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IDENTIFICATION AND EVALUATION OF THE CAPTIVE ENVIRONMENTAL FACTORS THAT AFFECT THE BEHAVIOUR OF SULAWESI CRESTED BLACK MACAQUES (*MACACA NIGRA*)

by

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A thesis submitted in partial fulfilment of the
requirements for the degree of Doctor of Philosophy

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VMelfi

Victoria Ann Melfi

I would like to dedicate this thesis to two women who inspired my interest in science,
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I will be forever grateful for their encouragement and love of science.

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ABSTRACT

IDENTIFICATION AND EVALUTION OF THE CAPTIVE ENVIRONMENTAL FACTORS THAT AFFECT THE BEHAVIOUR OF SULAWESI CRESTED BLACK MACAQUES (*MACACA NIGRA*)

Observations of eight Sulawesi macaque troops in the UK and Ireland, were used in four main studies that investigated: 1) The influence of season on the behavioural expression and enclosure use of Sulawesi macaques in a number of zoos; 2) A comparison of captive Sulawesi macaque behaviour and enclosure and substrate use between zoos; 3) A comparison of wild and captive Sulawesi macaque behaviour, using previously published data of wild macaques (O'Brien & Kinnaird, 1997); 4) The influence of captive environmental variables on the behaviour of Sulawesi macaques.

In captivity, Sulawesi macaque behaviour differed significantly between seasons, as did the climate and management practices. In the winter the occurrence of social behaviour significantly rose, while foraging behaviour significantly declined. Differences in the environmental conditions between zoos also significantly affected Sulawesi macaque behaviour, and enclosure and substrate use. Equally, the behaviour of wild Sulawesi macaque troops was reported to vary according to different environmental factors (O'Brien & Kinnaird, 1997). The behavioural variation observed in both sets of data, meant that behaviour between wild and captive troops was not significantly different.

The results of the multiple regression analyses identified five key features of the captive housing and husbandry regime that significantly affected captive Sulawesi macaque behaviour: enclosure size and complexity; troop size; the use of bark as an inside flooring material; and feeding frequency. Not unexpectedly, various combinations of these environmental factors determined behavioural expression. Practicalities influenced which environmental factors could be tested quantitatively, which were: enclosure complexity (useable area); flooring material; feeding frequency; and social composition. Appropriate modifications were made to the captive environment of one Sulawesi macaque troop, to quantify the effects of these environmental factors on behaviour. All the factors tested significantly affected captive Sulawesi macaque behaviour and/or enclosure use. Changes to the captive environment that reflected the concept of 'naturalistic' housing, promoted active behaviours.

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INTRODUCTION

1.1 STUDY RATIONALE

Sulawesi crested black macaques (*Macaca nigra*) are highly endangered in the wild; their habitat is fragmented and dwindling, and they are keenly hunted by local villagers (Kinnaird & O'Brien, 1996; Rosenbaum *et al.*, 1998; Hilton-Taylor, 2000). Measures to conserve Sulawesi macaques involve both *in-situ* (habitat protection and a reduction in hunting pressure) and *ex-situ* strategies (the use of captive breeding programmes in zoos, Norcup, 2000).

Captive management of endangered populations needs to integrate the requirements of conservation and welfare (Redshaw & Mallinson, 1991). Fundamental to maintaining primates in captivity, is the understanding of how captive environmental factors affect their behaviour. In this study, the effect of captive environmental factors on primate behaviour was expanded, using a two-step methodology and the captive population of Sulawesi macaques in the UK and Ireland, as a model.

1.2 STUDY AIM

This study aimed to identify which environmental factors altered the behaviour of captive Sulawesi crested black macaque. Activity budget comparisons were made to investigate how Sulawesi macaque behaviour varied between zoos and season (Chapter 2). Multiple-regression analyses were used to establish links between the different environmental variables found across zoos and how they affected Sulawesi macaque behaviour (Chapter 3). On the basis of these results, quantitative experiments were carried out to investigate how the manipulation of single aspects of the captive environment would affect the Sulawesi macaque behaviour (Chapter 4).

1.3 THE ROLE OF PRIMATES IN CAPTIVITY

The role of primates in captivity has changed greatly in the last century, as a consequence of major transformations in zoo ethos, husbandry and research (Mench & Kreger, 1996). As a result many zoos have committed themselves to meet the goals of primate conservation, research and education as outlined in the world conservation strategy (Halle, 1985; Waugh, 1988).

1.3.1 Conservation

Many primate species are at risk of extinction from anthropogenic hostilities, which are destroying their natural habitats and removing them from the wild for research, food or the pet trade (Kinnaird & O'Brien, 1996; Rosenbaum *et al.*, 1998; Pimm & Raven, 2000). Zoos can provide a short-term safeguard against extinction through the management and breeding of primate species *ex-situ*, which also reduces the need to take animals out of the wild for exhibition or research (Rawlins, 1985). Captive breeding programmes aim to maintain the genetic diversity of endangered primates, with the long-term goal of reintroducing them back into the wild when it is safe (Halle, 1985). This goal depends on the successful breeding of endangered primates that will be able to reproduce and nurture their young in captivity and when released back into their native habitat, which will require specialised survival skills (Snowdon, 1989). Many of the behaviours required for survival in the wild are adaptations to a specialised and challenging environment that can be different from captivity (Reinhardt & Roberts, 1997). Recent studies have highlighted behavioural inadequacies in reintroduced primate species, e.g. the inability to find food or recognise predators, which lead Snowdon (1989) to caution that the expression of survival skills by captive primates could not be expected, as there was the possibility that they may be lost during a lifetime in captivity. It is plausible that primates in captivity will become behaviourally adapted to their new environment, either through changes in their genetic makeup or as socially learnt behaviours are lost between generations. In captive populations gene frequencies will be affected by: artificial selection, as humans breed for desirable traits; natural selection, resulting in animals that become adapted to the captive environment; and relaxation of selection pressures, when the absence of ‘wild’ selection pressures allows behavioural traits to proliferate in captivity, that would otherwise be disadvantageous and selected against in the wild (Carlstead, 1996). Primates rely heavily on socially learnt behaviours, and as long-lived, large-brained animals, Box (1991) has asserted that they would be especially at risk of losing essential skills required for survival in the wild. This has been reflected in the extensive training and provisioning given to mammal species pre and post-release, while bird species get less and amphibians and reptiles usually receive none at all (Beck *et al.*, 1994). Although simplistic, it does appear that reintroduction programmes involving primates encounter greater problems compared to those that reintroduce bird and ungulate species. For example the Arabian Oryx (*Oryx leucoryx*) and Mauritius kestrel (*Falconidae naumanni*) were both threatened species and now represent viable wild populations, whereas the golden lion tamarin (*Leontopithecus rosalia rosalia*), Geoffroy's marmoset (*Saguinus geoffroyi*) and black and white ruffed lemur (*Varecia variegata variegata)* have all encountered numerous problems which have lead to many deaths (Dixson & Jones, 1988; Beck *et al.*, 1991; Passamani & Passamani, 1995; Beck *et al.*, 1998; Britt *et al.*, 1999). This could indicate that reintroduction success is inversely related to the species' reliance on socially learnt behaviours or their behavioural complexity.

At present the success rate of reintroduction programmes is low, but even if all the captive breeding programmes were effective only a small proportion of the world's endangered species could be saved, which has lead some to debate over whether is it a practical conservation option (Lindburg, 1992). Captive breeding programmes are associated with research that aims to improve animal welfare and further our understanding of animals. In addition, a zoo that holds endangered species can provide a resource for public conservation education, which can result in beneficial consequences.

1.3.2 Education

Zoos offer an unequalled chance to gain access to exotic animals, providing public education and resources for specialists undertaking further studies in the field of exotic zoo biology (Waugh, 1988; Fa *et al.*, 1995). Live exhibits at zoos attract a large body of people from a wide spectrum of society, increasing awareness of animal related issues, especially the need for conservation, and contributing to the creation of positive attitudes to wildlife, all without the need to handle any of the animals (Schaaf, 1984; Saunders & Young, 1985 cited in Sherwood *et al.*, 1989). Contact with animals from an early age has been associated with positive attitudes to wildlife and conservation and can be provided through visits to a zoo (Wheater, 1985; Kidd & Kidd, 1996). Many methods are implemented to convey the urgency of conservation efforts including interpretation signs for all animal exhibits, as well as more formalised education programmes (Thompson, 1989).

Evaluating the efficacy of pubic education in zoos has been approached in many ways, including investigations into the time spent reading information signs beside animal enclosures (McGough & Marples, 1998; Lacey, 2001). Enclosure style and the activity level of the animals held within them, affect the publics' perception of zoos and the type of information that they take away from them (Wolf & Tymitz, 1981; Bitgood *et al.*, 1988; Reade & Waran, 1996). In general, the public perceive active animals and natural looking enclosures positively (Shepherdson, 1993). In a classic study based at Chessington Zoo, a survey recorded the attitudes of people viewing several cat enclosures across two conditions (Young, pers. comm.). The two conditions were identical, except that in the second treatment the front of the exhibits that had been constructed of bars, were replaced with glass. Surveys of the public after each treatment revealed that the bars were associated with negative perceptions and assumptions about zoos and their treatment of animals. In a similar situation at Dublin Zoo, after the transfer of jaguars (*Panthera onca*), lions (*Panthera leo*) and snow leopards (*Panthero uncia*) to new exhibits, people were frequently heard to exclaim that they 'preferred the new animals' and that the new animals 'looked healthier than the old ones' (Healy, pers. comm.). Actions taken by zoos to promote positive perceptions of both the animals and the zoo, include the provision of more 'naturalistic' looking enclosures, objects within the enclosure that stimulate active behaviours in the animals and more accessible education facilities (Shepherdson, 1989; Thompson, 1989; Shepherdson, 1993).

1.3.3 Research

Primate species that would otherwise be difficult to locate *in-situ* can be studied in zoos. Research in zoos is usually restricted to non-invasive studies to limit stress and disturbance. Studies of behaviour are especially suited to zoo research as they are cheap, non-invasive and investigate a diversity of pure and applied scientific hypotheses. For example, pure scientific studies have investigated whether golden-lion tamarins use optimal foraging principals when feeding and applied studies have explored which flooring material primates prefer in captivity (Anderson & Chamove, 1984; Rapport, 1998). Many zoo-based studies have implications for the housing, husbandry, breeding and the welfare of captive primates and the implementation of recommendations resulting from these projects is essential for the improvement of zoo conditions and goals (Eisenberg & Kleiman, 1977; Hutchings *et al.*, 1978b; Schaaf, 1984; Kleiman, 1992; Kleiman, 1994a; Kleiman, 1994b; Seidensticker & Doherty, 1996). Zoo biology also provides an opportunity for the criticisms of zoos to be explored and solutions to be sought that will promote animal welfare and conservation, as well as provide information for educational programmes (Mallinson, 1995).

1.4 ACHIEVING THE GOALS PROMOTED BY ZOOS

It is generally accepted that alongside the goals of conservation, education and research, modern zoos also aim to meet the physical and psychological needs of primates in captivity. There are a variety of methods that can be used to meet these demands, from enclosure design and tailored husbandry regimes to the implementation of environmental enrichment. Integral to these approaches are the simulation or stimulation of 'wild-type' (those expressed by wild con-specifics) behaviours and activity budgets (Forthman-Quick, 1984; Maple & Finlay, 1989; Shepherdson, 1994; Newberry, 1995; Seidensticker & Forthman, 1998).

1.4.1 ‘Wild-type’ behaviour expression vs. domestication

‘Wild-type’ behaviour is the consequence of adaptations necessary for life in the wild, and the physical and cognitive complexities this involves. Intuitively, it seems sensible that the expression of these behaviours by captive primates would aid conservation efforts, but arguments are also made that these behaviours can also lead to improved welfare (Seidensticker & Forthman, 1998; section 1.3.1, 1.4.1.b and 1.4.1.c). Despite the universal implementation of programmes that aim to stimulate ‘wild-type’ behaviour in captive primates, there are some fundamental objections to the use of ‘wild-type’ behaviour as a phenomenon (Woolverton *et al.*, 1989; Veasey *et al.*, 1996; section 1.4.1.c). However, in the following sections ‘wild-type’ behaviour, defined as those behaviours or level of behaviour observed in wild primates, will be discussed, so that its importance to captive primates can be evaluated.

1.4.1.a Domestication

Primate species that breed most successfully in captivity represent those that have adapted more effectively to the captive conditions and therefore adaptation to the captive environment will be promoted through successive generations (Lovejoy, 1980). The ultimate aim of captive management is to support species survival, which is undertaken by preserving genetic diversity and preventing inbreeding within the captive population, as it is hoped: 1) that the captive population will then retain some genetic characteristics present in wild populations; 2) genetic variation will provide a basis for the species to adapt to changes in the environment: and 3) this will also aid in the promotion of individual and population fitness (de Boer, 1994; Ballou & Foose, 1996). Genetic management limits the process of phenotypic domestication, although as described in section 1.3.1 behaviours could still be lost over time in captivity. Few studies have investigated domestication in exotic species, however, the expression of 'wild-type' behaviours in long domesticated species like pigs and dogs, may suggest that some behaviours are far more difficult to extinguish than expected (Hale, 1969, cited in Carlstead, 1996; Stolba & Wood-Gush, 1989). Carlstead (1996) suggests that the behavioural difference between wild and captive animals is probably quantitative and not qualitative.

1.4.1.b Implications for conservation

The loss of behaviours which function as survival skills in the wild may hinder future conservation goals and so it has been suggested the behaviours required for survival in the wild should be maintained in captive populations (Shepherdson, 1994; Balmford *et al.*, 1996; Britt, 1998). However, evidence from the long-running reintroduction programme for golden lion tamarins suggests that the ability of to express 'wild-type' behaviours prior to release has a negligible impact on survival (Beck *et al.*, 1998). Beck *et al.* (1998) demonstrated that the information gained immediately prior to release i.e. in soft release areas, or after release during provisioning, increased the chances of a successful reintroduction above those afforded from a lifetime in an enclosure that allowed 'wild-type' behaviours to be expressed. As few primate reintroduction programmes have been conducted it is difficult to say with any certainty, whether 'wild-type' behavioural conservation is necessary for them to work.

1.4.1.c Implications for animal welfare

The welfare of captive primates is frequently determined through a comparison of their behaviour or activity budget with that observed in their wild counter-parts, and deviations from the 'wild-type' behavioural template are associated with impaired welfare (Hediger, 1955; Maki & Bloomsmith, 1989). It is argued that: 1) 'wild-type' behaviour is natural therefore best; 2) primates are highly motivated to perform these behaviours, so restricting their expression will reduce welfare (Stolba & Wood-Gush, 1984; Shepherdson *et al.*, 1993; Lutz & Novak, 1995); 3) these behaviours have evolved over time and therefore represent optimal behaviour; 4) if these behaviours are not performed a 'void' will be created, which could be filled with 'abnormal' behaviours (Anderson & Chamove, 1984; Chamove, 1988); 5) if they do not express these behaviours they may forego cognitive stimulation (Reinhardt & Roberts, 1997); and that 6) the expression of 'wild-type' behaviours by captive primates is the panacea to the restrictions placed upon them by living in captivity (Hutchings *et al.*, 1978b; Redshaw & Mallinson, 1991).

The term, 'wild-type' behaviour, is itself ambiguous as the behaviour of wild primates varies according to many environmental factors (section 1.5.1.c). Emphasis placed on 'wild-type' behaviour or activity budgets is further misleading, as only a selection of the behaviours observed in the wild are thought appropriate for captive animals to display. In general, activity levels are compared between wild and captive primate populations, resulting in the assertion that captive primates should be more active.

The concept that 'natural' is best, depends on the interpretation, as the welfare of many wild primates could be considered to be very poor (Barnard & Hurst, 1996). In zoos, primates are usually maintained with minimal stress, thus predation, infection, competition for resources and exposure to the climate do not shape behaviour, as it would if they were in the wild (section 1.5.1.c). Recently, the addition of some stress back into the lives of captive primates has been suggested, both from a conservation and welfare perspective. A group of cotton-top tamarins (*Saguinus oedipus*) were exposed to short intense stressful events, analogous to a stressful event that would occur in the wild as for example when a bird of prey flies overhead (Chamove & Moodie, 1990). The results of this study revealed that tamarins exposed to this stressful event displayed lower levels of abnormal, agonistic and locomotion behaviours and higher levels of affiliative behaviours, all of which the investigators concluded to be beneficial to welfare (Chamove & Moodie, 1990). It has also been suggested that primates intended for re-introduction should be exposed to all the selection pressures present in their native habitat, in an effort to select for competent individuals that would be able to survive and reproduce post-release (Beck *et al.*, 1998). The exposure of captive primates to fatal selective pressures may serve conservation efforts but would reduce individual welfare.

Arguments that suggest 'wild-type' behaviour is optimal, ignore the fact that behaviour observed in the wild varies according to many biotic and abiotic factors. The behaviour observed for one primate troop may vary significantly from another, but both patterns of behaviour could be considered optimal for the conditions each group are living in (O'Brien & Kinnaird, 1997). Therefore, the concept of a 'wild-type optimality' is flawed, though the range of behaviours observed in many wild troops could be used to provide an indication of how variable behaviours are in the wild.

Anderson & Chamove (1984) proposed that if captive primates did not express 'wild-type' behaviours, 'abnormal' behaviours might manifest in their stead. It is equally credible that if a void is created that behaviours of a negligible or beneficial nature may be performed rather than abnormal behaviours (those performed at extreme levels or to the exclusion of other behaviours like stereotyped pacing, or those that cause harm like self-mutilation) (Reinhardt & Roberts, 1997).

Some 'wild-type' behaviour include a sequence of behaviours, in which a highly motivated appetitive behaviour is followed by a rewarding consummatory behaviour for example, a primate is motivated to forage (appetitive) and when food is found will eat it (consummatory) (Hughes & Duncan, 1988). In a captive situation the appropriate rewards may not exist within the enclosure to allow the expression of consummatory behaviour after appetitive behaviours. In the wild, appetitive behaviours are not always rewarded, but in the absence of a reward, the animal is able to perform the behaviour in a different situation that may then deliver the appropriate reward and the consummatory behaviour can follow. It has been suggested that the inability of captive animals to perform this contingent link between behaviours, may result in the development of a myriad of undesirable behaviours including the formation of re-directed and displacement behaviour and stereotypies (Reinhardt & Roberts, 1997).

The concept that 'wild-type' behaviours may provide cognitive stimulation and captive primates are highly motivated to perform them, support the incorporation of 'wild-type' behaviours into the repertoire of captive primates. To survive in the wild, primates have developed complex behaviour patterns. In captivity many wild selection pressures do not exist, so there is no need to express many 'wild-type' behaviour patterns. Therefore, the stimulation associated with the expression of 'wild-type' behaviour patterns, would also be lost. Many measures could be taken to provide cognitive stimulation for captive primates, including the use of artificial apparatus; however, the aesthetics of these types of devices are rarely appreciated and the 'natural' alternative is usually sought which includes the stimulation of 'wild-type' behaviours (Hutchings *et al.*, 1978a; Hutchings *et al.*, 1978b).

Preference tests use the concept that an animal's willingness to 'work' for a resource, whether freely available or not, reflects their level of motivation to gain the resource or carryout the behaviour (section 2.3.3). Shepherdson (1993) observed that captive felids would work to catch live fish, in the presence of an alternative free food supply. He explained these observations in terms of two theories, 1) the appetitive/consummatory theory reported by Hughes & Duncan (1988) (see above), and 2) Inglis & Ferguson's (1986) theory that animals would forfeit free food to gain more information about their environment. Research reported by Elson & Marples (2001) revealed that a variety of parrot species would work harder to gain food if it was presented in a manner that reflected their 'wild-type' feeding habits. Instead of feeding from dishes in the enclosure the parrots would work to get food from enrichment devices that were tailored to their wild feeding behaviour. For example, captive golden-shouldered parrots (*Psephotus chrysopterygius*) selectively used hanging branches with seeds glued to them, which enabled them to employ manipulative behaviours used by wild counterparts to gain food from seedpods and/or grassheads, whereas wild scarlet-chested parrots (*Neophema splendida*) which feed mainly on the ground, showed a preference for foraging trays placed on the ground.

If the expression of 'wild-type' behaviour is not essential for reintroduction then a degree of domestication in captive primates should be considered. Domesticated animals are associated with successful reproductive lives in captivity, as they are not affected by many of the stressors integral to captive living; as such a degree of domestication could be considered as beneficial to individual welfare (Broom & Johnson, 1993; Harrington, 1996). The process of socialisation, where familiarisation and interaction occurs between keepers and their animals, could result in animals becoming more domesticated (Harrington, 1996; Mellen & Ellis, 1996). In the past, attempts have been made to limit the socialisation of captive animals especially if they were destined for reintroduction. Endangered bird species targeted for reintroduction extreme measures have been used to limit the interactions between keepers and chicks; however in a study of houbara bustards (*Chlamydotis undulata*), the long-term survival of reintroduced birds was not significantly affected by rearing conditions (Heezik *et al.*, 1999). Results from this study revealed that the style of training prior to release did significantly affect the bustards' long-term survival rate, though it should be noted that the ability of the birds to reproduce was not measured and this could be adversely affected by rearing condition (Heezik *et al.*, 1999). Welfare benefits have been associated with captive animals that have undergone some degree of socialisation, e.g. increased levels of interaction between keepers and small exotic felids were associated with elevated reproductive rates, indicating that socialisation may improve health parameters which indirectly promoted reproduction (Mellen, 1991). Furthermore, evidence that the management style adopted (negative, positive, neutral) when interacting with captive animals has been shown to affect health and reproductive rates of farm and exotic animals (Waran, 1995; Harrington, 1996; Mellen & Ellis, 1996). Designating animals as far as possible as either destined for conservation programmes or as those that are to live their life in captivity might be difficult, so degrees of domestication should be recommended whereby ‘wild-type’ behaviours are promoted but animals still interact with keepers (Newberry, 1995). On this basis, the benefits of adaptations required for life in the wild and those that may better serve life in captivity can be enjoyed.

Despite the ambiguity surrounding the welfare implications of ‘wild-type’ behavioural expression in captive primates, many researchers advocate its use as a reference point indicating enhanced welfare, and accordingly zoo managers attempt to provide adequate opportunities for captive primates to express these behaviours (Hutchings *et al.*, 1978b; Maple & Finlay, 1989; Seidensticker & Doherty, 1996). Less ambiguous claims suggest that wild activity budgets can serve as a guideline to illustrate the range of behaviours expressed, and so can provide an indication of whether behaviours observed in captive animals have diverged significantly from those expressed in the wild (Stolba & Wood-Gush, 1984; Chamove, 1988). Captive primates that express ‘wild-type’ behaviours and activity budgets are considered more appropriate subjects for education and research, as they can convey how wild animals live and with the exception of studies that attempt to alleviate any deleterious consequences of captivity, animals displaying ‘wild-type’ behaviours are considered better models for research (Newberry, 1995).

1.4.2 Environmental Enrichment

Environmental enrichment (EE) is the incorporation of stimuli into the captive environment, to promote the expression of ‘wild-type’ behaviour. Since the beginning of the 20th century the term EE has become broader, incorporating aims to promote many animal welfare indices e.g. providing the opportunities necessary to gain some control over the environment and express a range of behaviours, which is accomplished through a variety of methods (Chamove, 1989; Shepherdson, 1991). There are three main categories of EE, though there is some overlap: 1) active EE, uses operant conditioning to stimulate desirable behaviour. For example, in an attempt to increase the activity of four Diana monkeys (*Cercopithecus diana*), a complex exhibit was constructed in which food rewards were given to monkeys when they completed a complex series of movements around the enclosure (Markowitz *et al.*, 1978); 2) passive EE, provides species-specific opportunities to express ‘wild-type’ behaviours. For example, the group of Diana monkeys would be provided with a large and complex enclosure, provisioned with many interesting features that the monkeys could interact with and manipulate; and 3) social enrichment, manipulating social composition (Markowitz *et al.*, 1978; Visalberghi & Anderson, 1993).

