups of lion-tailed macaques studied were natal to the females. It may therefore be possible that the low levels of sexual inspection and mating displayed are a result of inbreeding avoidance (Pusey & Wolf, 1996).

Social play was performed the most by juveniles followed by infants. The opposite was found in baboons, Coelho Jr and Bramblett (1982) found infant baboons to play more than juveniles. The difference in levels of play and age group may be due to a difference in age group classification in lion-tailed macaques and baboons or simply the difference in play between different species. Play is common in all primate species and is useful in physical and social development. Play usually decreases when animals get older and is replaced with behaviours more suitable for an individual's survival. In support of this, De Oliveira et al (2003) found infant golden lion tamarins to spend significantly more time performing play behaviour than adults. The same was found in woolly monkeys by Defler (1995) which is consistent with this research.

In the current research levels of locomotion decreased across the age groups. Infants performed the highest levels of locomotion followed by juveniles and the lowest levels were performed by adults. Similar results have been found in European brown bears by Montaudouin and Le Pape (2004) who found increased resting time to be the main effect of increased age. Similarly, Wells and Turnquist (2001) found the frequency of locomotion to be greater in juvenile rhesus macaques and to decrease with age. Levels of locomotion may decrease with age due to young animals having more

energy for play behaviours than adults. Adult animals may use their energy for other activities such as strengthening bonds with individuals by allo-grooming or investing in reproductive activities. Due to energy required in mating, pregnancy and lactation, adults may spend more time resting than young.

Levels of agonistic, appeasement, foraging, social and threat behaviours were not modified by age. It is surprising that levels of agonistic behaviour, threat and foraging were not modified by age, as you would expect adult animals to spend more time performing agonistic and threat behaviours than infants and juveniles, since the latter behaviours play a significant role in reproduction. Adults could also be expected to spend less time foraging than younger individuals as they are more skilled and therefore efficient (Johnson & Bock, 2004).

4.4.3 Effect of sex on lion-tailed macaque behaviour

There was no significant effect of sex in modifying lion-tailed macaque behaviour which is a surprising result. A similar result has been found in wild woolly monkeys (Defler, 1995) for whom no sex differences were observed. The above result could reflect similarities in behaviour in animals in the three institutions studied or the non-significant result may be due to the behavioural observation period being too short to detect slight changes in behaviour. Data were not collected on animals over the course of a whole year or at the same time period per institution. As a result seasonal behaviour changes may not have been accurately recorded as one would expect sex differences to be more pronounced across the seasons. As mentioned above however lion-tailed macaques do not tend to display mating and birth seasonality in captivity (Lindburg & Harvey, 1996).

It is also possible that the variation in the social structure (for example, number of males and females) of the three groups studied may have masked potentially interesting results. If lion-tailed macaque groups were similar in size and social structure and more captive groups were studied, it is possible

that different results would have been found. Social structure and group size varied across groups due to limitations with availability of captive lion-tailed macaque groups. Unfortunately due to the nature of zoo research this could not be avoided.

The results from this study indicate that energy allocation to behaviour is significantly modified by external factors in captive lion-tailed macaques. Further long term research is required to thoroughly understand the factors that modify behaviour in this species of macaque. It would be interesting to carry out a similar study with wild groups of lion-tailed macaques in fragmented habitats, to see if behaviour is modified by similar factors.