1.4.2.a Active Environmental Enrichment

Markowitz and his colleagues developed active EE or environmental engineering and concluded that it was successful in stimulating desirable behaviours, increasing activity and also provided a easy method of monitoring health (Markowitz *et al.*, 1978; Markowitz, 1982). Despite the fact that this approach satisfies the aims of EE, as it can bring the behaviour of captive animals closer to their wild counterparts, it received strong criticisms (Hutchings *et al.*, 1978b). The main objection to environmental engineering was that the behaviour elicited was not 'natural', and the assertion that captive animals may be motivated to 'work' was anthropomorphic (Hutchings *et al.*, 1978b; Forthman-Quick, 1984). Ironically, later studies that demonstrated animals were motivated or willing to 'work' to perform species-specific behaviours were used in support of the implementation of EE (discussed in section 1.4.1.c). The behaviour that resulted from environmental engineering was considered artificial as no association was made between the behaviour and the environment, also these behaviours would sometimes be expressed indiscriminately or at abnormally high levels (Hutchings *et al.*, 1978b). The reward schedule appointed to the apparatus determined the rates of behaviour, so the abnormally high rates of behaviour associated with some engineering apparatus could be reduced by a change in reward rate (Forthman-Quick, 1984). Most of the arguments against environmental engineering were offered on the basis that an alternative passive EE approach was superior; however, comparisons of the two styles indicate that neither are particularly natural nor represent the panacea to behavioural problems in captive animals. For example, larger natural looking enclosures do not necessarily lead to an elevation in activity levels and a feeding device did not alter the stereotypical behaviour of zoo-housed bears, but hiding food throughout the enclosure did (Forthman-Quick, 1984; Spinelli & Markowitz, 1985; Carlstead *et al.*, 1991). Support for the mechanistic approach to behavioural modification has been overshadowed by the controversy that it has provoked; however, more recently it has been used in conjunction with passive EE, usually to stimulate feeding and foraging behaviours (Forthman-Quick, 1984; Reinhardt & Roberts, 1997).

1.4.2.b Passive environmental enrichment

Passive environmental enrichment advocates that natural stimuli be incorporated into enclosure design and husbandry regimes to promote 'wild-type' behaviours (Hutchings *et al.*, 1978b; Maple & Finlay, 1989). In contrast to active enrichment, passive enrichment does not rely on training, but provides a multitude of factors that stimulate behaviour and the performance of the behaviour should in itself be rewarding. In some circumstances greater rewards may be achieved, for example, if a primate explores a log and finds a beetle. However, in passive enrichment the onus is on the animal to choose what it wants to do and the enclosure should provide ample opportunities for this. Naturalistic enclosures are key to passive EE, as they provide a structural basis for daily enrichment (section 1.4.3.a).

Passive enrichment is sometimes called passive training, and is considered useful for potential reintroduction candidates, so that they can become familiar with the conditions and foodstuffs present in the wild.

1.4.2.c Social enrichment

The provision for social behaviour and its manipulation in captivity can be problematic, as mistakes can result in a failure to reproduce or lead to fatal fighting (Visalberghi & Anderson, 1993). Maintaining captive primates in social groups that are similar to those that occur 'naturally' is a generally accepted goal (Hediger, 1955; Hutchings *et al.*, 1978b). Active and passive enrichment are used to alleviate problems associated with unnatural social situations as for example when high levels of aggression or stereotypies (de Waal, 1989).

The formation of 'natural' social groups contributes to a surplus of animals, such as offspring from family groups or maturing males from harem systems (Graham, 1996). The problem of surplus males in the European Sulawesi macaque population is one that is becoming critical (Norcup, 2000). Attempts have been made to form bachelor groups to house surplus males for both Sulawesi macaques and long-tailed macaques (*Macaca silenus*) (Matthews, 1998; Asvestas & Reininger, 1999). The long-term stability of all male groups is not certain, especially as adolescents mature and competition for dominance heightens. In the wild ex-alpha males are not usually tolerated within the group and leave, but in captivity this is not usually an option. In addition to the possible behavioural problems which may compromise bachelor groups, the absence of young animals may also make this type of exhibit less attractive to zoo visitors and subsequently few zoos may be willing to hold all male groups.

The movement of individuals into and out of groups is a frequent occurrence in many 'wild' primate social groups (Pusey & Packer, 1987). Its simulation in captivity is associated with potential risks, which can reduce animal welfare, but replication of 'natural' migrations for captive primates provides genetic management, as well as social stimulation (Visalberghi & Anderson, 1993). This method of genetic management was recommended for Sulawesi macaques held as part of the European studbook and would involve moving males between participating zoos every three to five years, but due to logistical problems this recommendation has not yet been implemented (Lees, 1993; Norcup, 2001).

1.4.2.d Evaluation of enrichment

The goal of enrichment to modify behaviour to resemble a 'natural' template, or to promote 'wild-type' behaviour, is an ambiguous aim that makes evaluation and comparison of enrichment techniques difficult (Newberry, 1995). EE therefore should be implemented when a discrepancy between wild and captive con-specifics is evident. A two-step evaluation of the chosen EE, should involve a comparison of the captive primate behaviour before and after enrichment to reveal the impact of EE. Then a second comparison should be made between the behaviour resulting from the EE and the wild con-specifics. However few comparisons have been made between wild and captive primates, which suggests that this method is not frequently followed (section 2.3.1.c). Most enrichment studies are not evaluated on their ability to stimulate 'wild-type' behaviour, but by their ability to stimulate desirable and inhibit undesirable behaviours, or increase activity, as there is an underlying assumption that captive animals are too inactive (Nash & Chilton, 1986; Maple & Finlay, 1989). The drive for greater activity may not necessarily reflect the captive animal's wild counter-parts. For example, lions spend many hours resting in the wild, but in an effort to increase activity, lions in Busch Gardens, Florida are trained to move when they hear a whistle, which is operated every 30 min. In these situations, it seems that the visitors benefit more from these elevations in activity than the animals, as it has been reported that visitors view animals more positively if they are active (Shepherdson, 1991).

The majority of EE studies operate on a 'trial and error' basis, whereby stimuli are added or removed from an enclosure and the resultant behaviour observed (section 1.5). The success of EE as it is currently practised, may be a result of the vast number of studies undertaken using this approach, rather than the suitability of the stimuli that are used to promote activity or desirable behaviours. The use of systematic methods to evaluate behaviour in response to the current diversity of environmental factors between zoos should help to identify appropriate enrichment (section 1.5.1.a).

1.4.2.e Benefits of environmental enrichment

Reports of EE in zoo biology usually detail its successful implementation and the benefits accrued by the recipient. The stimulation of 'natural' behaviours and the amelioration of 'abnormal' behaviours are the most frequently quoted benefits of EE; examples include the reduction of stereotypies and the expression of species specific feeding behaviours in felids, bears and primates (Bayne *et al.*, 1991; Carlstead *et al.*, 1991; Shepherdson *et al.*, 1993; Baker, 1997; Britt, 1998; Healy, 2000). Improved physical fitness, spatial coordination and enclosure use have also been observed and reported for captive animals in enriched enclosures (Chamove, 1989; Shepherdson *et al.*, 1993; Kessel & Brent, 1996). Carlstead and Shepherdson (1994) reviewed the impact of EE on the reproduction of captive animals, and concluded that physical and psychological aspects of reproduction benefited from enrichment (e.g. modulation of stress and socio-sexual stimulation). Reinhardt & Reinhardt (2000) argue that social enrichment is essential for captive primate welfare and many studies have shown the even in very small cages the provision of a cage-mate can be greatly beneficial (Reinhardt, 1994; Reinhardt *et al.*, 1995; Reinhardt *et al.*, 1998). Conversely, Woolverton *et al.* (1989) asserted that there was no substantiated evidence that demonstrated that individually housed adult primates had impaired welfare, though they conceded that behavioural development of infant primates was deleteriously affected by single housing.

The methods used in EE are highly variable and their actions cannot necessarily be generalised between species, therefore a success in one situation might not translate well to another (Maple & Finlay, 1989). General aspects of the housing and husbandry routine have been identified which can be modified to reflect species-specific needs and, therefore, provide enrichment (Chamove, 1989; Boinski *et al.*, 1994). However, changes that reflect enrichment can be made to the enclosure and no visible change in behaviour observed. Spinelli & Markowitz (1985) reported that changes in enclosure size and complexity had no significant affects on the behaviour of some laboratory and zoo-housed primates (section 1.4.3.b). The widespread incorporation of EE into housing and husbandry demonstrates the popularity of the belief that its implementation is beneficial. Indeed, as the definition of EE broadens to encompass many of the possible and progressive housing and husbandry modifications that can be achieved, it is difficult to see how it cannot be beneficial. Developments that have no visible effect on captive animal behaviour may simply provide a more dynamic environment in which animals can display more choice and control over their lives, both of which would be hard to quantify. Finally, the aesthetics of EE can positively enhance public education (Wolf & Tymitz, 1981; Carlstead *et al.*, 1991; Reade & Waran, 1996; see section 1.3.2).

1.4.3 Enclosure design

Many managers of captive animals acknowledge that exhibits that allow the expression of 'wild-type' behaviours are beneficial, and try to provide them accordingly (Seidensticker & Doherty 1996). The modification of captive animal behaviour is attempted and in some cases achieved through environmental enrichment and naturalistic housing, both of which are fundamental to modern primate housing (Hutchings *et al.*, 1978b; Chamove, 1989; Maple & Finlay, 1989; section 1.4.2.a and 1.4.2.b).

Enclosure design and the considerations on which it is based have developed to incorporate the needs of the occupants (both psychological and physical), visitors (educational) and keepers (husbandry and hygiene) (Coe, 1996). Despite the variety of terms used to describe captive primate environments, two dichotomous architectural styles are generally recognised, that of 'hard' and 'soft' enclosures (Sommer, 1974, cited in Maple & Finlay, 1989). Maple & Finlay (1989) considered that physical and psychological complexity, privacy from visitors and con-specifics, temporal and manipulative objects and ample space to allow social distancing, were all factors that should be included in the construction of primate enclosures. These factors are seldom found in 'hard' enclosures, though the use of concrete, bars and few if any flexible objects are associated with them and often perceived negatively by zoo visitors and researchers alike (section 1.3.2). Conversely, 'soft' enclosures (naturalistic) provide natural materials that can be manipulated, a complex environment and many of the factors suggested by Maple & Finlay (1989) that provide passive enrichment. The process of creating enclosure complexity or adding natural materials is sometimes referred to as 'naturalizing' the habitat and can be applied to 'hard' enclosures (Coe, 1989).

1.4.3.a Naturalistic vs. hard enclosures

Naturalistic (or soft) enclosures are considered to be inherently more complex and atheistically pleasing than 'hard' enclosures. Naturalistic enclosures have been demonstrated to stimulate captive primates physically and psychologically, by providing a complex and dynamic enclosure (Redshaw & Mallinson, 1991; Ogden *et al.*, 1993). In two studies, the behaviour of mandrills (*Sphinx mandrillus*) and three species of big cat (lion, snow leopard and jaguar), were compared between 'hard' and 'soft' enclosures (Chang *et* *al.*, 1999; Healy & Marples, *in prep*). The animals were primarily resident in the 'hard' enclosures and then moved to the 'soft' enclosures. Healy & Marples (*in prep*) and Chang (1999) interpreted changes in behaviour as evidence that the 'soft' enclosures were beneficial, as stereotypical behaviour in the 'big cats' declined and activity levels in the mandrills increased. However, 'soft' enclosure design has been interpreted and implemented in many different ways and Seidensticker & Doherty (1996) categorised these enclosures according to their function: 1) the realistic, reproduces the wild habitat including land formation and plant life; 2) the modified, simulates the wild substituting available materials for example, using different vegetation and land formations present at the zoo; and finally 3) the naturalistic, where no attempt is made to duplicate the wild, and natural materials are used in a stylistic way, frequently for aesthetics not animal function. There is an obvious difference between the types of stimulation a captive primate would gain from each of these 'soft' enclosures, which indicates that aesthetically acceptable enclosures do not automatically convey health and welfare benefits to primates. Similarly, 'hard' environments can be modified to provide a more complex environment for captive primates. In a study conducted by Bayne *et al.* (1991) a 'hard' laboratory cage was altered to hold a social group of capuchins (*Cebus apella*) and furniture was added to provide a complex environment. These changes resulted in the reduction of stereotypical behaviour. Enclosures should contain substrates and structures that can be used in species-specific activities. This can only be achieved through an understanding of primate behaviour and how it is affected by captive environmental factors (Kerridge, 1996; Britt, 1998).

1.4.3.b Enclosure complexity vs. space

Theoretical discussions concerned with the improvement of captive housing for primates suggest that enclosures should be large, complex and dynamic facilities that are able to hold appropriate social groups (Mallinson, 1995; Newberry, 1995). Enclosure size can be considered important for animal welfare, as behaviours required to limit stress can be restricted by enclosures that are too small, like distancing and comforting behaviours (Hediger, 1955; Berkson *et al.*, 1963). Boot *et al.* (1985) also reported that unsuccessful pregnancies in long-tailed macaques were reduced when the macaques were housed in the larger of two differently sized enclosures. Woolverton *et al.* (1989) argued against the use of large enclosures, because they claimed that there would be an increased risk of injury and far greater opportunities to destroy the enclosure and either use parts thereof as projectiles or ingest them. Empirical studies have also refuted the importance of enclosure size in relation to captive primate welfare. In one series of studies there was no observed change in the behaviour of rhesus (*Macaca mulatta)*, long-tailed and pig-tailed macaques *(Macaca nemestrina*), when they were housed in different sized cages (Line *et al.*, 1989; Line *et al.*, 1990; Line *et al.*, 1991; Crockett & Bowden, 1994). Furthermore, no significant difference in cortisol level was measured when long-tailed and pig-tailed macaques were housed in different sized cages (Crockett *et al.*, 1993a; Crockett *et al.*, 1993b). These studies conclude that enclosure size does not affect captive primate welfare: although it seems more likely that the index chosen to reflect animal welfare may be robust to changes in enclosure size and a multi-disciplinary approach may help to interpret the results, as the enclosure sizes used restricted full body movement (0.05m x 2m x 0.36m; 0.1m x2m x 0.43m; Crockett & Bowden, 1994). Reinhardt *et al.* (1996) argued further, asserting that studies of cage size were unimportant, as more or less barren space was of no consequence to captive primates, but the contents of space was (complexity). This was supported by the results reported by Leu *et al.* (1993), where a significant decline in stereotypical behaviour was observed in long-tailed macaques after they were transferred from a small barren enclosure into the larger compartmentalised cage. The frequency of stereotypical behaviour in captive primates was also observed to decline when modifications were made to the enclosure's complexity while its size remained the same (Whitney & Wickings, 1987).

Space alone, therefore, may only affect captive primate welfare if it falls below a certain threshold, above which enclosure complexity may contribute more to captive primate welfare and behaviour. This is supported by the observations of primates and other zoo-housed animals that are provided with large enclosures which they do not fully utilise, but display distinct preferences for certain areas (Ogden *et al.*, 1993; Pullen & Buchan, 2001; Lammers, 2001). In zoo enclosures, complexity is provided through the implementation of environmental enrichment, which increases the primate's 'psychological space'; a term coined by Chamove (1989) that conceptualises how captive primates view their surroundings (Forthman-Quick, 1984; section 2.2.2). In a study by Wilson (1982) enclosure complexity was identified as more important in the determination of gorilla (*Gorilla gorilla)* and orang-utan (*Pongo pygmaeus*) behaviour than enclosure space. However, when Perkins (1992) replicated this study, enclosure space and complexity were considered highly interrelated and, therefore, considered to affect behaviour together. Dramatic changes in the way captive primates are exhibited may in part explain the discrepancy between the results of these two studies and suggests that enclosure complexity and size were not uniform in older exhibits (Wilson, 1982). The acceptance by zoo managers that complex enclosures are beneficial to captive primate welfare and behaviour, has lead to the incorporation of complexity into enclosure design and appears to have resulted in zoo enclosure size and complexity increasing in parallel (Perkins, 1992).

1.5 MEASURING THE IMPACT OF CAPTIVITY ON BEHAVIOUR

It is generally accepted that captivity affects primate behaviour and that it is detrimental (Morris, 1964). This is surprising because zoos furnish captive primates with all the resources they need food, shelter and mates, while attempting to limit competition and potential conflict and also reduce the risk of predation and disease. This suggests that either the removal of liberty or some aspect of the facilities holding primates have damaging affects, if zoos truly affect captive primates negatively.

Studies have been conducted to investigate how captivity affects the behaviour of primates, which have followed two main approaches, which could be described as 'bottom-up' and 'top-down'. The bottom-up approach makes speculative changes to the captive enclosure or husbandry routine until behaviours are modified. This approach predominates as most environmental enrichment studies use this method. For example, many attempts have been made to modify or reduce undesirable behaviour and promote desirable behaviours in captive primates, by making alterations to the captive environment (Chamove, 1989; Reinhardt & Reinhardt, 2000). The top-down approach first establishes which captive environmental factors affect behaviour. If it is then felt necessary to modify behaviour, environmental factors can be altered accordingly. The two approaches can be used in conjunction, by first identifying the environmental factors that affect behaviour and then modifying that factor until behaviour is altered.

Both 'top-down' and 'bottom-up' approaches reveal similar information; however, by definition the 'bottom-up' approach is less comprehensive as the goal is to modify behaviour and if this occurs after changing one aspect of captive management the investigation is concluded, so no further information about how other environmental factors alter behaviour is gathered.

In the following section, methods that have been used to establish the effect of captivity on captive animal behaviour are explored and include the use and comparison of activity budgets, multivariate statistical analyses and preference testing.

1.5.1 Activity budget comparisons

Behaviours can be categorised as states or events depending on their duration. Events occur momentarily while states are longer lasting. Events are recorded and expressed as frequencies, while the duration of a state behaviour can be calculated and is used in the construction of activity budgets. An activity budget represents the time allocation to certain behaviours and can be constructed for individuals or groups (Martin & Bateson, 1996).

The time available to behavioural expression remains constant, though the time devoted to particular behaviours can vary. If restrictions or demands are placed on the activity budget, 'fixed' (high priority) behaviours will be satiated at the cost to other 'flexible' behaviours, which will inevitably have less time devoted to them. For example, as infants grow and need more energy, feeding behaviour (fixed behaviour) is increased and the performance of play (flexible behaviour) may decline. Where fixed behaviours cannot be fully satiated, animal welfare may be infringed (Bubier, 1996). In addition, though the time spent performing flexible behaviours can be modified, there may be a limited time range within which these behaviours should be expressed and if conditions push flexible behaviour expression beyond this range then animal welfare can also be compromised (Bubier, 1996).

1.5.1.a Factors that affect activity budgets

Individual differences and the environment in which an animal is reared and lives, will influence the time spent performing behaviours and determine where behavioural priorities lie. Individual differences include genetic make-up, temperament, rank, reproductive status, disease load and sex-age class (Hawkins, 1999). Identifying genes that are responsible for behavioural expression is beyond the scope of the project, so too is the impact of temperament. However, in a recent series of studies Carlstead *et al.* (1999a) found that the individual temperament of black rhinoceroses (*Diceros bicornis*) influenced how they reacted to environmental factors present in their enclosure. In captive primates disease load should be minimal and therefore not affect behaviour, but other factors occur in captivity that can influence an individual's behaviour. For example, hand-rearing has been reported to affect behavioural development significantly and consequently behavioural expression (Martin, 2000). All primates in this study were parent-reared.

In this thesis, individual activity budgets are assessed by sex-age class and, to a limited extent, rank. The decisions that drive activity budgets are different between the sexes, in part because of differences in body size, investment in reproduction and dominance status within the group. Sulawesi macaques are sexually dimorphic, so males are larger than females. Larger animals have higher energy demands, but a more efficient metabolism than smaller animals so the time and amount of food they need to gather, declines proportionally as their body size increases (Schmidt-Nielsen, 1990). Larger animals are also more likely to attain positions of higher rank and therefore enjoy priority access to resources. This was demonstrated in a study of feeding behaviour in Sulawesi macaques, where the dominant male and female frequently monopolised food after they were provisioned resulting in them spending less time feeding (Ettah, 1997; Smith *et al.*, 1989). Individuals of low rank have been associated with poor access to food, high levels of stress and low reproductive success, which will all contribute to the activity budget (Silk, 1989). Females of high rank have been observed to suffer from a greater number of failed pregnancies, however, as they begin breeding younger and have shorter inter-birth intervals their overall reproductive success is greater relative to lower ranked females (Melnick & Pearl, 1987; Silk, 1989). Investment in reproduction varies between sexes and females depending on the stage of their reproductive cycle. As pregnancy progresses the energetic demand increases and persists during lactation until the infant is weaned, suggesting that females will require more food during these months (Lee, 1987). Social interactions may also be affected by the reproductive status of the females, as the dominant male tries to monopolise the ovulating female and subordinate males attempt 'sneaky matings'.

Age will also affect an individual's activity budget, due to many of the same differences explored above (for example body size and reproductive status). Social interactions are also different between age classes with juveniles spending at least 10% of their time playing socially (Beckoff & Byers, 1992). It would be reasonable to assume that as individuals become older, the time spent moving would decline, especially in a captive situation were they are provisioned with food.

To understand how environmental factors affect behaviour, group activity budgets can be constructed by averaging the activity budgets for individuals in a group. Although some environmental factors may be similar between captive and wild primates (season and intra-troop sociality) it is the environmental factors unique to captivity (visitor disturbance and lack of predation), which probably have most effect on their activity budgets.

Variations in rainfall, temperature and vegetation are associated with changes in season. Many wild primate species exhibit seasonal behaviour, which reflects changes in resources and the need to regulate their internal temperature (Oates, 1989; Menzel, 1991). Seasonal changes experienced by captive and wild primates are probably different, due to climatic differences between regions and indirectly due to changes in the captive management of primates between seasons. Captive Sulawesi macaques have been observed to avoid extremes in weather conditions, if they have access to sheltered areas (Bernstein & Baker, 1988).

Numerous environmental factors associated with the captive management of primates have been identified which influence their activity budgets, which can be grouped into four categories: enclosure size and enclosure complexity (section 1.4.3.b), husbandry routine and inside flooring substrates (section 3.3.4 and 4.1). The group's activity budget will also be affected by its social composition, as the behaviour of different sex-age classes is expected to differ, so the group's activity budget will be biased towards the most abundant sex-age class.

Husbandry broadly encompasses the actions taken by the zoo management to maintain primates and include, the number of feeds provided per day and the style in which they are presented. Few studies have been carried out in zoos to quantify the effects of these different husbandry factors, though more extensive research has been undertaken on captive primates under laboratory conditions, especially studying the influence of flooring materials on the behaviour (Chamove *et al.*, 1982). Aspects of captive management that have been explored are the effects of visitors, and factors associated with feeding and foraging behaviours and troop size (in primates and other species). It has been demonstrated that zoo visitors significantly affect the behaviour of captive primates, especially if they are noisy or in big groups (Hosey & Druck, 1987; Birke, 2001). In a comparative study of golden-bellied mangabey (*Cercocebus galeritus chrysogaster)* behaviour in enclosures that received high, moderate and low levels of visitors, levels of aggressive behaviour towards visitors and inter-group aggression (between the focal primate group and surrounding primate groups in other enclosures) were observed to increase with visitor number, while aggression toward neighbouring primates in other enclosures was observed to decline (Mitchell *et al.*, 1991). Chamove *et al.* (1988) asserted that behavioural changes associated with visitors represented stressful excitement and did not provide stimulation analogous to enrichment. The impact of visitors on captive orang-utans was lessened, by providing them with areas within their enclosure where they could hide from the public (Herbert & Bard, 2000).

Reinhardt & Roberts (1997) reviewed many of the techniques and devices used to modify the time captive primates spent feeding and foraging. These included the use of puzzles, probes and inside flooring materials in which food was hidden. The style of food presentation has also been shown to significantly affect captive primate and feline behaviour (Shepherdson *et al.*, 1993; Reinhardt & Roberts, 1997). In two studies, the time spent feeding significantly increased when whole food rather than 'chopped' food was provided (Ettah, 1997, Sulawesi macaques; Smith *et al.*, 1989, lion-tailed macaques). This elevation in feeding time was considered beneficial as it brought the captive activity budget closer to that observed for wild con-specifics, though there was some concern that monopolisation of choicest foods was easier and a nutritional balance might not be achieved (Ettah, 1997; Smith *et al.*, 1989).

The effect of troop size on behaviour and reproductive success varies considerably between species. Large group sizes have been associated with significant elevations in Orang-utan activity, a reduction in reproductive success in small captive exotic felids and increases in reproductive success in Chilean flamingos (*Phoenicopterus chilensis*) which require at least 40 birds to breed and Caribbean flocks (*Phoenicopterus ruber ruber*) which require over 20 birds (Wilson, 1982; Mellen, 1991; Stevens, 1991; Pickering *et al.*, 1992).

1.5.1.b Multi-zoo studies

Comparing the behaviour of one species across several zoos provides the best opportunity to investigate the effects of captive environmental factors on behaviour and has been used to evaluate how these factors affect reproductive success, activity levels and enclosure use (Ogden *et al.*, 1993; Mellen, 1994). Most of these studies have used multiple regression analyses to identify which of the environmental factors measured were most successful at predicting behaviour. In a pioneering multi-zoo study, Wilson (1982) indicated that troop size and the type of objects in the enclosure significantly influenced the activity levels of captive orang-utans and gorillas. As the results of multiple-regression analyses are based on correlations, the relationships identified are not necessarily causal and so they need to be quantitatively tested (Chang *et al.*, 1999).

Multi-zoo studies are seldom conducted despite their benefits, probably because their demand of finance and time is considered too high (Mellen, 1994). However, a series of multi-zoo studies have recently been initiated in the USA, using the data collected by surveys at 45 American zoos to investigate the effects of current housing and husbandry regimes on the breeding success of endangered species which are known to show poor reproduction in captivity (Kleiman, 1994a). These studies use a method classified as the 'measuring behavioural assessment' (MBA), which evaluates how different individuals react to captive environmental conditions according to their 'personality traits'. For example, the breeding success and mortality of captive black rhinoceros were shown to be affected by enclosure size and the personality combination of the pair put together to breed (Carlstead *et al.*, 1999a; Carlstead *et al.*, 1999b).

1.5.1.c Wild vs. captive

To date few studies have quantitatively compared the behaviour of wild and captive con-specifics, though many studies frequently refer to 'wild-type' primate behaviour when they attempt to alter captive primate behaviour. These studies consider that the behaviour expressed by wild animals is optimal and therefore efforts should be made to achieve similar behavioural expression in captive animals (section 1.4.1). Veasey *et al.* (1996) succinctly countered the calls for achieving 'wild-type' behaviour in captive animals by indicating six main discrepancies in wild-captive comparisons of animal behaviour, which they claimed invalidated such comparisons. Dissatisfaction with previous wild-captive comparisons can be summarised as four points: 1) behaviour of wild animals changes according to geographical, topographical and temporal variation, therefore a single 'wild activity budget' is meaningless; 2) there may be genetic differences between wild and captive animals (Eisenberg & Kleiman, 1977); 3) behavioural observations made in the wild are affected by the investigator, so may not reflect undisturbed wild animal behaviour; 4) most comparisons involve small sample sizes and different researchers, thus creating an element of experimental error.

Not only are wild primate troops variable in their behavioural expression, but the behaviour observed in captive primate troops is also highly variable as it is affected by enclosure and/or social group changes (Mitchell *et al.*, 1991; Boinski & Mitchell, 1992; O'Brien & Kinnaird, 1997). Indeed some recognise that differences between captive animals in large free-ranging enclosures and some wild troops are fewer than those between wild troops in different habitats or different captive enclosures. Thus environments should be categorised as being more 'wild-like' or 'captive-like' (Carlstead, 1996; Chang *et al.*, 1999). Rowell (1967) was one of the first to discredit the wild-captive dichotomy. Given that primates bred in both locations, she considered that they were extreme points on a habitat continuum. Wild-captive comparisons should not be disregarded as long as an adequate quantification of environmental and temporal variables that may affect behavioural expression is recorded.

Methodological inconsistencies between captive and wild behavioural data may also invalidate comparisons (Veasey *et al.*, 1996). As wild animals are easily disturbed and generally difficult to locate and observe, a variety of observational techniques have been developed to minimise the impact of the observer on the animal but these still provide data of variable validity due to factors like habituation of the target animals and/or provisioning (Martin & Bateson, 1996). In a study carried out by O'Brien & Kinnaird (1997), observations of wild Sulawesi macaques were achieved through habituation; a process that supposedly removes the effect of observer bias, as the animal no longer reacts to the observer. However, in a study conducted by Isbell & Young (1993) observer bias was displayed in sympatric species and their interactions with the focal animals, resulting in modified behavioural observation. Isbell & Young (1993) found that the African herbivores they were studying were killed at statistically lower levels when an observer was present. If wild-captive comparisons are made, a method of behavioural observation should be chosen which reduces the risk of being conspicuous to target animals. If investigations of behavioural interactions are required between species, habituation should be attempted for both species, or remote observations employed. Practically this may not be possible and so observer bias should be considered when interpreting results. However, in terms of wild-captive comparative studies, the effect of observer bias is probably minimal compared to the effects of different environmental factors.

The use of small sample sizes is the bane of zoo biology, as the number of animals held restricts sample size. An approach that increases sample size is multi-zoo research, which gathers information across many zoos (section 1.4.2.a). In addition, there are statistical methods designed specifically for use with small sample sizes and though larger sample sizes may represent greater precision, or generality of the result, this does not disqualify the data collected from small samples.

Many research projects use multiple observers and there are many methods of testing that inter-observer variation did not occur or is negligible (Ralls *et al.*, 1982; Martin & Bateson, 1996; Herbert & Bard, 2000). When comparisons are made between sources that do not check for inter-observer reliability there is a risk that the perceived behavioural definitions may be dissimilar, resulting in inconsistent data. These risks can be reduced with the use of clear ethograms (Martin & Bateson, 1996).

In summary, the arguments made against wild-captive comparisons of behaviour are valid but by considering these arguments an improved wild-captive comparison can be made.

1.5.1.d Variation between macaque species

The genus *Macaca* is widespread and includes 15 species, 7 of which are endemic to Sulawesi, Indonesia (Fooden, 1969; MacDonald, 1984). The geographic range of macaques is far-reaching and their behaviour and social systems are diverse (MacDonald, 1984; Whitney & Wickings, 1987). In captivity, the influence of environmental change on macaque behaviour can vary depending on the species. In a classic series of experiments, pig-tailed macaques and stump-tailed macaques (*Macaca arctoides*) were provided with visual barriers in their enclosures, which lead to increased and decreased levels of aggression, respectively (reported in Carlstead & Shepherdson, 1994). These macaque species are governed by different social systems. The dominant male pig-tailed macaque mediates female-female aggression, so when his view of the troop was impaired with visual barriers, female-female aggression rose (Erwin, 1979). Whereas, aggression in the stump-tailed macaque troop was primarily caused by the dominant male trying to monopolise copulations, so the visual barrier hampered his view of the group and therefore lead to a reduction in aggression (Estep & Baker, 1991). Macaques maintain complex social networks in part by the ability of individuals to behave co-operatively after aggressive confrontations (Call *et al.*, 1999). The pattern of retaliation and reconciliation after aggressive incidences can be used to categorise and compare macaque social groups (Kappeler & Schaik, 1992). Sulawesi crested black macaques were ready to retaliate after an aggressive encounter, and would then reconcile within a minute of the conflict using intense and elaborate reconciliatory behaviours (Petit & Thierry, 1994). This was categorised as a egalitarianism social system, due to the low asymmetry between individuals (Petit & Thierry, 1994). This pattern was also observed in Tonkean macaque (*Macaca tonkeana*), another endemic of Sulawesi (Fooden, 1969). Both Sulawesi macaque species differ from the strict hierarchies of the rhesus, Japanese (*Macaca fascicularis*) and long-tailed macaques, which were observed to have a low repertoire of reconciliatory behaviours that were displayed at low frequencies (reported in Petit & Thierry, 1994). Differences between macaque species are also evident in the interactions of females and infants (allomothering) and between infants. Rhesus macaques with their strict hierarchies were observed only to allow similar ranking peers to interact with their babies, whereas bonnet macaques were observed to place few restrictions on those that could interact with their infants reflecting a more 'liberal' social organisation (Caine & Mitchell, 1980).

1.5.2 Multiple regression analysis

Multiple-regression (MR) analysis is an extension of bivariate correlation, where several independent variables (IVs) including enclosure size, troop size and feeding regime, are used to predict the value of a dependant variable (DV) for example the time spent resting, foraging and feeding. The goal of MR is to use as few IVs as possible to achieve a good prediction of the DV (the predictive model). Depending on the MR model used the unique and combined contribution made by each IV to the predictive model can be established, therefore the relationship between each IV and the DV, as well as the relationship between all the IVs in the model and the DV can be deduced.

1.5.2.a Correlation data

Multiple regression analysis is based on the significance of correlation coefficients that have inherent limitations and need to be borne in mind when interpreting results. A correlation between IV and DV is not necessarily causal, as a third IV not included in the analysis may be responsible for changes in both the DV and IV. The strength of the correlation is not necessarily reflected by its significance, as the probability of finding a significant relationship increases with sample size. Sprinthall (1987) (quoted in Martin & Bateson, 1996) proposed an arbitrary set of definitions to interpret the strength of the correlation coefficient, which recognise that some correlations are so weak that they may be negligible.

1.5.2.b Data entry

There are three main methods of entering data into multiple-regression equations, standard, hierarchical and statistical. Each model requires different data stipulations and provides alternative interpretations of the results. In statistical MR, IVs enter and/or leave the equation depending on whether they meet a predetermined statistical value (either F or *p* value). There are then 3 methods of data entry into the statistical MR: forward selection, backward deletion and stepwise regression. In forward selection IVs are added to the equation one at a time if they meet the statistical criteria of entry and their addition to the model is permanent. Additional IVs enter the equation if their contribution to the model increases the ability to predict the DV (elevates R^2). Backward deletion starts off with all the IVs in the equation and removes them one by one if they do not contribute to the statistical significance of the regression. Stepwise regression is a compromise of both the forward and backward methods. IVs are added to the model one by one if they improve the regression model, but also removed if, after the addition of successive IVs, their contribution to the model no longer contributes significantly to the regression. Statistical MR is considered to be effective when addressing the question 'what is the best linear combination of the IVs to predict the DV in this sample?' (Tabachnick & Fidell, 1996). In addition, statistical MR can provide information on the sequential and combined contribution of the IVs to the prediction of the DV, which is especially important when there is a degree of multicollinearity between the IVs (intercorrelation between more than one IV). The forward selection version is recommended if several MR analyses are to be carried out on the same set of data (Wilkinson & Dallal, 1981). In this study, statistical MR using forward selection was used.

1.5.2.c Interpretation of MR results

The significance of the MR model is determined by calculating the F ratio for the multiple R, where the multiple R is the correlation coefficient for the final multiple regression model. A significant MR result (rejection of the null hypothesis) occurs when there are significant correlations between the IVs and the DVs.

The degree to which the IVs included in the MR model can predict the DV, is indicated by R^2, the coefficient of determination, which describes how much of the observed variation in the DV can be ascribed to the model. As the sample size increases and more IVs are included in the MR, the potential to overestimate the multiple R rises, leading to overestimated R^2 values and the chance of accepting the null hypothesis becomes negligible. Adjusted values of multiple R should be calculated to compensate for sample size and number of IVs included in the MR (Tabachnick & Fidell, 1996).

The unique contribution (sr_i^2, semi-partial correlation coefficient) made to the MR model by an IV, is the value by which R^2 will reduce if that IV is removed. In statistical MR the sequential sr_i^2 value is calculated, which indicates the contribution made to the MR model at the point that the IV enters the equation. Therefore, any overlap in the contribution made to the model by previously entered IVs will be deducted from the contribution made by newly entered IV. For example if the first IV to enter the equation is intercorrelated with the second, the sr_i^2 made by the second IV will appear smaller as the overlap in variation will be credited to the first IV. Therefore the contribution made to the final R^2 value by each IV will depend on the order of IV entry into the equation. The contribution made to the MR model by each IV is represented by a β correlation coefficient, whose significance is established using a t-test. A β coefficient should range between >2 or <-2, therefore not include 0.

The degree of multicollinearity (intercorrelation between more than two IVs) can be established by evaluating the tolerance values. Tolerance values range between zero and one, where zero reflects a linear relationship between IVs in the model and therefore high intercorrelation. Multicollinearity in a MR model reduces the accuracy of interpreting how individual IVs affect the DV. Therefore, the direct effect of each IV on the expression of the DV can only be implied.

1.5.3 Preference testing

Preference tests establish which resources animals prefer, thus providing a mechanism to interpret how an animal perceives its own needs. Animal behaviour and animal welfare studies have extensively used preference testing to determine how behaviour is influenced by genetic differences, reproductive status and numerous different environmental factors (Hughes & Black, 1973). In order to evaluate the preferences of animals fully, it is very important not to underestimate their environmental complexity and to provide them with sufficient options from which to choose a resource they prefer (Fraser & Matthews, 1997). The preferred choice may also be affected by previous experience, therefore use of new resources may temporarily reflect the animal's tendency to avoid or use the novel resource. To date the majority of preference testing has been carried out with animals housed either in laboratories or farms, but more recently preference testing has been used to evaluate the preferences of zoo housed animals (Ogden *et al.*, 1993; Ludes & Anderson, 1996; Kinahan & Marples, 2000).

Simultaneous presentation of different resources provides information about which resource the animal prefers from the selection provided. Equally apparatus can be used to calculate how much time or energy the animal is willing to expend to get access to a resource. The latter method has been developed to measure the strength of the animal's preference for a resource (Cooper & Mason, 2000). Dawkins (1983) highlighted how the choices of shoppers in economic theory, parallel the choices made by animals, thus providing a mechanism to interpret preference strength and its implications for animal welfare. There are two main assumptions in this theory: 1) that the resources available are wanted and 2) that budget constraints will affect choice. When restrictions are placed on the animal, it is expected that the most important resource will be chosen, which is considered to be an inelastic 'product' and a necessity, whereas in a situation where there are no constraints on animal choice a 'elastic' or luxury 'product' can be chosen.

Several methods have developed to measure an animal's preference strength: 1) will an animal learn a behaviour in order to gain the resource? If not, then the demonstrated preference for that resource is considered weak;

2) an obstruction test puts something between the animals and its reward e.g. door and considers how hard the animal is willing to work in order to gain the reward;

3) animals are restricted by the amount of time they have to use a choice of rewards, as the time allowed to gain the reward diminishes, it is assumed the animal will choose the reward it most prefers or needs;

4) aversion tests, usually consider the choice of an animal to undergo something unfavourable for example, an electric shock. Comparisons are made to identify how vigorously an animal will avoid different unpleasant situations (Fraser & Matthews, 1997).

The number and appropriateness of the resources presented to an animal during a preference test, determines the value of the results. The choices made by animals are not necessarily those which promote animal welfare, for example, they may choose a tastier rather than healthier food, and the animals' decisions may only satiate short-term and not long-term biological functioning (Duncan, 1978). Therefore, the ability of preference tests to provide an insight into the needs of animals is only as good as the experimental design.

1.5.4 Behavioural diversity and single site comparisons

Single site studies are defined as those carried out at one location (zoo enclosure). Usually this style of study compares behaviour before and after an event to evaluate its repercussions. This style of study is typical of evaluations made of zoo enrichments, as the influence of enclosure or husbandry changes can be assessed in terms of changes in behaviour.

The benefits of this approach are that it is relatively cheap, quick and easy. In these situations, extraneous variables should not confound the results as they are matched between treatments. Order effects and those contributed by the passing of time can be reduced through design modifications e.g. using a Latin square design (Lehner, 1979). Unfortunately, this method usually suffers by having a small sample size, which is further reduced, as sub-groups may exist within the group (sex-age classes). The interpretation of results from a study of small sample size is limited, as the results may be influenced by individual or group variation, which becomes apparent when a similar study with different animals leads to different results. In addition, the variables present at one site may vary considerably from those found at another and although these 'background' variables were not modified during the experiment, they may alter the animal's perception of the changes and therefore contribute to the behavioural changes. For instance, in a complex enclosure the addition of another substrate e.g. a log may affect behaviour less dramatically than if it were incorporated into a more barren enclosure. Therefore, results from these single site studies do not lend themselves to generalisations, though studies of this type cautiously predict how changes in the environment might affect behaviour (Carlstead *et al.*, 1991; Baker, 1997). Changes in food presentation, enclosure structure and complexity and the effect of visitors, are examples of studies that have been investigated using single-site studies (McKenzie *et al.*, 1986; Smith *et al.*, 1989; Mitchell *et al.*, 1991).

Chapter 2

INTRA-SPECIFIC VARIATION

2.1 THE EFFECT OF ZOO AND SEX-AGE CLASS ON BEHAVIOUR

This section explores the extent to which captive environmental variables present at each of the study zoos affect behaviour, by considering whether differences in behaviour between zoos might be a result of behavioural patterns associated with different sex-age classes.

2.1.1 Methodology

2.1.1.a Subjects

The macaques in this study are part of a European population that are managed through a captive-breeding programme (Norcup, 2000). This means that breeding and exchanges of Sulawesi macaques in the twenty-two European zoos are managed centrally in an endeavour to maximise genetic diversity (or retain the genetic information of the founder population) and minimise inbreeding. Lees (1993) suggested that exchanges of Sulawesi macaques between European zoos should occur every three to five years to maintain genetic diversity and reduce inbreeding. Due to managerial and practical constraints Sulawesi macaque exchanges between zoos have not reached this level. Between 1995 and 1998 the mean gene retention of the population dropped from 0.772 to 0.729 and the wild source of gene diversity remained constant at 0.977 (Norcup, 2000). Norcup (2000) believes that breeding from genetically important dams and sires in the future could increase the genetic diversity.

The performance of behaviour is always determined to some extent by both genetic and environmental factors; however, in some circumstances it may be possible to consider one more influential than another. In this project, the behaviour of several troops of macaques is compared and where there are differences, environmental factors are assumed to be the cause. This rationale rests on the assumption that the macaques in each troop (zoo) are not genetically distinct from others in the population (sample) and so no troop has a genetic predisposition to perform certain types or levels of behaviour relative to the other troops. The genetic differences between the troops should not exceed the differences within a troop. Pedigrees for each of the study troops have been constructed which illustrate at least two different genetic lines that have a contributed to the genotype of that troop (figures 2.1.1 – 2.1.7). There are obvious genetic overlaps between these study troops, with the exception of macaques at Jersey and Chester Zoo, which do not appear to share any genes (in the form of ancestors) with London (though London does share genetic lines with the other troops, as do Jersey and Chester). From the pedigrees it also appears that the genetic diversity between the macaques studied at each troop is comparable across the troops. On the basis of the pedigrees for each troop, it would seem that the integral assumption of this project is valid; namely that each troop's genotype is similar.

Table 2.1.1 Captive group composition and age range of Sulawesi macaques observed (summer of 1997† and 1999‡).

Zoo	Troop size (*number observed if different*)	Sex ratio of troop m:f:unk*	Sex-age categories of individuals studied					Age range
			Adult		Juvenile		Infant	
			male	female	big	small		
Chester†	14	4:10:0	2	4	5	3		2 yr–18 yr
Dublin‡	10 (9)	4:5:0	1	3	2	3	1	9 mth – 13 yr
Jersey I†	17 (16)	7:9:1	3	6	3	4	1	2 wk - 26 yr
Jersey II‡	14	4:10:0	1	6	4	3		2 yr – 13 yr
London‡	7	2:5:0	1	4	0	2		1 yr – 20 yr
Marwell†	10 (9)	2:7:1	1	4	1	3	1	4 mth - 13 yr
Paignton‡	13 (12)	7:6:0	3	4	3	2	1	7 mth - 15 yr
Thrigby‡	8 (7)	2:5:1	1	3	2	1	1	3mth – 16 yr

*m:f:unk = male:female:unknown

Troop size and composition of the macaques' studied are presented in table 2.1.1. Three troops were multi-male groups and 5 troops single-male harems. Individuals were classified into one of five sex-age categories:

Infant - under 1 yr,
Small juvenile –1-2 yr,
Big juvenile (female 3-5yrs or male 3-7yrs),
Adult female - 5yr & older and
Adult male - 7 yr & older

Figure 2.1.1 Pedigree for the macaques at Chester Zoo. Macaques observed in this study have double-bordered shapes and are named, males are represented by a square, females by a circle and infants of unknown sex by a triangle.

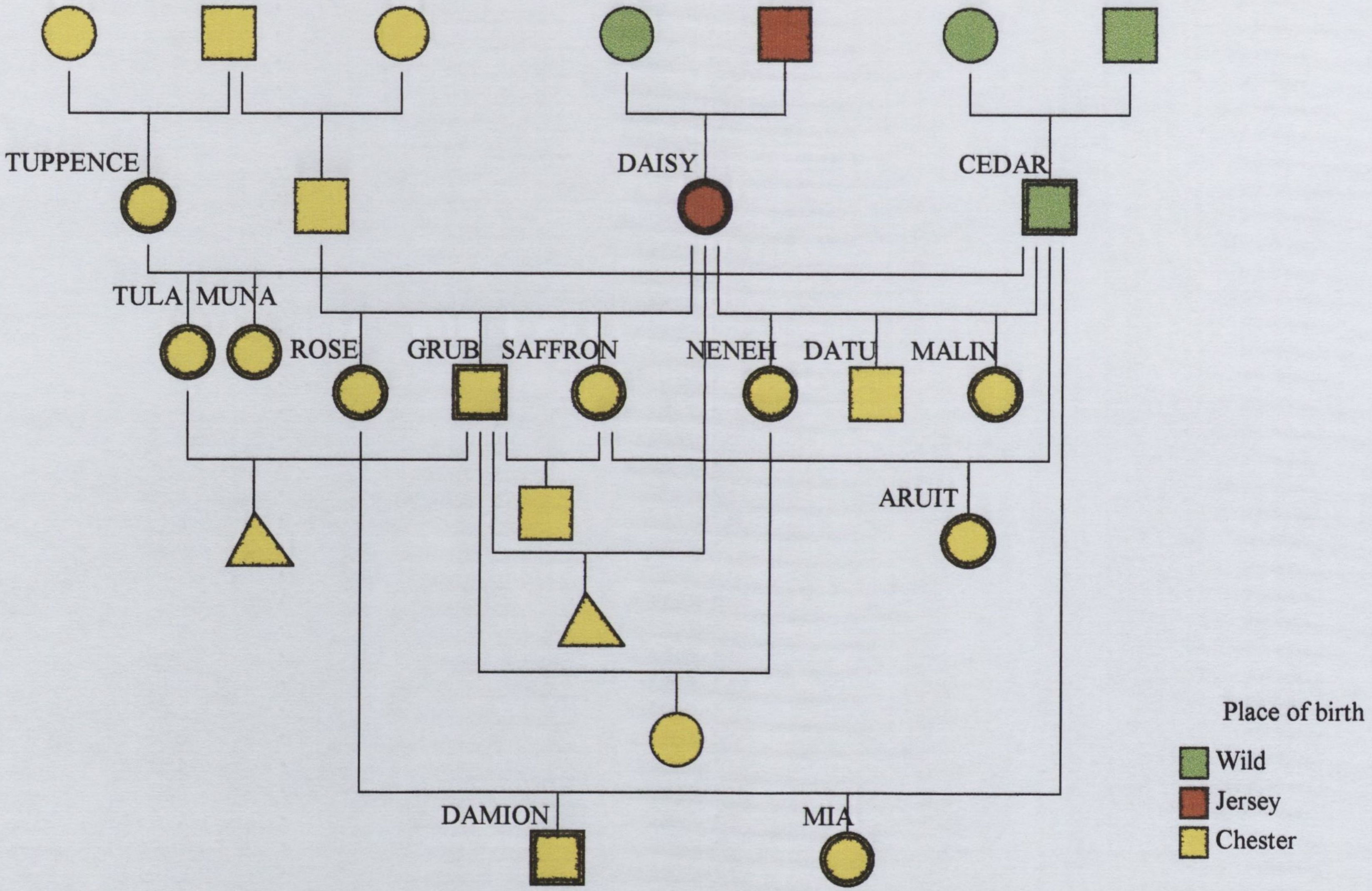


Figure 2.1.2 Pedigree for the macaques at Dublin Zoo. Macaques observed in this study have double-bordered shapes and are named, males are represented by a square and females by a circle.

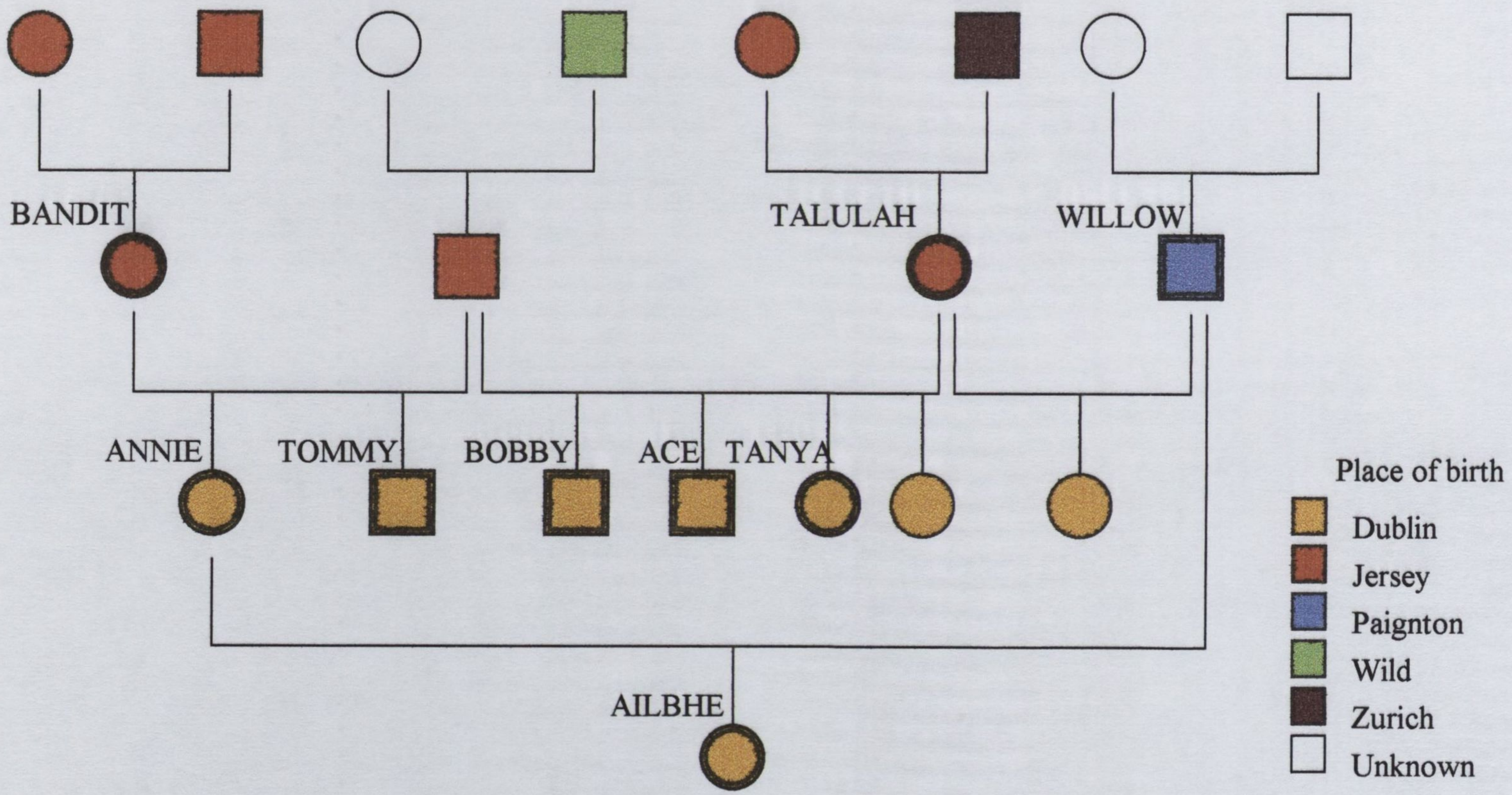


Figure 2.1.3.a Pedigree for the macaques at Jersey I Zoo (1997). Macaques observed in this study have double-bordered shapes and are named, males are represented by a square and females by a circle. A square with a question mark denotes a mating with an unidentified male.

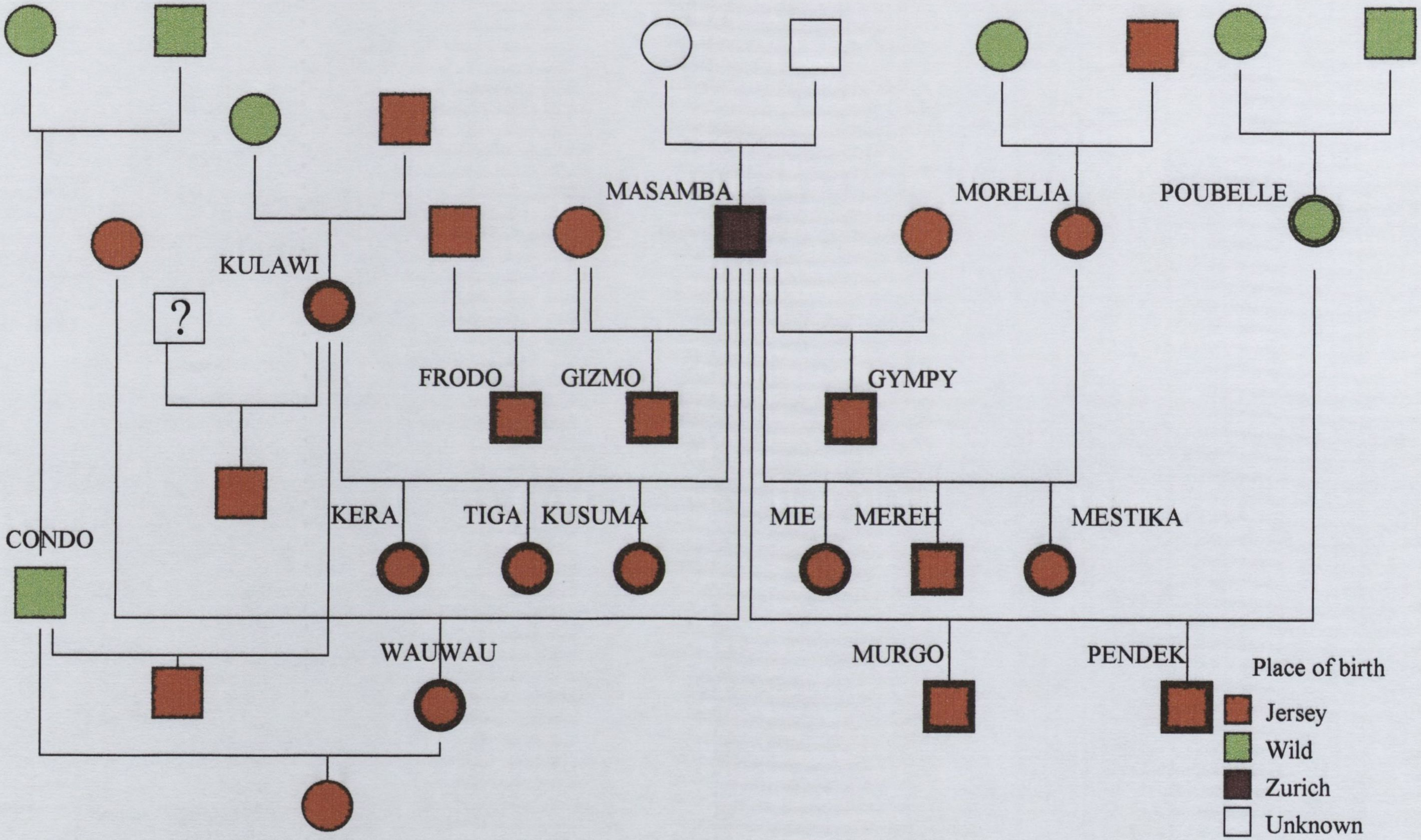


Figure 2.1.3.b Pedigree for the macaques at Jersey II Zoo (1999). Macaques observed in this study have double-bordered shapes and are named, males are represented by a square and females by a circle. A square with a question mark denotes a mating with an unidentified male.

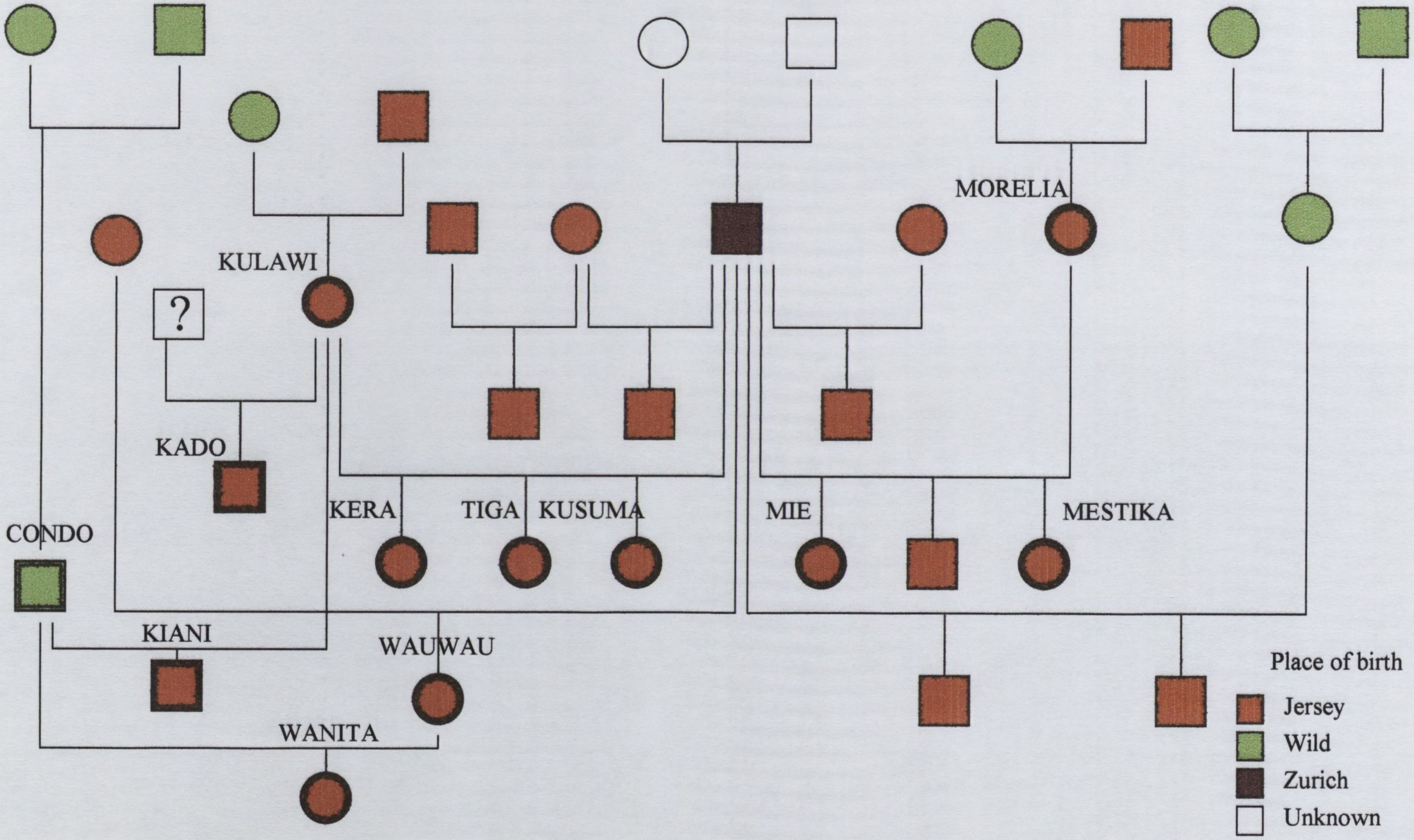


Figure 2.1.4 Pedigree for the macaques at London Zoo. Macaques observed in this study have double-bordered shapes and are named, males are represented by a square and females by a circle. A square with a question mark denotes a mating with an unidentified male.

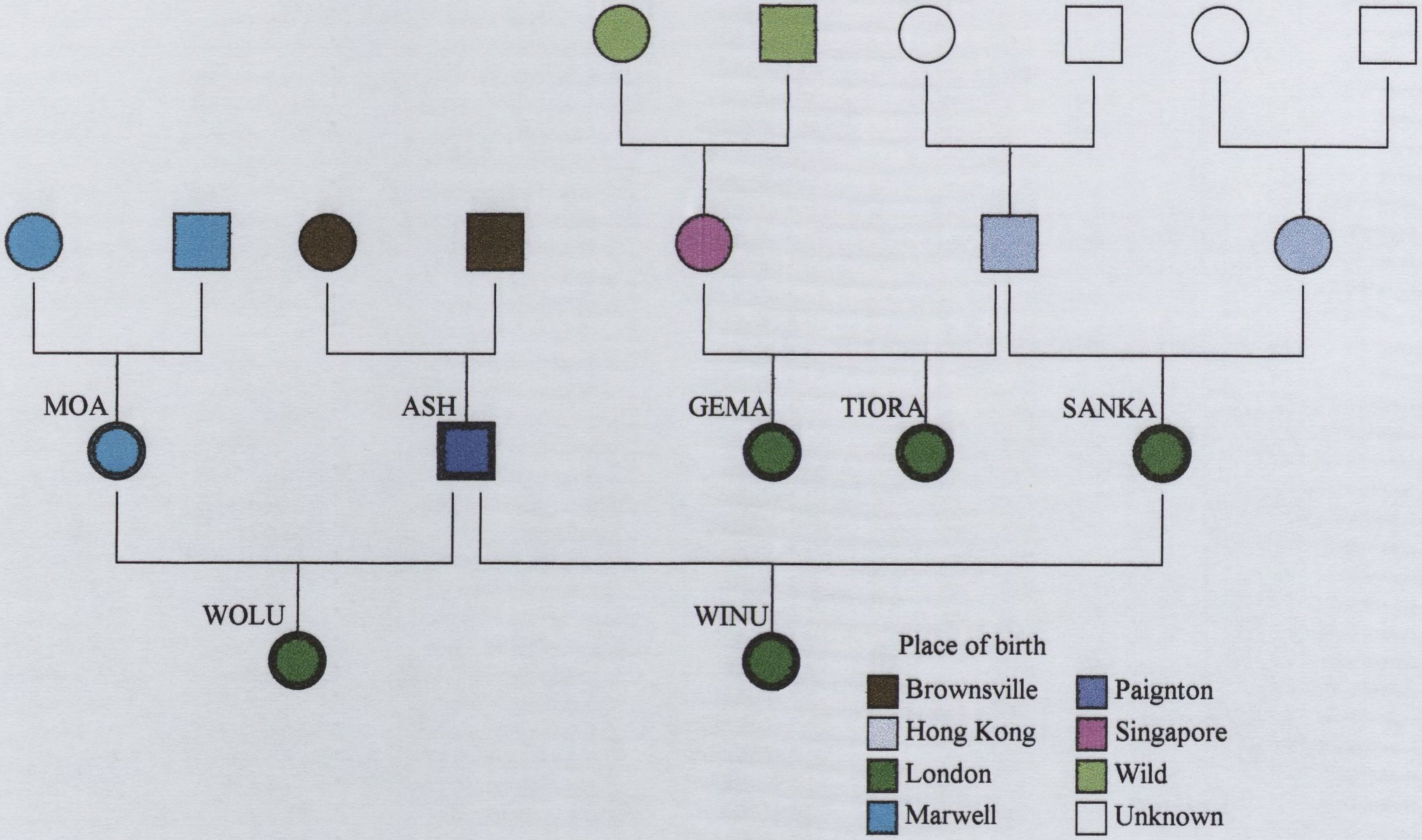


Figure 2.1.5 Pedigree for the macaques at Marwell Zoo. Macaques observed in this study have double-bordered shapes and are named, males are represented by a square and females by a circle. A square with a question mark denotes a mating with an unidentified male.

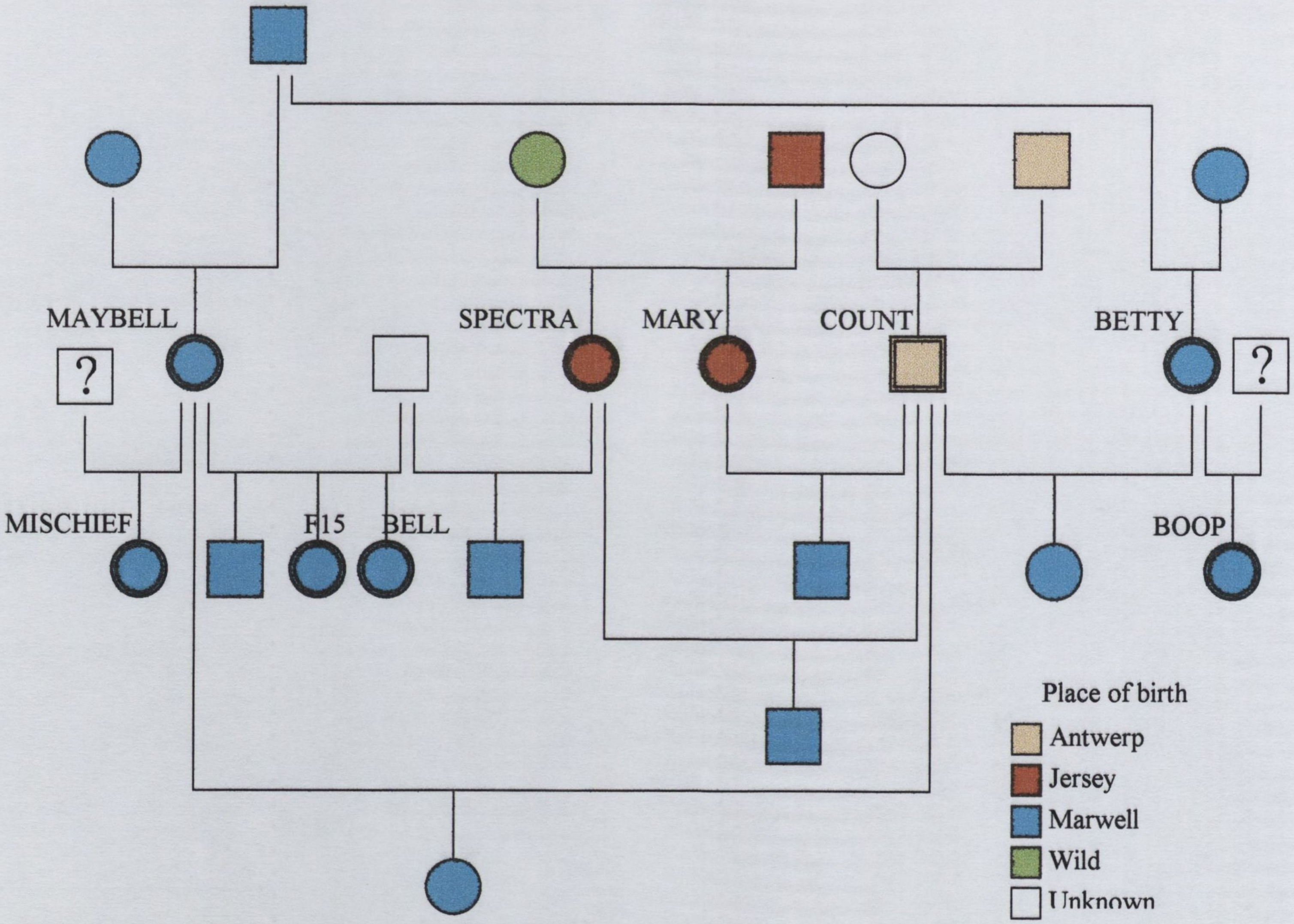


Figure 2.1.6 Pedigree for the macaques at Paignton Zoo. Macaques observed in this study have double-bordered shapes and are named, males are represented by a square and females by a circle. A square with a question mark denotes a mating with an unidentified male.

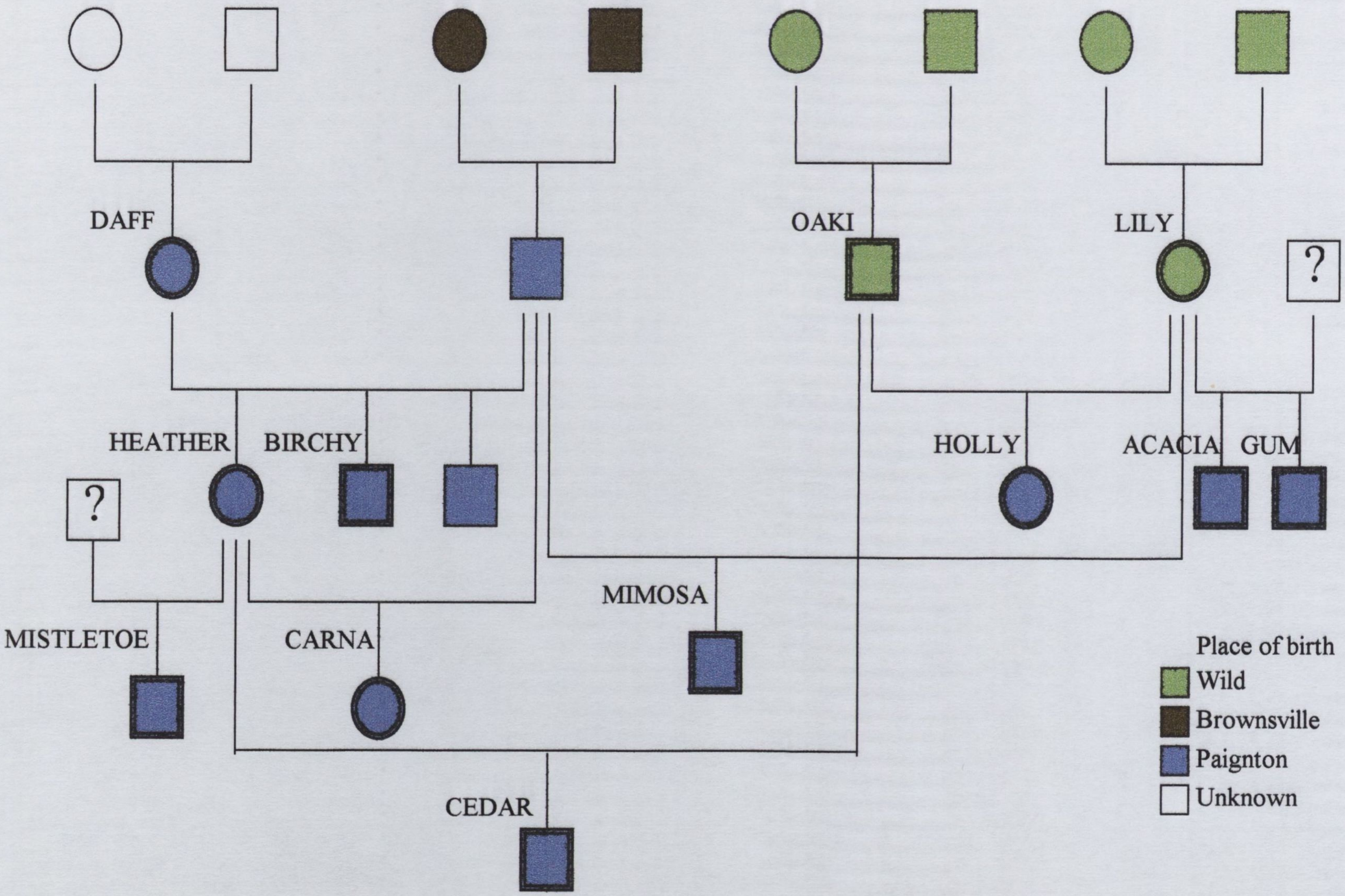
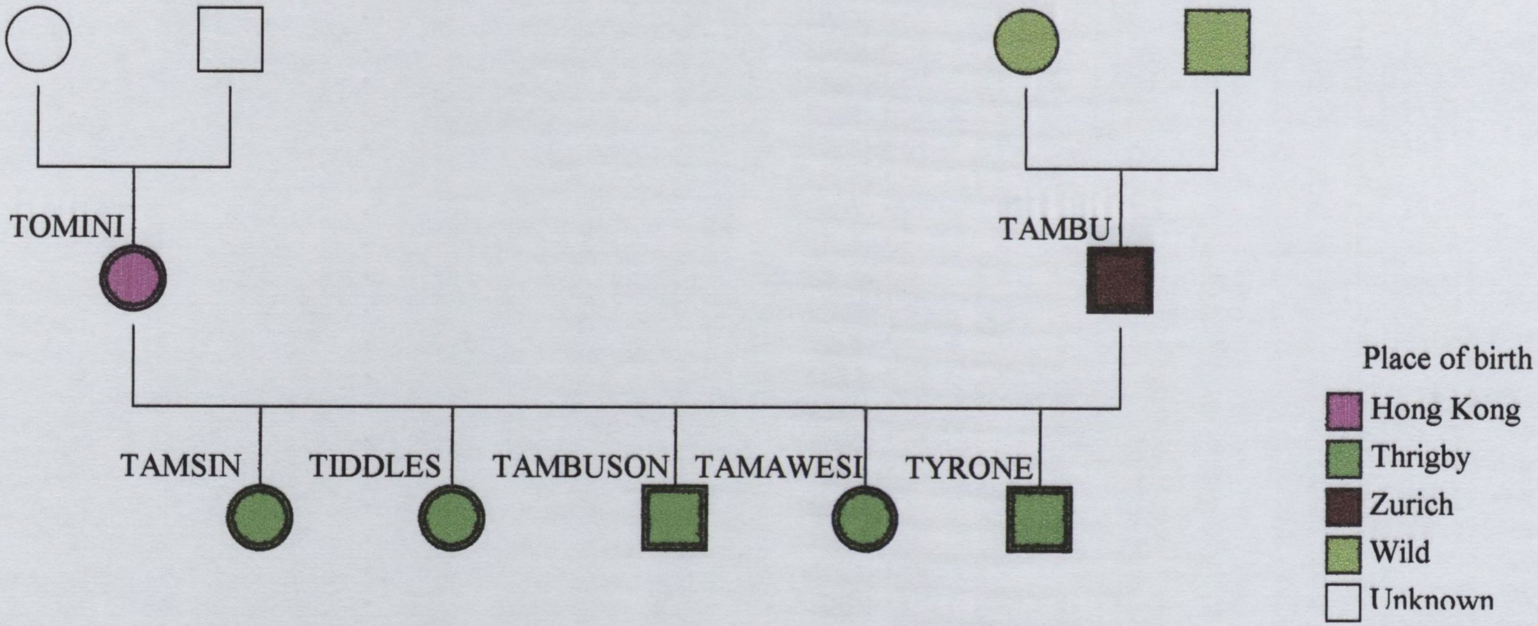


Figure 2.1.7 Pedigree for the macaques at Thrigby Hall. Macaques observed in this study have double-bordered shapes and are named, males are represented by a square and females by a circle.



Infants were excluded from data collection as it was thought that their activity budget was too dependent on their mother (Rowell, 1967). Due to changes in social composition and husbandry practises at Jersey Zoo during the study (see section 4.4), two activity budgets are included in data analyses (Jersey I and Jersey II). Most enclosure variables remained the same, but feeding frequency increased from four to five feeds a day (table 2.1.2).

2.1.1.b Study sites

Eight Sulawesi crested black macaque troops were observed at 7 zoos in the UK & Ireland. The macaques were all housed in enclosures made up of two main areas, one inside (sheltered house) and one outside (exposed to the elements). The outside areas incorporated aspects reminiscent of "naturalistic" enclosure design as they provided enclosure furniture representing structures seen in the wild, including natural vegetation and movable and elevated features (Hutchings *et al.*, 1978b; Seidensticker & Doherty, 1996). The inside enclosures were divided into three dens, to allow for separation of individuals.

The Chester Zoo enclosure was the largest study site. The outside island was surrounded by a moat and the macaques had access to their large inside enclosure via ropes (outside) and wire tunnels (inside). The island was well planted with trees, bushes and grass; the latter was allowed to grow tall in areas. There was also a waterfall, logs and rocks situated on the island. The inside enclosure was constructed mainly of wire, with one rendered wall (with a couple of caves and ledges) and a long window for public viewing. This area was divided into three areas to which the macaques had free access, but which could be used for separation. Enclosure furnishings included a pond, several 'tree-like' structures, logs, ropes and 'non-fixed objects' (mobile objects suspended from the ceiling).

The enclosure at Dublin Zoo had a well-planted outside island surrounded by a moat. The macaques had access between the inside and outside areas via ropes and two bridges. The island's plants were distributed in two discrete areas (on either side of the enclosure) that had at one time been protected by an electric fence; hence the vegetation had had time to establish and grow. A large wooden climbing frame occupied the centre of the enclosure and provided a sheltered platform. The inside enclosure had separation areas but the macaques did not have access to these. Enclosure furnishings included a couple of logs and rocks (outside), and a rope suspended from the ceiling across the length of the inside enclosure.

Jersey Zoo was the second largest enclosure. An electric fence surrounded the perimeter of the outside area, which was undulating with two main hills. The vegetation included bushes (including gorse), grass of varying lengths and ivy. The inside area was relatively small, though the macaques had access to separation areas. The floor was raised (making two steps) on either side of the enclosure to provide elevated ledges. Enclosure furnishings inside were limited to two suspended hoses, while the outside area had a pond (and stream), small platform, rocks and large horizontal and vertical logs with ropes suspended between them.

The London Zoo enclosure was the smallest, but had the second largest inside area (second to Chester Zoo). The outside area was a wire cage with some grass and paving slabs, with bushes growing between the cage and the 'stand-off' barriers. The outside area was full of furnishings including a pond, ropes, logs, rocks, ledges and many 'non-fixed objects' suspended from the wire ceiling. The inside area included a large 'off-exhibit' area that the macaques had access to, out of sight of the public. A large frame occupied most of the visible inside area, alongside ledges and handles fixed to walls.

The enclosure at Marwell Zoo had an outside island surrounded by a moat and the second smallest inside area. The island was covered in grass and had a waterfall, rocks, three very large logs and a very tall and thin climbing structure in the middle of the enclosure which had a cargo net suspended between it and one of the large logs. The inside area was dominated by a wire structure of horizontal poles and uprights (some had sloping platforms on top). Access between areas was granted through a wire tunnel and lead to a small wire cage inside.

The inside and outside areas of the Paignton Zoo enclosure rated third largest. The outside area sloped slightly and was surrounded by an electric fence. This area was covered in grass, with the exception of a small gravelled area and some paving. Several wooden uprights were linked together by rope, from which a couple of tyres and 'monkey fists' (rope knots) were suspended. There was also a platform and some logs. The macaques had variable access to 'off-show' areas inside. The inside area was predominated by and a large wooden climbing frame with three platforms. There were also ledges and some 'non-fixed objects' suspended from the wire ceiling.

The inside area at Thrigby Hall was the smallest amongst the sites visited, though the outside area was an average size (sharing the approximate dimensions with three of the other enclosures visited). The outside area had an electric fence perimeter with a wire tunnel that lead to an all wire outside cage and then onto a sheltered inside area. The outside area was covered with grass and had a substantial area of nettles (that the macaques ate). There were also several wooden uprights and a couple of rocks in the outside enclosure. The outside wire cage had limited perching, while the inside area had two elevated perches and ledges.

A comparison of the study sites and management regimes for the different captive Sulawesi macaque troops is presented in table 2.1.2 and diagrams of the enclosures are provided in appendix 2 – 9.

A comparison of the study sites and management regimes for the different captive Sulawesi macaque troops is presented in table 2.1.2 and diagrams of the enclosures are provided in the appendices.

Table 2.1.2 A comparison of the captive study sites and management of Sulawesi macaques during the summer period of 1997 and 1999.

Enclosure	Chester Zoo	Dublin Zoo	Jersey Zoo	London Zoo	Marwell Zoo	Paignton Zoo	Thrigby Hall
Inside area (max. height)	190 m^2 (5.7m)	24.12 m^2 (2.7m)	33.2m^2 (3.2m)	41 m^2 (4m)	20 m^2 (3m)	37.2 m^2 (3.8m)	15.82 m^2 (2.1m)
Outside area	1660 m^2	350 m^2	1000 m^2	81 m^2	375 m^2	750 m^2	300 m^2
Access between inside and outside areas	Restricted: access to outside for a few hrs between 0800 – 1600 h*.	24 hr: concurrent access to both inside and outside areas.	24 hr: as Dublin zoo.	24 hr: as Dublin zoo.	Restricted: locked in 1800 – 0800; locked out 0800 – 1800.	Semi-restricted: concurrent access 1000 – 1800; locked in 1800-0800.	24 hr: as Dublin zoo.
Feeding regime	1) Concentrates, (am) 2) Enrichment* feed (am) 3) Fruit and vegetable (pm)	1) Occasionally fruit & vegetables (am) 2) Fruit, vegetables & concentrates (pm).	1) Fruit & concentrate (am), 2) Scatter of seeds or mealworms (am), 3) Enrichment feed (pm) 4) Fruit and vegetable (pm). (Jersey II, had an additional scatter feed, am).	1) Concentrate (am) 2) Occasional roof-top scatter feed of fruit & vegetables 3) Fruit and vegetables (pm).	1) Occasional eggs or scatter feed of concentrate (am). 2) Fruit, vegetable & concentrate (pm).	1) Occasional seeds and concentrate (am), 2) Fruit & vegetables (pm).	1) Fruit, vegetables & concentrate, 2) As above (pm).

* This restricted access was temporary as the enclosure was new.

** Enrichment feeds included, frozen seed cakes, frozen fruit and juice, shelled nuts, bamboo filled with jelly and yoghurt.

2.1.1.b Behavioural observations

The following methodology was chosen to enable comparisons to be made with behavioural data published on wild Sulawesi macaques (O'Brien & Kinnaird, 1997). Instantaneous scan sampling was used to record behaviour, location and substrate use for each individual in the troop (Altmann, 1974; Martin & Bateson, 1996). Scan observations were made every 30 minutes and finished when the last individual in the troop was identified or after 10 min whichever was first. Animals that could not be located were recorded as "not seen". Some enclosures provided access to off-show areas and in cases where an individual was 'not seen' but known to be in this area, the location and substrate use could be scored. Data were collected for 10 days at each zoo, from 7am - 7pm each day. Troops at Chester, Jersey I and Marwell were observed for 10 h per day at half-hourly intervals (20 scans/day). Troops at Dublin, Jersey II, London, Paignton and Thrigby were observed for 12 hr/day (24 scans/day). Thus, at least 200 scans were amassed for each individual per troop (including instances when the individual was not seen).

Behavioural data were collected using an extended version of the categories used by O'Brien & Kinnaird (1997) as additional behaviours could be readily observed in the captive situation (Table 2.1.3). The additional behavioural categories of negative social behaviour (fights etc.) and object manipulation were rarely observed, so these few observations were grouped together with a similar pre-existing behavioural category and not analysed separately. Negative social behaviour was amalgamated with other social behaviours, and object manipulation grouped with foraging, which lead to broad definitions for these behavioural categories. However as these data were used to construct activity budgets for broad state behaviours, this was not considered problematic, as information would still be gained regarding the time captive macaques attribute to broad behavioural categories.

Given that behaviours are not mutually exclusive, a recording hierarchy was constructed which determined the order that behaviours were recorded if two or more were expressed concurrently. In this study behaviours were noted in the following order of priority, social; foraging; moving; feeding and then resting behaviour. This method means that as behaviours descend the hierarchy, the risk of being underrepresented in the activity budget increases which has been considered when interpreting results. Data were collected at Chester, Jersey I and Marwell Zoos in May and June 1997 and at Thrigby Hall and Dublin, Jersey II, London and Paignton Zoos from April to August 1999.

The methodology used to record area and substrate use is detailed in section 2.3, along with analyses of the data collected.

Table 2.1.3 Behavioural categories scored. Italics indicate where categories and definitions have been expanded from O'Brien & Kinnaird (1997).

Behaviour	Description
Social	Allogrooming, play, non-copulatory mounting and copulation *(excluding manipulation of objects).* *Fights (chasing including attacks, usually associated with vocalisations), strutting, yawning, biting, pulling hair (usually from the crest) and grimacing (submissive) (Dixson, 1977).*
Moving	Locomotion, including walking, running, climbing and jumping.
Resting	Body stationary, usually sitting or lying and not engaged in social activity. Autogrooming included.
Foraging	Moving slowly with attention directed toward potential food source or manipulating substrates in search of potential foods *Manipulation of the environment (e.g. furnishings)*
Feeding	Reaching for, picking up, manipulating, masticating, placing food in mouth, or manipulating cheek-pouch contents
Miscellaneous	*Behaviours that cannot be described by any of the above categories, including the situation when the macaque was not visible.*

2.1.1.c Statistical analysis

Activity budgets were created for each zoo, using the mean percentage time spent performing behaviours. Daily counts of each of the behaviours were summed for each day and an average for the 10 days' observations was calculated for each macaque. The mean percentage time spent performing the behaviour/macaque/scan was calculated by dividing the average counts of behaviour by the number of scans per day used to observe behaviour (either 20 or 24) and multiplying the result by 100. An activity budget for each zoo was then calculated by averaging the mean percentage time spent performing behaviours by all the macaques in that troop (N = 7-16).

The behavioural data were normally distributed so parametric analyses were conducted. A two-way analysis of variance was carried out for each behavioural category with zoo and sex-age class as the fixed factors. To determine where the significant differences lay, post-hoc multiple pair-wise comparisons were carried out. The Bonferroni adjustment was made to the level of significance to allow for the number of comparisons made; also this test is more powerful for small numbers of pairs (SPSS, 1999b). All the analyses were conducted on SPSS version 8.0 for Windows (1997).

2.1.2 Results

The behaviour of macaques between zoos was significantly different for all behavioural categories, perhaps demonstrating the importance of environment and husbandry in the formation of every aspect of their activity budget (Figure 2.1.8). The behaviour observed for each of the sex-age classes was also significantly different, with the exception of miscellaneous behaviour (Figure 2.1.9). There was also an interaction between sex-age class and zoo in the feeding behaviour displayed, indicating that the time spent feeding by sex-age classes was not similar across zoos and possibly monopolisation of food by adult males differed between zoos. The results of the 2-way ANOVA for these differences are shown in table 2.1.4.

Post-hoc analyses (Table 2.1.5) showed that macaques at Dublin Zoo spent significantly more time feeding and significantly less time foraging than macaques at other zoos. Macaques at London Zoo were significantly more social than other troops and also spent significantly more time out of sight or exhibiting miscellaneous behaviours. Macaques at Chester Zoo rested significantly less than macaques at other zoos and moved significantly more than two other troops (London and Paignton), but the macaques that made up Jersey II moved significantly more than those at Chester and other zoo troops in the study.

Post-hoc results investigating the behaviour performed by sex-age classes are reported in table 2.1.6 and reveal that adult females were significantly more social than other sex-age classes, but moved significantly less than adult males and big juveniles. Adult males fed and foraged significantly less but rested significantly more than other sex-age classes. Small juveniles spent significantly less time resting than either adult males or females, but there were no significant differences between small juveniles and big juveniles in their resting behaviour.

Figure 2.1.8 Mean ± SE percentage time spent performing behaviours between zoos (Mis = miscellaneous behaviour).

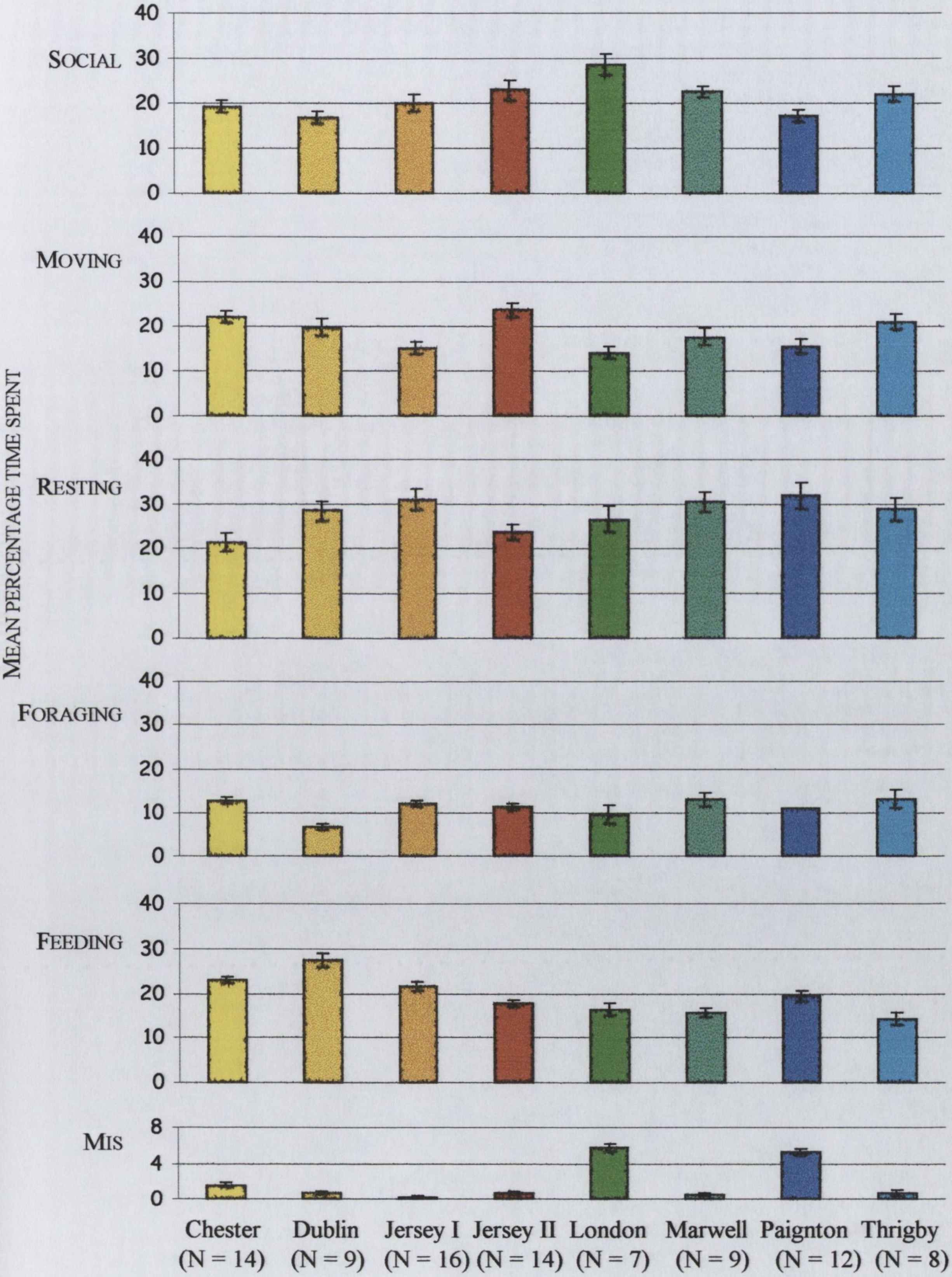


Figure 2.1.9 Mean ± SE percentage time spent performing behaviours by different sex-age classes, with standard error bars (mis = miscellaneous behaviour).

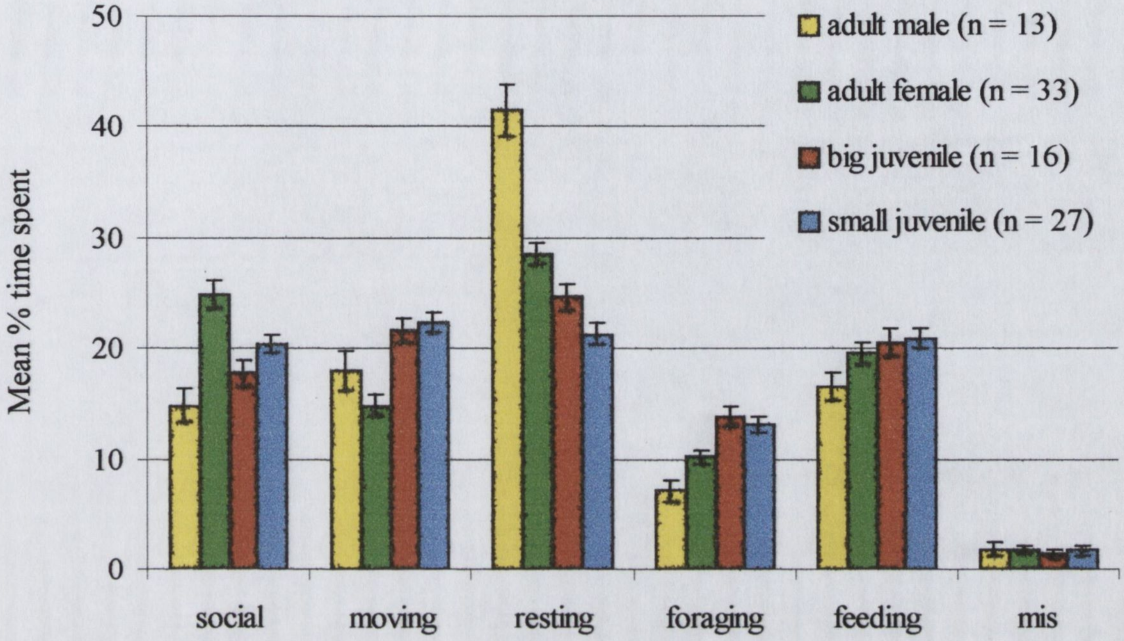


Table 2.1.4 Summary of two-way ANOVA results investigating how zoo and sex-age class relates to the mean % time spent performing behaviour (Miscell. = miscellaneous behaviour).

	Zoo x sex-age (df = 20)	Sex-age (df = 3)	Zoo (df = 7)
Behaviour	F value	F value	F value
Social	0.63	8.52***	3.48***
Moving	0.65	13.8***	4.38***
Resting	0.91	36.74***	5.33***
Foraging	1.01	19.5***	3.95***
Feeding	2.09*	4.27**	17.54***
Miscell	0.93	0.95	63.91***

*$p<0.05$, ***$p\leq0.001$ level of significance.

Table 2.1.5 Summary of significant results from the Bonferroni inequality post-hoc test, comparing the mean % time spent performing behaviours between zoos.

Behaviour	Zoo comparisons		Mean difference
Social	London (N = 7)	Dublin (N = 9)	11.67*
		Paignton (N = 12)	11.42*
		Chester (N = 13)	9.21*
		Jersey I (N = 16)	8.44*
Moving	Jersey II (N = 14)	Jersey I	13.96***
		Chester	12.34**
		London	2.75**
		Paignton	2.24**
	Chester	London	1.13**
		Paignton	0.62*
Resting	Chester	Paignton	-10.62***
		Jersey I	-9.8***
		Marwell (N = 9)	-9.33*
		Thrigby (N = 7)	-7.52*
		Dublin	-7.33*
Foraging	Dublin	Marwell	-6.33**
		Chester	-6.15*
		Thrigby	-6.15**
		Jersey I	-5.29*
		Jersey II	-4.61*
Feeding	Dublin	Thrigby	12.99***
		Marwell	11.8***
		London	10.89***
		Jersey II	9.7***
		Paignton	8.01***
		Jersey I	5.89***
		Chester	4.46*
Miscell.	London	Jersey I	5.5***
		Marwell	5.21***
		Jersey II	5.06***
		Thrigby	5.04***
		Dublin	5.02***
		Chester	4.11***

* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$ level of significance.

Table 2.1.6 Summary of significant results from the Bonferroni inequality post-hoc test, comparing the mean % time spent performing behaviours between sex-age classes.

Behaviour	Sex-age class comparisons		Mean difference
Social	Adult female (N = 33)	Adult male (N = 13)	10.07***
		Big juvenile (N = 16)	7.13*
		Small juvenile (N = 27)	4.45***
Moving	Adult female	Big juvenile	-7.47***
		Adult male	-6.81***
Resting	Small juveniles	Adult male	-20.2***
		Adult female	-7.3***
	Adult male	Small juvenile	20.2***
		Big juvenile	16.85***
		Adult female	12.9***
Foraging	Adult male	Big juvenile	-6.76***
		Small juvenile	-6.02***
		Adult female	-3.05*
Feeding	Adult male	Small juvenile	-3.93**
		Big juvenile	-3.49*
		Adult female	-3.04*

* $p = 0.05$, ** $p = 0.01$, *** $p = 0.001$ level of significance

2.1.3 Discussion

The amount of time allocated to each of the behaviours varied with the captive environment and the sex-age class of the captive macaques in this study. The time spent feeding was significantly influenced by an interaction between zoo and sex-age class. This interaction indicates that the time spent feeding by sex-age classes varied between zoos, which could be accounted for by environmental conditions between zoos that either promoted or inhibited feeding in some sex-age classes. Thus the pattern of feeding was different between sex-age classes in some zoos and not in others. Adult males fed at significantly lower levels than other sex-age classes, which may be a consequence of gaining preferential access to choicest foods (Ettah, 1997). Variation in this trend from one zoo to another, would have led to the observed interaction of zoo and sex-age class on the expression of feeding behaviour. It is possible that housing and/or husbandry differences between zoos may have resulted in adult males feeding for longer, reducing the difference in feeding behaviour between sex-age classes. This could have arisen at Dublin Zoo where an abundance of easily accessible vegetation led to significantly higher levels of feeding in all sex/age classes. Alternatively, the provision of food in some zoos may have inhibited the ability of the adult male to monopolise food and therefore once again, reduced the difference in feeding time observed between sex-age classes.

Miscellaneous behaviour, which included observations when the macaques were not visible, was significantly affected by zoo. The miscellaneous behaviour category was significantly different between zoos but not between sex-age classes. Observations of miscellaneous behaviour were infrequent, and there was no reason to expect one sex-age class to use the off-show areas any more than another. The difference found between zoos was expected however, as some zoos (London Zoo) had larger off-show enclosures than other zoos and so observations of miscellaneous behaviour were greater at these zoos, reflecting the greater opportunities to be off-exhibit and therefore not seen.

Social, moving, resting & foraging behaviours were significantly influenced by both zoo and sex-age class independently. The effect of different captive environmental factors on the activity budget of Sulawesi macaques is fully explored using multivariate analyses and further experiments in chapters 3 and 4, and therefore this discussion will explore only the effects of sex-age class on activity budgets.

The activity budgets recorded for the different sex-age classes followed a pattern observed in a study of wild Sulawesi crested black macaques (O'Brien & Kinnaird, 1997). Macaques live in matriarchal social groups, where females remain in the natal group and males migrate when they reach puberty, leading to suggestions that the social bonds between females are more important than either male-female or male-male relationships (de Waal, 1995). Females would therefore be expected to spend more time in social behaviours, as was the case in this study, where females spent significantly more time in social behaviours than other age-sex classes (Table 2.1.6). Females also moved the least around the enclosure, which in part is probably due to the high investment they placed in social behaviour.

The activity budgets constructed for captive adult male and juvenile Sulawesi macaques are similar to those recorded for their wild counterparts, as adult males were observed to spend significantly more time resting than other sex-age classes and juveniles were observed to be the most active (Figure 2.1.9; O'Brien & Kinnaird, 1997). A comparison of the time spent resting and moving between adult male and adult female wild Sulawesi macaques, demonstrated that adult males moved more and rested more, which was considered to reflect the guarding and patrolling duties of the adult males in the group (Reed *et al.*, 1997). A similar pattern was revealed in this present study, for captive Sulawesi macaques, where the level of resting behaviour by adult males was significantly higher than that observed in adult females, though the difference in moving behaviour was not significant. In captivity, the level of moving required to patrol and guard the adult females in the group is reduced, especially when macaques are kept in single-male groups, as there is not competition from other adult males. Small enclosures make it possible for the adult male to fulfil his guarding duties without moving, even in multi-male groups.

Captive juvenile Sulawesi macaques in captivity were observed to perform higher levels of active behaviours for example, foraging and moving and less resting relative to other sex/age classes, which was similar to observations of wild counterparts, where the small juveniles were observed to rest least and also take part in significantly more social play behaviours (O'Brien & Kinnaird, 1997). Unfortunately, the broad state behaviours recorded in this study do not allow play to be identified from the results, but self-directed play such as jumping and leaping would have been recorded as moving and social play would have been recorded as social behaviour. The high levels of play activities associated with young mammals, could therefore be reflected in this study, by the high level of moving behaviour by both small and large juveniles and the high level of social behaviour observed in the small juveniles (Figure 2.1.9; Beckoff & Byers, 1998).

The contribution foraging made to the captive Sulawesi macaque activity budget was nominal, adult males spent significantly less time foraging than any other sex-age class, representing less than ten per cent of their day (Figures 2.1.8 and 2.1.9). As previously mentioned adult males enjoy priority access to food and therefore could be considered to benefit from higher-quality foods when provisioned, relative to other sex-age classes (Dittus, 1977; Ettah, 1997). This observation both explains low levels of foraging in adult males and high levels of foraging in juveniles, as the latter gained access to food last and therefore might forage more to address a short fall in calories or nutrients.

Data were collected using a hierarchical method of behavioural observation, resulting in an artificial inflation of behaviours that were higher up the hierarchy. Behaviours that were most frequently performed simultaneously were feeding, foraging and moving, and social and feeding. Though resting behaviour was lowest on the hierarchy of behaviours, its actual performance is fairly reflected by the recorded activity budget, as it was not performed at the same time as other behaviours. However the time spent feeding and moving may possibly be artificially lower than performed as concurrent social and foraging behaviours were noted in their stead.

Low levels of moving and foraging behaviour are frequently used as evidence of the detrimental conditions of captivity (Macedonia, 1987; Chamove, 1988). With respect to the Sulawesi macaque these types of assumptions may be unfounded and require comparison with activity budgets of wild Sulawesi macaques, to establish how they have adapted to apportion time to different behaviours (Stolba & Wood-Gush, 1984; Maple & Finlay, 1989). A high level of variation in the activity budgets constructed for wild Sulawesi macaques suggests that low levels of moving and foraging behaviour may just represent a diverse activity budget (O'Brien & Kinnaird, 1997; section 2.4).

In summary, these data indicate Sulawesi macaques in captivity are motivated to perform behaviours at a similar level to their sex-age class counter-parts in the wild. Captive environmental conditions significantly affected troop behaviour, suggesting that differences between zoos, excluding the effects of different social compositions, have a dramatic effect on captive Sulawesi macaque behaviour.

2.2 THE EFFECT OF SEASON ON CAPTIVE BEHAVIOUR

North Sulawesi experiences significant variations in rainfall, which has not been found to affect the activity budgets of Sulawesi crested black macaques significantly (O'Brien & Kinnaird, 1997). Sulawesi macaques in captivity are exposed to a changeable temperate climate, changes in day length and variations in captive management, all which were explored for their effect on the Sulawesi macaques' activity budget.

2.2.1 Methodology

Behavioural observations described in section 3.1.2, were made at five zoos (Chester, Dublin, Jersey II, Marwell, Paignton). Following this, a second series of observations (winter) were performed for 8 hr a day between 0800 and 1600 h, for 10 days (N = 16 scans per individual per day). These winter observations were carried out between November and March 1998-1999 and December and January 2000.

2.2.1.a Statistical analysis

Activity budgets were constructed following the methodology described in section 2.1.3. In addition to summer and winter activity budgets, a 'short summer' activity budget was created that used summer observations recorded between 0800 and 1600 hr, thus data collected in the summer were matched by the hours used for sampling in the winter and so the 'short summer' activity budget reflected the amount of the time apportioned to behaviours in the summer, during the winter day-length.

Data from each zoo were analysed separately using a multivariate analysis of variance (MANOVA) to investigate the relationship between activity budget and season. Activity budgets were composed of social, moving, resting, foraging and feeding behaviours; miscellaneous and not seen behaviour were excluded from analyses (Table 2.1.3). Significant MANOVA results were followed by univariate ANOVA tests to determine which behaviours were significantly affected by season. Bonferroni post-hoc multiple pair-wise comparisons were then calculated.

The data in this study met the assumptions required to perform ANOVA and MANOVA tests. ANOVA tests require normally distributed data that have homogenous variances; the data in this study were normally distributed and in most cases the results of the Levene's Test for homogeneity of variances were not significant. MANOVA tests require data to have a normal multivariate normal distribution and that the variances are homogenous. These features can be tested for by using the Box's M test for the equality of the group covariance matrices, which tests for homogeneity of variances and is sensitive to deviations from a multivariate normal distribution (SPSS, 1999b). The results from the Box's M test revealed that data collected at Chester and Dublin Zoos had significantly different variances or did not come from a multivariate normal distribution (Chester, M = 81.63, $p = 0.001$; Dublin, M = 72.57, $p = 0.03$; Jersey, M = 32.52, $p = 0.68$; Marwell, M = 5.78, $p = 0.99$; Paignton, M = 34.92, $p = 0.62$). Although data collected from Chester and Dublin Zoos, did not meet one of the MANOVA assumptions, the data were still analysed as ANOVA and MANOVA tests have been reported to be robust to deviations in normality (Tabachnick & Fidell, 1996). Data collected at the other zoos met both MANOVA assumptions. Group sizes were equalised between treatments by matching sex-age classes, which resulted in discarding behavioural data collected for one macaque for Chester, Dublin and Paignton Zoos, and three macaques from Jersey Zoo. All statistical analyses were carried out using SPSS for Windows, version 8 (1997).

2.2.2 Results

The results in table 2.2.1 demonstrate that the behaviour of captive Sulawesi macaques differed significantly between different seasons. For most of the zoos, there was a significant decline in the time observed foraging and feeding in winter compared to summer; conversely the time spent feeding and foraging rose significantly at Marwell and Dublin Zoos, respectively (Figure 2.2.1).

The expression of social behaviour by macaques at Chester Zoo was observed to increase significantly in the winter compared to the summer. At Jersey Zoo the macaques moving behaviour was shown to vary significantly between seasons. This was not however supported by the results of the post-hoc tests and the increased level of moving displayed in winter was not found to be significantly different from that observed in the summer. Season affected the behaviour of Sulawesi macaques differently between zoos, which probably reflects the influence of the different housing and husbandry regimes implemented.

Figure 2.2.1 Mean ± SE percentage time spent performing behaviours during the summer (12hr sampling), short summer (8hr sampling matched with winter) and winter (8hr sampling). Concurrent access between inside and outside areas of the enclosure varies along the x-axis, from restricted access e.g. locked in/out (Chester) to 24 hr access to both areas (Jersey II and Dublin).

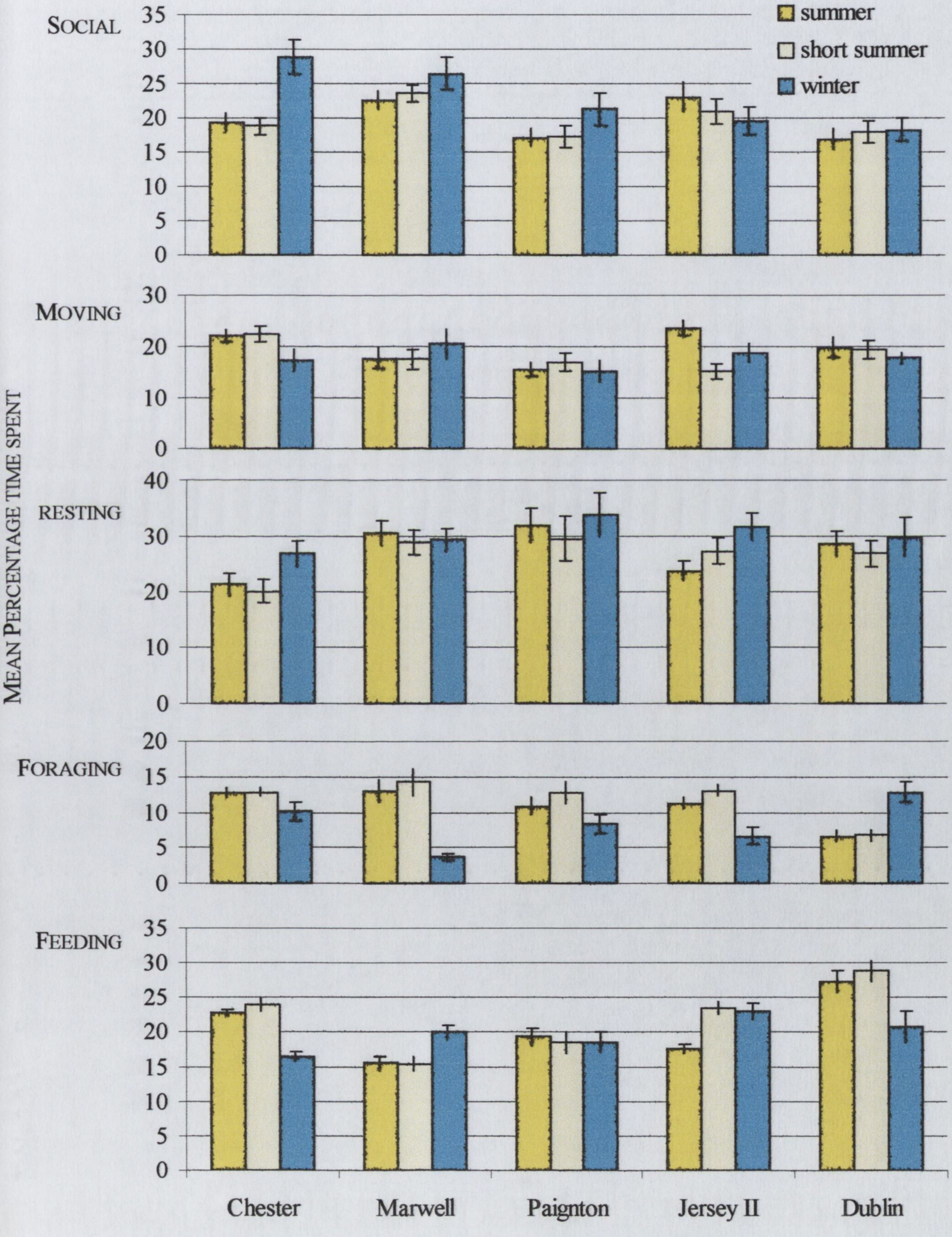


Table 2.2.1 Summary of significant multivariate and univariate analyses of variance results, investigating the effect of season and on behavioural expression in Sulawesi macaques.

Zoo	MANOVA			ANOVA			Post-hoc		
	df	Wilk's λ	F-value	Behaviour	df	F-value	Pair-wise comparison		Mean difference
Chester (N = 14)	10	0.294	5.9***	Social	2	8.35**	Winter	Summer	9.39**
								Short summer	9.96**
				Feed	2	24.48***	Winter	Summer	-6.3***
								Short summer	-7.4***
Dublin (N = 8)	10	0.22	3.9*	Forage	2	11.1**	Winter	Summer	6.46**
								Short summer	6.2**
				Feed	2	7.26**	Winter	Summer	-7.51*
								Short summer	-8.76**
Jersey (N = 13)	10	0.48	2.86**	Moving	2	3.74*	Winter	Summer	$5.39^{(p = 0.063)}$
								Short summer	$5.19^{(p = 0.078)}$
				Forage	2	11.1***	Winter	Summer	-5.32**
								Short summer	-6.35***
Marwell (N = 13)	10	0.28	3.59**	Forage	2	16.81***	Winter	Summer	-9.32***
								Short summer	-10.52***
				Feed	2	6.86**	Winter	Summer	4.44*
								Short summer	4.56**
Paignton (N = 12)	10	0.35	3.9***	Forage	2	4.1*	Winter	Summer	-5.38*

$^{*}p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$.

Seasonal differences in behaviour existed regardless of day-length, with the exception of foraging behaviour as observed in the macaques at Paignton Zoo. In this example, the macaques were observed to forage at significantly lower levels during the winter compared to the short summer, whereas foraging behaviour during the winter and summer were not significantly different. Figure 2.2.1, illustrates that the time spent foraging was lowest in the winter, highest in the short summer and at an intermediate level during summer, hence summer and short summer were not significantly different as the variation in the time spent foraging during each overlapped.

2.2.3 Discussion

Season was demonstrated to have significant effects on the behaviour of captive Sulawesi macaques; however the variation in seasonal effect observed between zoos implies that factors related to each zoo were also influencing behaviour. Indeed, the behavioural differences between seasons can be categorised into two main classes, firstly, those affected by changes in vegetation and those that were a consequence of housing and husbandry factors.

A decrease in the time spent feeding and foraging during winter was expected, as vegetation declined in abundance during this season; therefore the significant reduction in feeding and foraging behaviour observed in the macaques at most zoos was acknowledged as a seasonal effect. The macaques at Dublin and Marwell Zoos displayed an unexpected elevation of feeding and foraging behaviour during the winter, respectively. These unexpected seasonal changes in behaviour can be related to housing and husbandry factors. Macaques at Marwell Zoo received their main feed just before the end of the keepers' day, and as the keepers left earlier in the winter this meant that the main feed was delivered much later in the day during the summer. As a result, fewer observations were made after the provision of food during the summer period compared to the winter and the level of feeding appeared to be shorter during the summer. Both management changes and an artefact of the methodology used to record behaviour, resulted in the seasonal difference in feeding behaviour observed at Marwell.

Levels of foraging behaviour observed at Dublin Zoo were also considered to be a consequence of housing and husbandry factors. The outside enclosure at Dublin Zoo included two heavily planted areas which were protected by an electric fence preventing access by the macaques; however prior to this study the electric fence failed and the macaques had full access to these sources of abundant vegetation. In a comparison of

Sulawesi macaque behaviour between zoos, data collected during the summer revealed that macaques at Dublin Zoo displayed high feeding and low foraging levels, which was attributed to the abundance of vegetation recently made available to them (Melfi & Marples, 2000). Conversely, during the winter these macaques displayed low feeding and high foraging levels. As the area of vegetation was relatively novel, the macaques may not have adapted to the fact that much of the vegetation would die back during the winter and the reward for foraging would be low; as such macaques at Dublin Zoo spent significantly longer foraging than macaques at other zoos which had become accustomed to the decreased abundance of vegetation during the winter and so apportion less time to this behaviour in the winter.

Seasonal changes in social and moving behaviour observed in Sulawesi macaques at Chester and Jersey Zoos may also represent influences from the housing and husbandry regime. Social behaviours were most frequent at zoos that had restricted access between the inside and outside areas of the enclosure (Marwell and Chester) and lowest where 24 hr access was provided (Dublin), though social behaviour was only significantly different at Chester Zoo. Restricted access for the macaques at Chester Zoo meant that they were locked in throughout winter. Despite the inside enclosure area at Chester being relatively large compared to other macaque enclosures at different zoos, being locked in did reduce the opportunities available to the macaques to disperse and therefore bought them into closer proximity. Similar results were reported for gorillas (section 3.3.2; Hoff *et al.*, 1997). These results support the predictions made by de Waal (1989), that primates will exhibit high levels of social behaviour when there is an increased risk of aggression (section 3.3.1). The seasonal change in moving behaviour observed at Jersey Zoo is thought to reflect a change in feeding frequency. In the summer the macaques received four feeds/day compared to five feeds/day in the winter. Just before feeding time the macaques ran around their enclosure, until provisioned. It therefore makes sense, that if the number of feeds/day were increased that they would move more.

The inclusion of three levels of seasonal data (summer, short summer and winter) was used to investigate the impact of day length on the captive Sulawesi macaques' activity budget. With one exception, day length did not appear to affect the time apportioned to behaviour significantly. The exception took place at Paignton Zoo, where macaques were observed to spend significantly more time foraging during the short summer period compared to the winter, but no difference was observed between summer and short summer, or summer and winter. This reveals that the macaques at Paignton Zoo spent more of their time foraging during the 0800 – 1600 time period, when observations were recorded for the short summer period, compared to 0700 – 0800 and 1600 – 1900 time periods that represented the additional hours of observations included in the summer period. Once again, it seems that this difference does not reflect seasonal differences, but is influenced by the amount of access provided between areas of the enclosure; as macaques at Paignton Zoo were locked in between 1600-1000, and so unable to forage in the outside enclosure area where the vegetation was.

Contrary to the observations of wild Sulawesi macaque troops, where season was established to have negligible affects on activity budgets, this study indicates that season affects the time spent in feeding and foraging, which decline in the winter (O'Brien & Kinnaird, 1997). Changes to housing and husbandry regimes that occur seasonally could be considered as indirect seasonal effects, for example the change of feeding time that occurs every year. Other changes in the behaviour of captive Sulawesi macaques, which are entirely influenced by captive management routine, cannot be considered seasonal e.g. changes to the feeding frequency or access provided between areas of the enclosure.

In conclusion, the captive Sulawesi macaque activity budget appears to be relatively fixed and increases to fill the daylight hours available, so that when the daylight hours increase in the summer, the time apportioned to all the observed behaviours increases.

2.3 ENCLOSURE AND SUBSTRATE USE

The extent to which macaques at five zoos in the UK and Ireland used their enclosure area and the substrates provided for them was investigated in the next section.

2.3.1 Methodology

2.3.1.a Data collection

Five Sulawesi macaque troops housed in zoos at Dublin, Jersey II, London, Paignton and Thrigby Hall were included in this study. Instantaneous scan observations were made every 30 min for 12 hr from 0700 to 1900 for 10 days (N = 240) between June and August 1999 (described in section 2.1.1.b). During these observations enclosure and substrate use were noted.

Zoo enclosures were divided into easily identifiable sites, resulting in sites of unequal size (relative size of enclosures, appendix 1; maps of the enclosures, appendices 2 – 6). Sites were identified as inside, outside and off-exhibit (when they were inside but not visible); macaques could not always be identified as being off-exhibit and sometimes were recorded as not seen. Vertical enclosure use was defined as the total time spent on than grass (outside) or on the inside flooring material (inside) which were collectively considered to be ground and the time spent on other substrates e.g. frame, was considered to above ground.

Substrates were defined as items within the enclosure, which the macaques were observed to manipulate. For each zoo a list of substrates was compiled and defined (Table 2.3.1 and 2.3.2). It was possible for macaques to be in contact with more than one substrate at any one time e.g. a macaque could sit on grass and manipulate a twig, as both grass and twig are substrates. In this situation the less frequently used substrate was noted, resulting in an underestimation of the most frequently used substrate i.e. grass.

3.3.1.b Spread of Participation Index

Both enclosure and substrate use were evaluated using a modified version of the Spread of Participation Index (SPI, Shepherdson *et al.*, 1993). The original SPI evaluated enclosure use, by establishing the frequency at which each site within the enclosure was used compared to the total number of observations recorded and all sites within the enclosure were assumed to be equal in size. The result was expressed as an index between 0 and 1, where 0 indicated maximum use and the animal used all the sites within their enclosure, and 1 indicated minimal use when some of the sites were used predominantly. The SPI equation used by Shepherdson *et al.* (1993) to establish the enclosure use of small confined cats was:-

$$S = \frac{M(n_b - n_a) + (F_a - F_b)}{2(N - M)}$$

where N = total number of observations of the subject; M = mean frequency of observations in all sites (N/number of sites); n_b = number of sites with frequencies less than M; n_a = number of sites with frequencies greater than M; F_a = total number of observations in sites with frequencies greater than M; F_b = total number of observations in sites with frequencies less than M.

The original SPI equation did not take into account differences in enclosure site size, but established whether frequencies observed for all the sites were different from the mean behavioural observations recorded (expected frequency). An adjusted SPI equation was used in this study, where comparisons of observed site use against expected site use were calculated separately for each site, thus the expected rate of site use could vary according the relative size of the site (Plowman, *pers. comm*). Expected site use was calculated by dividing the total number of observations recorded, by the relative size of the site e.g. total observations = 2000, relative site size 25%, expect 500 observations in that site. The sum of the difference between expected and observed frequencies for all the sites in the enclosure, made up the numerator part of the equation. As in the original SPI, the result of the adjusted SPI was expressed as an index between 0 and 1, where 0 indicated maximum use and 1 indicated minimum use. The denominator in both equations transforms the result of the numerator into a value between 0 – 1. In the adjusted SPI, the denominator was changed to incorporate the lowest F_e rather than M, which meant that the transformation of the numerator value varied according to the size (expected use) of the site, rather than using a mean value. To evaluate substrate use, the relative abundance of each substrate was used in the adjusted SPI equation and compared with the frequency of substrate use observed. The adjusted SPI equation:-

$$\text{Adjusted } S = \frac{\sum(F_e - F_o)}{2(N - \text{lowest } F_e)}$$

where the sum of the absolute value of $(F_e - F_o)$ is calculated for each site or substrate, N = total number of observations; F_o = the observed frequency of observations; F_e = the expected frequency of observations.

Table 2.3.1 Definitions of substrates recorded during observations at the zoos.

Substrate		Working definitions
Vegetation	Grass	Grass of all lengths
	Bush	Dense vegetation (not grass or trees)
	Tree	Living or dead, including vertical wooden objects > 1 m high
	Branch	Branches on trees, or wood with a diameter of less than approx. 8cm
Structural features	Inside ground	The ground of the inside enclosure area, whether provisioned with a flooring material or not
	Paving	Cement found in outside areas
	Frame inside Frame outside	Static structure, with platforms attached to uprights, sizes and styles varied between zoos
	Handles	U-shaped metal attachments to the wall of the inside enclosure
	Pond	Size and shape varied between zoos, but to be considered the pond had to be integral to the enclosure, a moat was not included
	Wire	Square weld of different sizes used in the construction of the enclosure
	Ledge	Opportunities within the inside enclosure that were wide enough for macaques to perch on. At Jersey zoo, ledge described the raised (by about 2ft) inside areas of the floor.
Temporary features	Ladder	A rope ladder, made by knotting rope between wooden slates
	Log	Wood with a diameter greater than approx. 8 cm, usually lying horizontally on the ground, but included vertical wooden objects < 1m high
	Non-fixed objects	Wooden objects hung from the ceiling of the enclosure, at London Zoo these also hung in the outside enclosure
	Rock	Rock or boulder over 15 cm in diameter
	Rope	Sisal rope or old fireman's hose pipe
	Tyre	Old car tyres

Table 2.3.2 List of substrates recorded at each zoo.

Substrate	Dublin	Jersey II	London	Paignton	Thrigby
Grass	X	X	X	X	X
Bush	X	X	X		X
Tree	X	X		X	X
Branch	X		X	X	X
Inside ground	X	X	X	X	X
Paving				X	
Frame inside			X	X	X
Frame outside	X	X	X	X	
Handles			X		
Pond		X	X		
Wire	X	X	X	X	X
Ledge	X	X	X	X	X
Ladder				X	
Log	X	X	X	X	X
Non-fixed objects			X		
Rock	X	X	X		X
Rope	X	X	X	X	X
Tyre	X			X	
Total number of substrates	12	11	14	13	11

3.3.1.c Statistical analyses

Mean adjusted SPI scores were established by averaging the adjusted SPI score for each macaque per troop (N = 9, 14, 7, 12 and 7, at Dublin, Jersey II, London, Paignton and Thrigby). The SPI scores of enclosure and substrate use were compared between zoos, using non-parametric Kruskall-Wallis tests and multiple post-hoc pair-wise comparisons. To control for differences between sex-age classes (described in section 2.1.1.a), an alternative analysis of these data was performed; activity budgets were compared that were generated from data collected from macaques of matched sex-age class (1 adult male, 2 adult females, 1 big juvenile and 1 small juvenile). So that the comparison could be made between each of the four sex-age categories across all zoos, London Zoo was assigned with the average SPI score for all big juveniles (BJ) studied, as London Zoo had no big juveniles. A non-parametric Friedman test was used to investigate whether the mean adjusted SPI scores were significantly different between zoos.

The mean percentage time spent on the ground and inside was calculated for each macaque, from the total daily counts for each category recorded. A daily average was calculated by finding the mean from the 10 daily observations for each macaque, which were divided by the number of scans per day used during observations and this score was then multiplied by 100, providing the percentage time spent in each category/scan/macaque. This score was averaged for all the macaques in a troop, to provide the mean percentage time spent in each category/scan/troop (N = 7 - 14). Non-parametric Kruskall-Wallis tests were used to establish whether the mean time observed in each category was different between zoos, which was followed by non-parametric post-hoc multiple pair-wise comparisons, using the mean rank for each category as calculated in the Kruskall-Wallis analyses.

Kruskall-Wallis and Friedman tests were carried out using SPSS for Windows version 10.0 and non-parametric post-hoc analyses were calculated manually (SPSS, 1999c; Siegal & Castallan, 1988).

2.3.2 Results

Area and substrate use by macaques in the same enclosure was fairly uniform, as indicated by the small error bars on figures 2.3.1 and 2.3.2. Area and substrate use between zoos was significantly different (Kruskall-Wallis, enclosure use, $\chi^2 = 34.76$, df = 4, $p < 0.001$, substrate use, $\chi^2 = 41.65$, df = 4, $p < 0.001$). Significant differences between the adjusted SPI scores for enclosure use and substrate use indicated that the macaques at Jersey and Thrigby Zoos used the sites within their enclosures more fully and equally than macaques at Paignton and Dublin Zoos, and exploited the substrates provided in their enclosures more evenly than macaques at Paignton Zoo (Figures 2.3.1 and 2.3.2; Table 2.3.3). Similar results were obtained when the social composition between zoos was matched, indicating that this was not the factor responsible for the significant differences in enclosure and substrate use (Friedman test, enclosure use, $\chi^2 = 13.0$, df = 4, $p = 0.011$, substrate use, $\chi^2 = 14.6$, df = 4, $p = 0.006$).

The relative size of a site or the abundance of a substrate within the enclosure was not related to the frequency with which the macaque's used it (Figures 2.3.3 and 2.3.4). Although, there was a significant difference in the time spent inside between zoos, the macaques spent an average of 44.2% of their time inside, despite these areas representing approximately 5% of the total enclosure size, with the exception of London Zoo where it made up 33.6% of the overall enclosure area ($\chi^2 = 39.99$, df = 4, $p < 0.001$; Figure 2.3.5). Most of the macaque troops had 24 hr access between inside and outside areas (macaques at Paignton Zoo were locked in between 1800 and 1000 hr) and therefore, the time they spent inside represents an active choice on the part of the macaques to be inside.

The types of substrates provided for macaques and their abundance within the enclosure differed between zoos (Figure 2.3.4). Relative substrate abundance was linked with its location within the enclosure: for example, outside areas are larger so therefore grass accounted for the most plentiful substrate available to the macaques, except at London Zoo where it was wire. Discrete items around the enclosure were available at relatively low levels for example, the tyre or rope. For some substrates abundance was estimated to be so low that they do not appear on figure 2.3.4, likewise neither do the substrates used infrequently. As with area use, the time spent using a substrate did not correspond to its relative abundance (Figure 2.3.4). The adjusted SPI values provide information about how much the macaques use the sites and substrates within the enclosure, while accounting for their approximate size and abundance. Unfortunately, these results do not provide information about the interaction between the site and substrates used, i.e. we are unable to distinguish whether sites were used because the macaques preferred the location of the site, or whether they used the site because of the number and/or types of substrates in it (section 5.3).

Substrate use was further explored by investigating whether the macaques used substrates on or above the ground. The time spent on the ground was significantly different between zoos, with macaques at Dublin and London Zoos spending the least amount of time on the ground, about 30 % of the day ($\chi^2 = 35.8$, df = 4, $p < 0.001$). The macaques were observed to use the ground between 30% and 50% of the time, which reveals that they use the vertical space and substrates within the enclosure most of the time (Figure 2.3.6).

Figure 2.3.1 Mean ± SE adjusted spread of participation index scores for enclosure use by Sulawesi macaques at five zoos in the UK and Ireland.

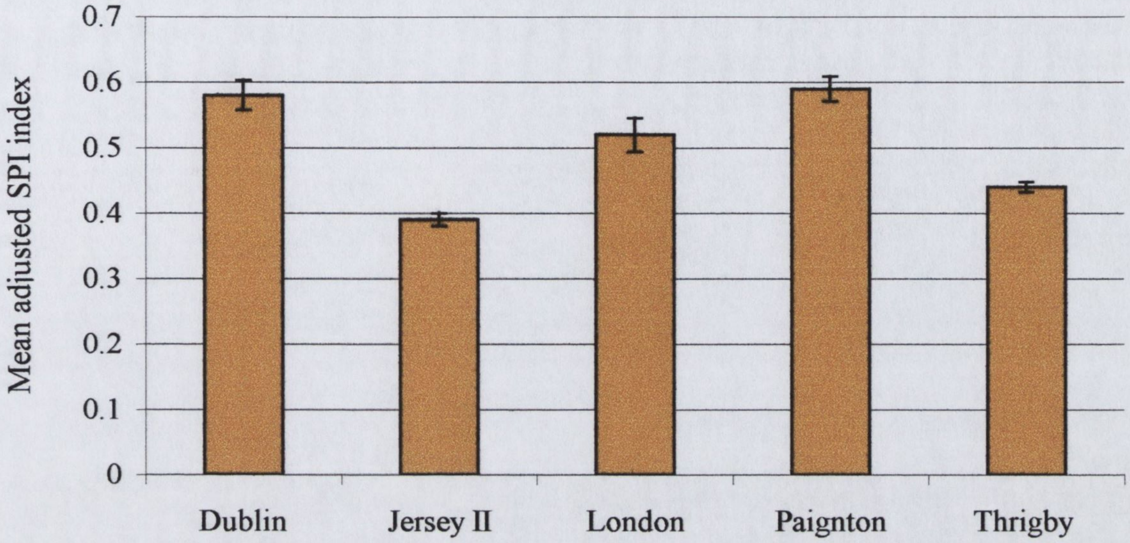


Figure 2.3.2 Mean ± SE adjusted spread of participation index scores for substrate use by Sulawesi macaques at five zoos in the UK and Ireland.

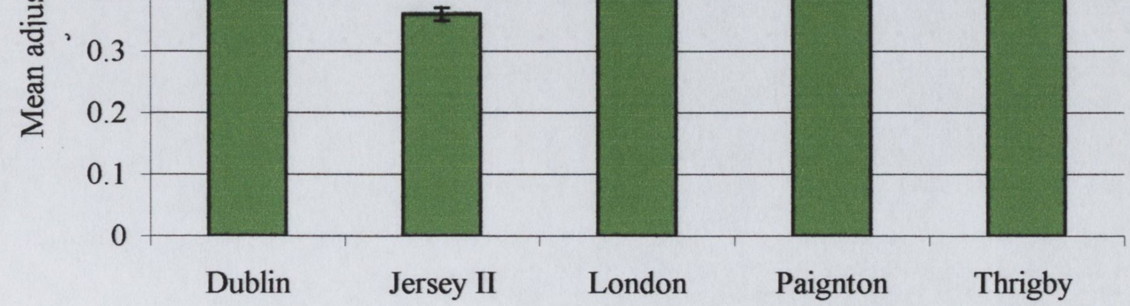


Figure 2.3.3 A comparison of enclosure site use (1 – 17) and its proportion of the total enclosure size (lighter shading highlights sites inside).

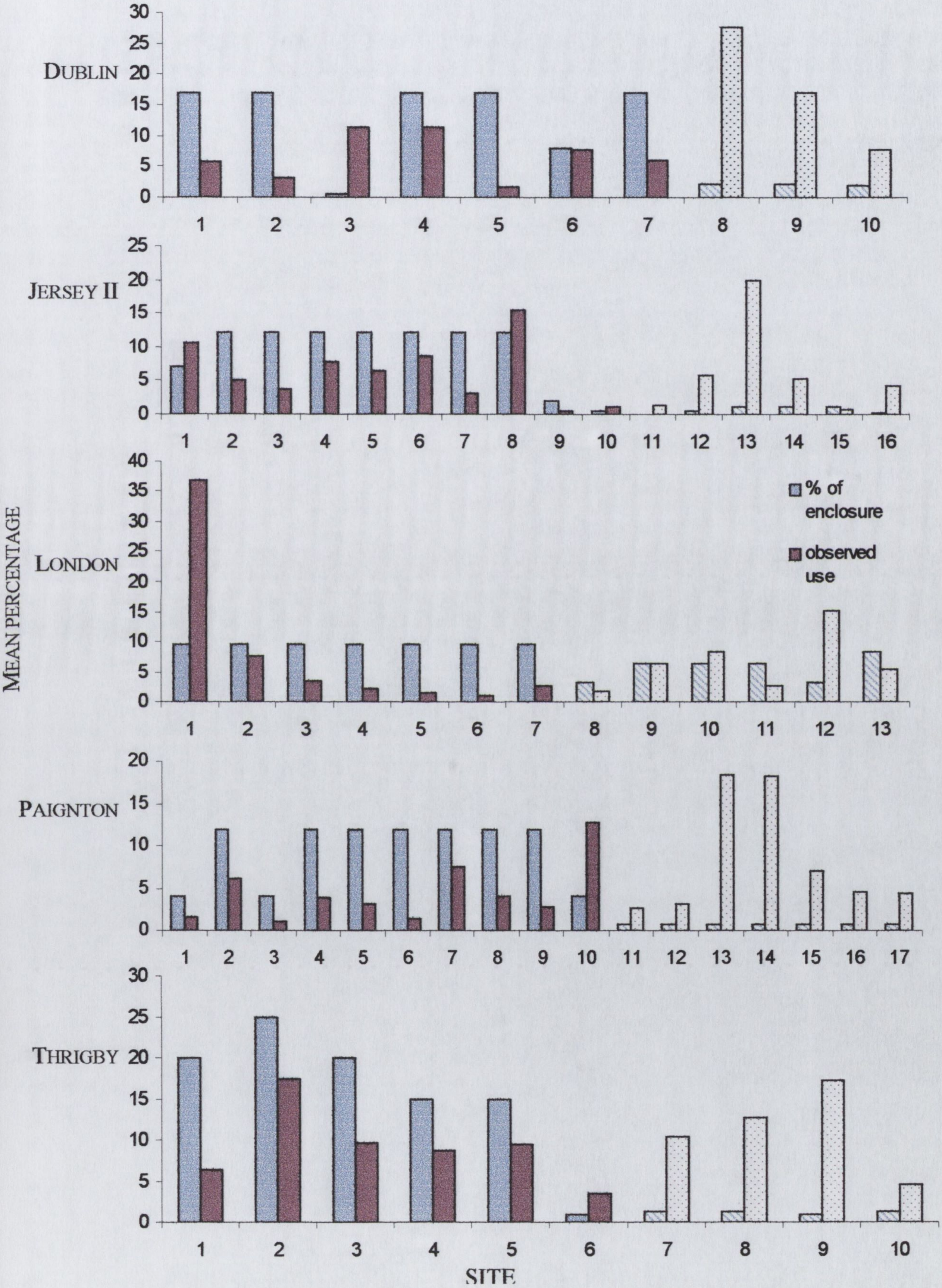


Figure 2.3.4 A comparison of substrate use and its approximate abundance within the zoo enclosure, which is illustrated with the most abundant substrates first on the y-axis (*non-fixed object, lighter shading denotes substrates found inside).

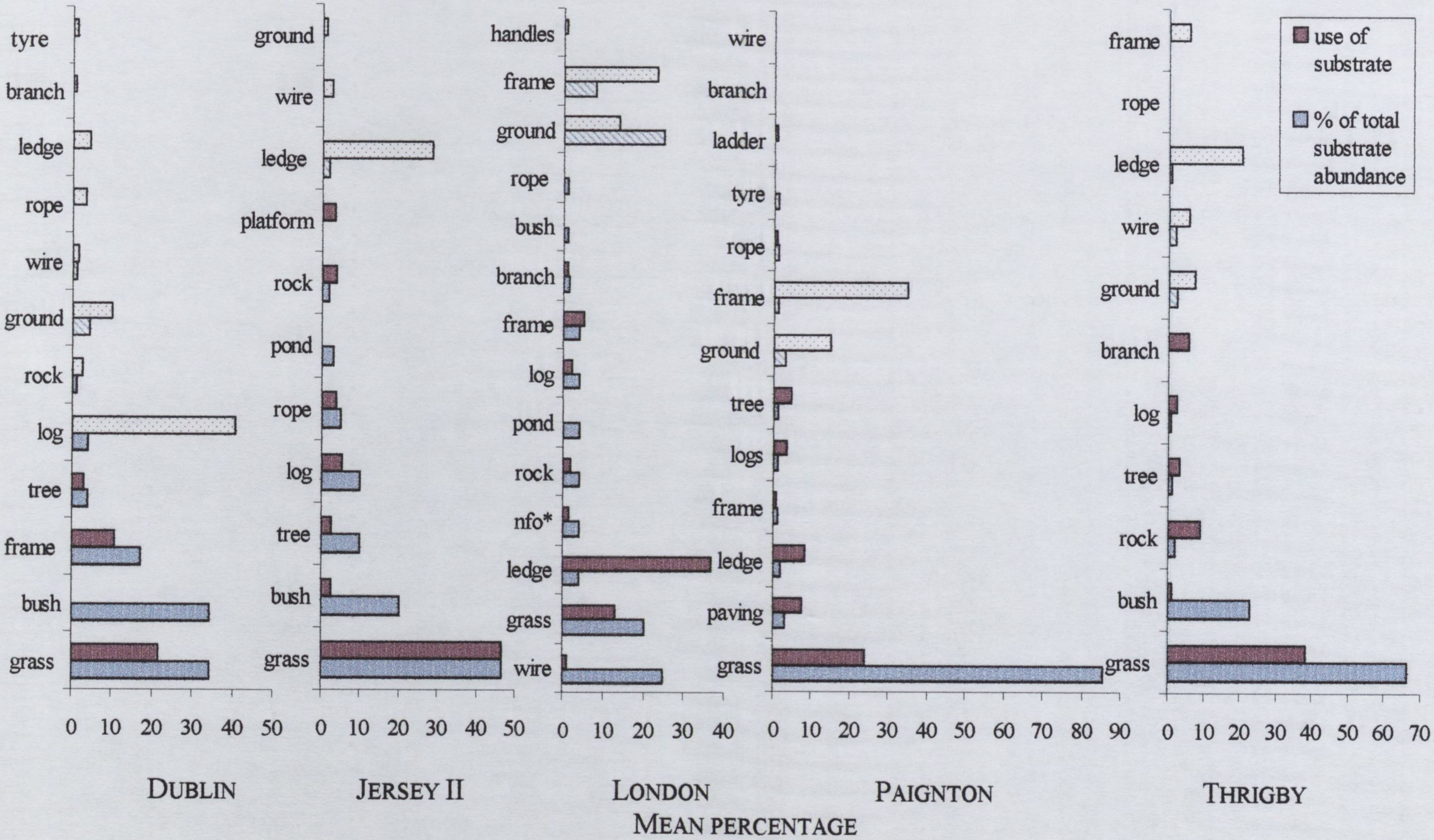


Figure 2.3.5 Mean ± SE percentage time spent using inside areas of the enclosure by captive Sulawesi macaques at zoos in the UK and Ireland.

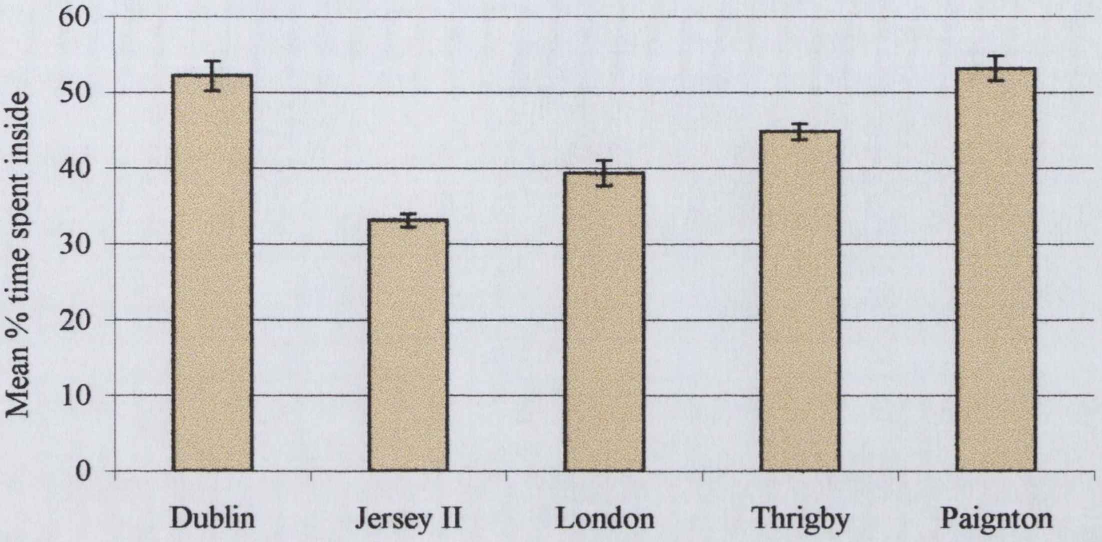


Figure 2.3.6 Mean ± SE percentage time spent on the ground by captive Sulawesi macaques at zoos in the UK and Ireland.

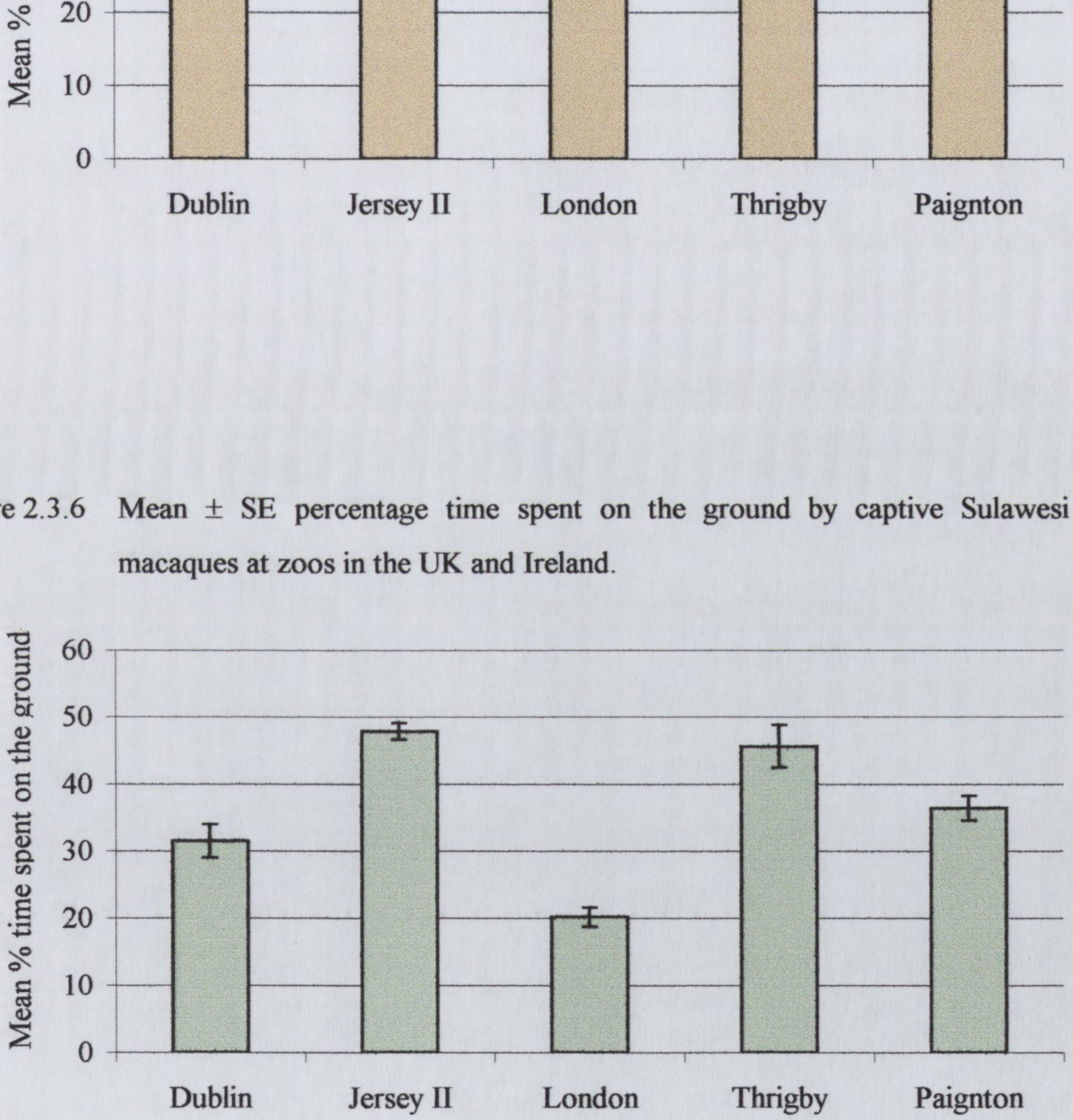


Table 2.3.3 Summary of significant results ($p < 0.05$) from the post-hoc analyses of enclosure and substrate use and mean time spent on the ground and inside.

Pair comparison		Mean rank difference				Critical value
		Enclosure use	Substrate use	Inside	Ground	
Dublin (N = 9)	Jersey II (N = 14)	27.37		30.24	24.64	17.99
	London (N = 7)			20.96		20.46
	Paignton (N = 12)					
	Thrigby (N = 7)	22.38				19.84
Jersey II	London				34.68	18.75
	Paignton	23.85	33.29	31.28	19.04	16.01
	Thrigby					
London	Paignton			22		18.75
	Thrigby				34.69	21.1
Paignton	Thrigby	18.86	20.98			18.66

2.3.3 Discussion

Enclosure and substrate use, as described by the adjusted spread of participation index (SPI), was fairly uniform between macaques in the same enclosure, but significantly different between macaques at different zoos. These data suggest a degree of homogeneity between macaques within a troop, which is supported by the fact that inter-group differences in the activity budgets of Sulawesi macaques are greater than intra-group differences (section 2.1). Adjusted SPI scores for the different troops indicate that sites and substrates within the enclosure were not uniformly used, but that the macaques displayed preferences for particular areas and substrates which are used more extensively. The macaques at Jersey Zoo scored the lowest adjusted SPI for both site and substrate use, revealing that they used their enclosure more evenly than macaques at the other zoos. However, predilections for enclosure sites and substrates were obvious for all troops, as time spent using certain enclosure areas and substrates was not proportional to the area designated for them.

A huge contrast existed between the size of inside and outside areas, where the majority of land was reserved for the outside areas, while the inside areas rarely appeared to exceed the minimum requirement to hold the troop comfortably with the provision of isolation areas. Consequently it is interesting to observe that the Sulawesi macaques in this study spent between 4 and 6 hr inside during the day (12 hr) and almost certainly much of the night. The zoos in this study have aimed to provide 'naturalistic' enclosures, whereby complexity and 'wild-type' substrates have been incorporated into the macaques' captive environment (Hutchings *et al.*, 1978b; Mallinson, 1990). A lack of consideration for inside areas may have resulted from attempts to provide large aesthetic landscaped outside areas, commensurate with 'naturalistic' enclosure design. Recently, moves towards improving inside enclosure areas have been made, by making them larger and more complex, for example the Chester Zoo Sulawesi macaque enclosure has an inside area equal in size (sometimes larger) to outside areas found at other zoos. Potentially smaller inside enclosure areas may restrict, both physically and socially, the types of behaviour performed by the macaques while inside. It has been demonstrated that when Sulawesi macaques spend more time inside they also spend more time performing social behaviours, which has been suggested to alleviate tension that increases in confined spaces (section 2.2).

Substrate diversity can be used as a measure of enclosure complexity, whereby an enclosure with a large variety of substrates is considered complex relative to an enclosure with few substrates. As substrate use was disproportionate to its relative abundance, so our perceptions of enclosure complexity may not be useful to the macaques. Alternatively enclosure and substrate use may have been underestimated by this study. Data collected in this study provided indications of which substrates were most frequently used and which were avoided. Use of some substrates was as infrequent as once or twice within the whole study, reflecting almost non-existent use of the substrates, at which point their contribution to any form of functional enclosure complexity becomes dubious. Low frequencies observed for the use of some substrates may have been an artefact of the recording method, as instantaneous scan sampling is biased toward recording substrate use which was protracted rather than brief. For example, when a macaque runs from rope, to tyre and comes to rest on the grass, it is most likely that neither rope nor tyre would be recorded as the macaques' use of these substrates was fleeting, whereas the use of grass would be recorded as the macaques spent longer on it. Assuming that the provision of many substrates for macaques is not harmful, the lack of correspondence between substrate abundance and use is not alarming. The incorporation of many substrates into the enclosure does provide the macaques with a variety of opportunities for utilisation, for example through exploration, movement or as objects in play.

Considering grass and the floor of the inside enclosures as ground and all other substrates to be above ground, provides a limited but interesting assessment of how Sulawesi macaques use vertical space. From the data it appeared that macaques preferred to be off the ground much of the time, though in many instances only by several centimetres e.g. on a log. This is particularly interesting given that the ground usually represented the most abundant substrate.

This study indicated that greater space should be assigned to inside enclosure areas as macaques chose to use them as much as outside enclosure areas. Sulawesi macaques have been observed to seek shelter in extreme weather conditions, which further supports the need for greater inside areas (Bernstein & Baker, 1988). As previously stated, the number and abundance of substrates within the enclosures differed between zoos. However, the provision of additional non-hazardous substrates in the enclosure can only be viewed as advantageous, as they provide the macaques with additional stimulation and choice.

2.4 A COMPARISON OF WILD AND CAPTIVE ACTIVITY BUDGETS

Many studies draw comparisons between the behaviour of captive primates and their wild counterparts, however few of these comparisons are quantitative; they compare captive primates against a generic wild primate activity budget which displays high levels of activity and little resting behaviour, or compare similar species between wild and captive settings. For example, Boccia & Hijazi (1998) used the fact that wild primates spent 30 – 70% of their time foraging to support their assertion that captive pig-tailed macaques should spend most of their active day foraging when in captivity. These studies emphasise that the expression of 'wild-type' behaviour by captive primates is beneficial for conservation, animal welfare, public education and research (Eisenberg & Kleiman 1977; Coe 1985; Snowdon 1989; Kleiman 1992; Reade & Waran 1996). In this present study, a quantitative comparison is made between the activity budgets of wild and captive Sulawesi macaques, to determine whether the behaviour of captive macaques deviates from that observed in wild Sulawesi macaques.

Table 2.4.1 Group composition, size and geographical range of the wild Sulawesi macaque troops observed by O'Brien & Kinnaird (1997).

Group	Troop size	Sex-age composition					Monthly home range (Km^2)	Amount of primary forest in home range
		Adult		Juvenile		Infant		
		Male	Female	Big	Small			
Rambo	97	7	28	31+	14	2	2.42	4%
Dua	61	5	20	12	19	2	1.13	20%
Malonda	50	6	14	7	13	8	0.69	15%

2.4.1 Methodology

2.4.1.a Data collected in the wild

O'Brien and Kinnaird (1997) compiled activity budgets for wild Sulawesi macaques in Tangkoko DuaSudara National Reserve in north Sulawesi. Of the eight troops regularly observed in all habitats and elevations of the reserve, three troops (Rambo, Malonda and Dua) comprising 50-97 individuals were habituated and followed for 18 months. Behavioural observations were carried out using instantaneous scan sampling with 30 min intervals; all data was recorded in the first 10 min of every half an hour between 0600 and 1740 h. Five individuals from each sex-age class (adult male, adult female, large juvenile, small juvenile) were observed in each scan (20 individuals/scan). Troop size, home range and quality of habitat varied between the three troops, though they had neighbouring ranges that overlapped in some areas (Table 2.4.1).

2.4.1.b Captive behavioural data collection

The data described in section 2.1.1.b were collected so as to be comparable to the wild data set.

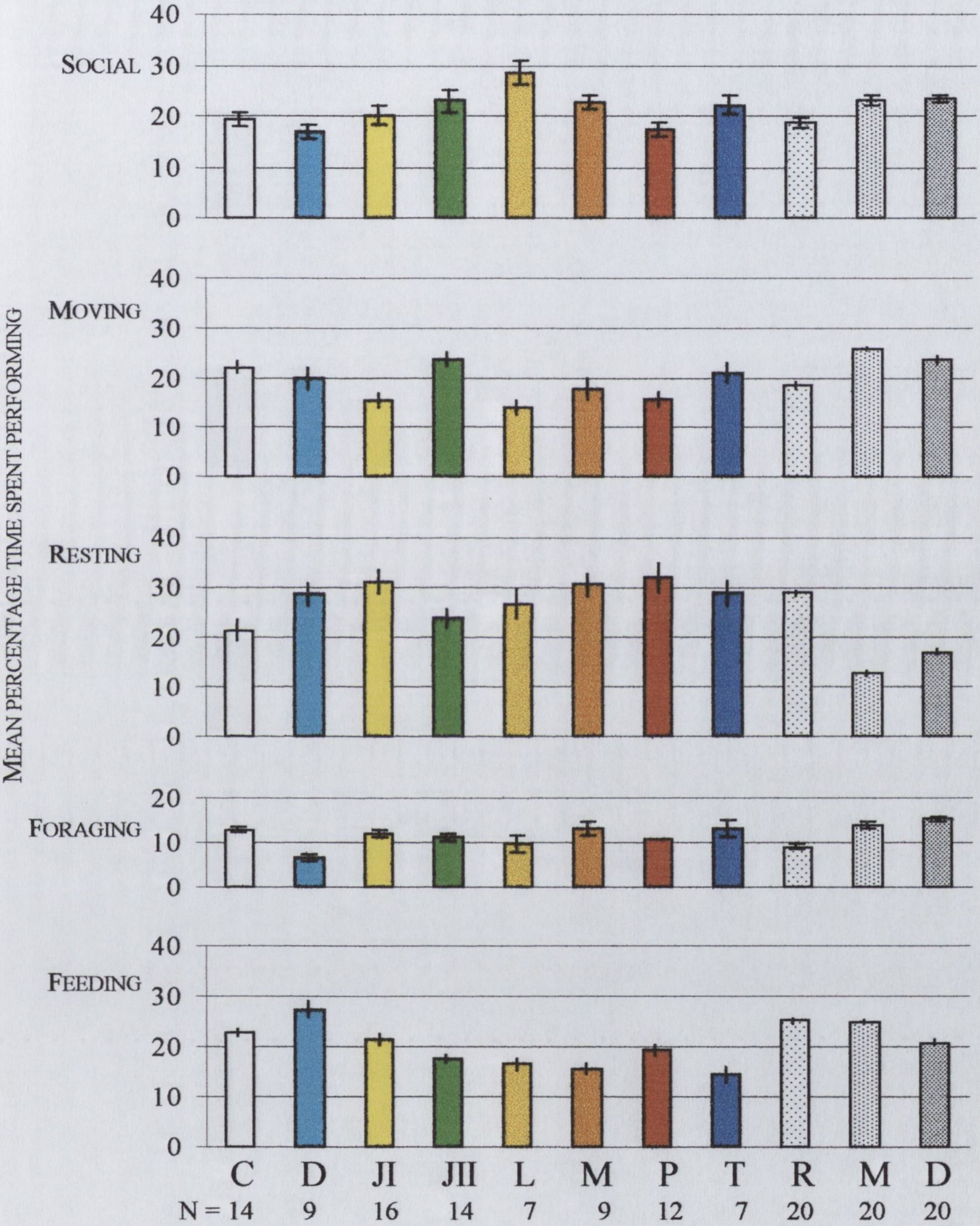
2.4.1.c Statistical analysis

Analyses were limited by the wild data, which were taken from a publication and provided the mean percentage time spent performing behaviours per group (N = 3). Therefore a non-parametric Mann-Whitney U test was performed on the data, as it can provide statistical information on unmatched pairs from small sample sizes e.g. N = 3, 5 (Fowler & Cohen, 1990). The 'miscellaneous and not seen' category recorded for captive Sulawesi macaques was not included in this comparison as no comparable data were available for the wild troops.

2.4.2 Results

Activity budgets generated from observations of wild and captive Sulawesi macaque troops are illustrated in figure 2.4.1. Mann-Whitney U tests revealed that the time attributed to behaviours was not significantly different between wild and captive troops (Table 2.4.2). When small sample sizes are used in Mann-Whitney U tests, any overlap in observations results in the acceptance of the null hypothesis; which explains why there is no significant difference between the two sets of activity budgets (Fowler & Cohen, 1990). The small sample sizes used in this analysis could therefore mask potential differences between wild and captive activity budgets. Pooling all wild data and all captive data to give two mean activity budgets, might clarify any differences (Figure 2.4.2). When the activity budgets generated for wild and captive troops are interpreted from figure 2.4.2, it appears that Sulawesi macaques in wild troops spent more time moving and feeding, and less time resting than captive troops. These differences were not significant because of the aforementioned overlap in observations.

Figure 2.4.1 Mean ± SE percentage time spent performing behaviour by wild and captive troops of Sulawesi macaque (SE bars do not appear on all columns, because they are too small).



Captive study sites, C = Chester, D = Dublin, JI & JII = Jersey, L = London, M = Marwell, P = Paignton and T = Thrigby. Columns with dots represent wild study sites, R = Rambo, M = Malonda and D = Dua (O'Brien & Kinnaird, 1997).

Figure 2.4.2 Mean ± SE percentage time spent performing behaviours, of the wild and captive troops of Sulawesi macaques (N = 8, captive; N = 3 wild). Wild data were recorded and published by O'Brien & Kinnaird (1997).

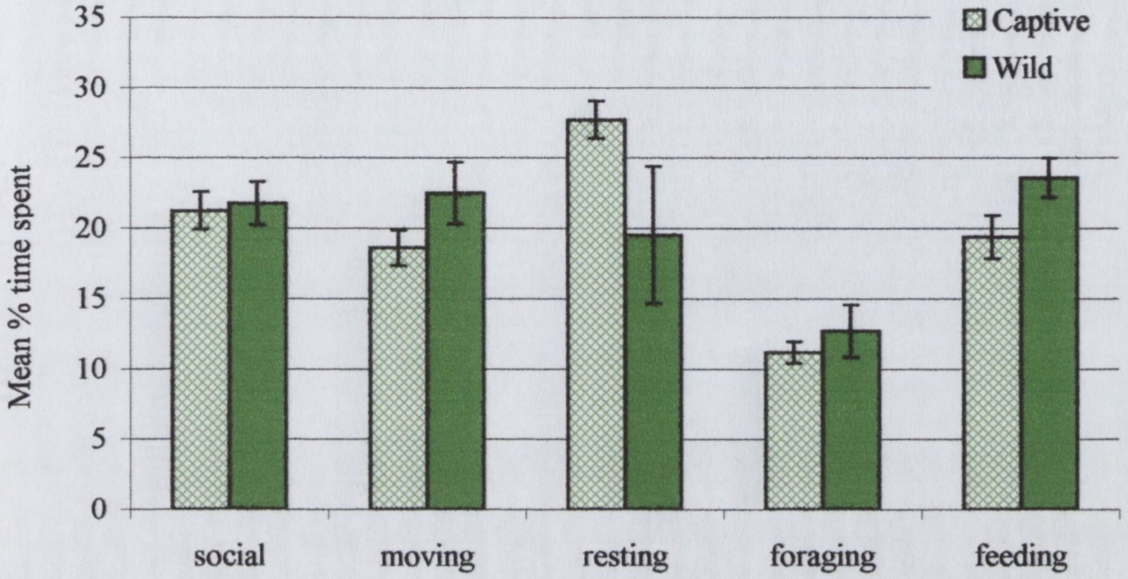


Table 2.4.2 Summary Mann-Whitney U test results that compared wild and captive Sulawesi macaque troops.

	Mean rank		Mann-Whitney U test		
	Wild (N = 3)	Captivity (N = 8)	U value	Z value	*P* value
Social	7.17	5.56	8.5	-0.72	0.47
Moving	8.33	5.13	5	-1.43	0.15
Resting	3.67	6.88	5	-1.43	0.15
Foraging	7.67	5.38	7	-1.02	0.31
Feeding	8.33	5.13	5	-1.43	0.15

2.4.3 Discussion

As behaviour is partly the product of environmental factors, and the contrast between wild and captive conditions is considerable, a difference in the time spent performing behaviours between sites would be expected. In this study no significant difference in the activity budgets of wild and captive Sulawesi crested black macaques was found, which could be the product of small sample sizes and high levels of variation between the activity budgets recorded in the wild and captive troops (Figure 2.4.1). The disparity between activity budgets in the wild macaque troops was credited in part to geographical diversity and consequent variations in food abundance available to each troop, which was demonstrated by the variation in the amount of primary rainforest in the home range of each troop (Table 2.4.1; O'Brien & Kinnaird, 1997). Similarly, the variation observed in the activity budgets of captive Sulawesi macaques has been attributed to the differences in the captive environmental conditions between zoos (Chapters 3 and 4).

Differences in the mean rank for behaviours (Figure 2.4.2) supported the generally accepted view that the time spent resting becomes elevated in captivity while active behaviours e.g. social, moving, foraging and feeding, decline. A reduction in activity is usually considered to result when wild selection pressures are absent in the captive environment, which is exaggerated by a lack of stimulation (Chamove, 1988).

'Wild-type' behaviour is considered to be inherently beneficial as animals have evolved over time to perform these adaptations and therefore 'wild-type' behaviour is considered 'natural' and 'good' (Stolba & Wood-Gush, 1984; Maki & Bloomsmith, 1989; Maple & Finlay, 1989; discussed in section 1.4.1). Same-species troops in the wild are influenced by the many variable climatic, geographical and social factors, which are reflected in the observation of highly different activity budgets; for example, the time spent feeding by neighbouring wild Sulawesi macaque troops varied from 20.8% to 25.1%, and resting behaviour was observed to range between 12.6% and 28.95%. The use of wild activity budgets as 'desirable' baselines of behaviour is therefore ambiguous (O'Brien & Kinnaird, 1997; discussed in section 1.4.1). To encompass the variation in activity budgets observed in wild primate troops, Chamove (1989) suggested that these wild observations should be used as a guide, and that captive primates should be housed in such a fashion that their activity budgets fall within the range observed in the wild.

Limitations associated with wild-captive comparative studies have been identified by Veasey *et al.* (1996) (see section 1.5.1.c). Consequently, the methodology used in this study sought to minimise disparities in data collection between wild and captive sites in the following ways: 1) minimising observer bias by habituating animals to observers at both sites, although it should be noted that there was possibly a bias in the wild data collection towards macaques that were more clearly visible i.e. those that were still or near to the ground; 2) the use of simple behavioural categories which were well defined reducing inter-observer variation between sites; 3) by attempting to gain a representative sample of captive and wild macaque behaviour (wild N = 3, captive N = 8); 4) unlike the study carried-out by Veasey *et al.* (1996), there was no obvious problem with hybrid macaques in this study and all subjects were *Macaca nigra*. No genetic comparison has been made between wild and captive Sulawesi macaques. However the aim of the captive management strategy in place for the Sulawesi macaques aims to maintain genetic diversity and, therefore, some overlap in the genetic make-up of wild and captive Sulawesi macaques is expected (Norcup, 2000).

The similarities between wild and captive activity budgets found in this study demonstrate that it is possible to maintain captive Sulawesi macaques that express 'wild-type' behaviours. The zoos in this study were able to stimulate 'wild-type' behaviours (explored further in chapters 3 and 4), which may be the product of the naturalistic approach to zoo enclosure design as it was a common feature of all the enclosures studied. Alternatively, variation in the activity budgets observed in the wild Sulawesi macaques may be so wide, that however divergent the captive Sulawesi macaque activity budget becomes, it will still be within the behavioural range observed in wild macaques. The nature of the enclosure may be of little consequence if this second hypothesis is true. There are a lot of studies that have demonstrated the negative repercussions of restricted captive conditions (laboratory cages) on macaque behaviour, which indicate that the captive environment certainly does affect captive primate behaviour (Bayne, 1989; Reinhardt *et al.*, 1998). In a zoo situation however, enclosures now tend to be more extensive and include social groups and a complex environment, which may not be sufficiently different from the Sulawesi macaque's wild habitat to alter the captive macaques' activity budgets beyond the range observed in the wild habitat. This is supported by the suggestion that in many situations there are greater similarities between wild and captive environments, than there are differences (Carlstead, 1996).

The results of this comparison can be interpreted in two ways: 1) Zoo enclosures are providing the correct conditions for captive primates as 'wild-type' behaviour is expressed, or 2) A greater understanding of wild and captive primate behaviour is necessary if wild-captive comparisons of behaviour are made, as the variation which exists in the wild is substantial and a fair representation of wild primate behaviour is not gained from a study which observed only three troops.

Chapter 3

MULTIPLE REGRESSION ANALYSES

3.1 METHODOLOGY

These analyses used data from 8 troops of Sulawesi macaques in 7 zoos in the UK and Ireland. The subjects, study sites and method of behavioural observations are described in section 2.1.1.

3.1.1 Environmental factors measured

Sixteen environmental variables (independent variables, IV) were measured at each zoo to evaluate current housing and husbandry regimes. These IVs represented enclosure size, enclosure complexity, inside flooring material and husbandry indices (Table 3.1.1). These factors did not represent an exhaustive selection of the captive environmental variables that could potentially affect Sulawesi macaque behaviour but they did provide a basis for comparison of housing and husbandry systems across zoos.

Table 3.1.1 Definition of the environmental variables measured between zoos.

ENCLOSURE SIZE

Enclosure out	Surface area of outside area (m^2)
Enclosure in - floor area	Surface area of inside flooring area (m^2)
Enclosure in - volume:	Inside flooring area x height of enclosure (m^3)
Enclosure in - useable area	"Useable" was defined as any surface that the macaques could sit on, or climb: sum of surface area of the enclosure, surface area of wire areas and ledges (m^2).
Total floor area	Enclosure out + enclosure in floor areas (m^2).
Ratio in /out	Enclosure floor area outside was divided by the inside floor area (m^2).
Area /Individual	Total floor area divided by troop size (m^2/individual).

ENCLOSURE COMPLEXITY

Number of substrates - inside	Substrate number was established by counting the different materials e.g. grass and cement flooring, and features of different function e.g. logs and ledge, within the enclosure.
Number of substrates - outside:	Ditto for outside enclosure e.g. tree, grass, bush, frame, electric fence and pond.
Total number of substrates	Number of substrates outside + inside

INSIDE FLOORING MATERIAL

The type of flooring material used inside (bark, straw, sawdust or nothing, when no material was used) was entered into the regression equation as dummy variables.

HUSBANDRY STYLE

Access between inside and outside areas	Categorised into one of the three classes: 24 hr access, semi-restricted and restricted access (defined in section 3.1.1).
Number of feeds/day	Total number of feeds given a day. In zoos where the number of feeds/day varied, an average was calculated.
Troop size	Total number of macaques in the troop

3.1.2 Analyses

Two statistical multiple regression (MR) analyses, with forward selection entry of IVs (see section 1.5.2.b) were employed for each of the 5 behaviours (dependant variables, DV) observed, totalling 10 MR analyses. The first MR analysis for each of the behaviours was used to explore the data and select four from the sixteen IVs measured to enter the second MR analysis, which was used for statistical inference. The number of IVs that could be incorporated into the second MR equation (M) was dependent on the number of cases (N) available for analysis. As $N = 89$ in this study and M is defined as equal to $(N-50)/8$, it was calculated that 4.88 IVs could be used in the MR equation (Tabachnick & Fidell, 1996). Thus a maximum of four IVs were selected and used in the second MR analyses, on the basis of their contribution to the first MR model. Previous research demonstrated that sex-age class affected captive Sulawesi macaque behaviour (Melfi and Marples, 2000), so different social compositions between zoos could affect activity budgets (section 2.1). To ensure that the effects of housing and husbandry were evaluated and not confounded by effects that resulted from different social compositions between zoos the behavioural data for each troop was weighted by sex-age class prior to the MR analyses. All statistics were carried out using SPSS for Windows version 8.0 (1997).

3.2 RESULTS

The results of the multiple-regression analyses for social, moving, resting, foraging and feeding behaviour are presented in the following: table 3.2.1, 3.2.2, 3.2.3, 3.2.4 and 3.2.5.

3.2.1 Social behaviour

Troop size, number of feeds per day (*feeds/day*) and 24 hour access between inside and outside areas (*24 hr access*) significantly predicted 19% of the variation observed in social behaviour ($R = 0.44$, $F_{3/85} = 6.72$, $p < 0.001$). Of the three variables included in the predictive model for social behaviour *feeds/day* contributed the most and accounted for 0.13 (sr_i^2) of the final coefficient of determination ($R^2 = 0.19$). Tolerance values indicated that there was a level of intercorrelation between the IVs, with *24hr access* demonstrating least intercorrelation with the other IVs (tolerance value = 0.57). Partial correlation coefficients suggest that the time spent in social behaviour was negatively related to *24hr access* and *troop size*, but positively related to *feeds/day* (Table 3.2.1).

These results suggest that of the variables selected in the MR model, *feeds/day* was a more important determinant of social behaviour than either *troop size* or *24 hr access*, with the level of social behaviour rising with *feeds/day*. *Troop size* and *24 hr access* were negatively correlated to social behaviour, which indicated that social behaviour was lower in larger troops relative to smaller groups and when the macaque troops received 24 hr access to inside and outside areas of the enclosure.

3.2.2 Moving behaviour

Troop size, area per individual *(area/individual)*, number of substrates in the outside area of the enclosure (*no. of subs. out*) and *useable area* were incorporated into a model that significantly predicted 28% of the variation observed in moving behaviour (R = 0.53, $F_{4/84} = 8.02$, $p<0.001$). The *no. of subs. out* and *useable area* accounted for the majority of variation observed in moving behaviour, contributing 0.12 and 0.08 respectively to the coefficient of determination ($R^2 = 0.28$). The tolerance values for the IVs in the model varied. *No. of subs out* showed little intercorrelation (tolerance value = 0.73). *Area per individual* and *useable area* were highly interrelated (tolerance values = 0.055 and 0.078 respectively), which is not surprising as both were measurements of enclosure size. Given the high level of intercorrelation between them, interpretation of their affects on moving behaviour was considered jointly and their combined influence on moving behaviour discussed in section 4.3.3. Partial correlation coefficients indicate that the time spent moving was negatively related to the *no. of subs. out* and *troop size* but positively related to enclosure size. These results suggest that the macaques moved more in larger enclosures and less if the enclosure was complex or they were in a large group.

3.2.3 Resting behaviour

Troop size, *feeds/day* and the number of substrates present in the inside area of the enclosure (*no. of subs. in*), were included in the multiple regression equation that significantly predicted 17 % of the variation observed in resting behaviour (R = 0.41, $F_{3/85} = 5.79$, $p<0.001$). The *no. of subs. in* contributed 0.098 (sr_i^2) to the coefficient of determination ($R^2 = 0.17$), which suggests that it is a very good predictor of resting behaviour. Its influence can be evaluated with a high degree of certainty, as there was a very low level of intercorrelation between this and the other IVs in the model (tolerance value = 0.99). A degree of intercorrelation existed between the remaining two variables indicated by tolerance values of 0.49. *Troop size* had a greater impact on the time spent resting accounting for almost 5% of the variation observed, compared to only 3% represented by *feeds/day*.

Correlation coefficients indicated that resting behaviour was negatively related to the *no. of subs. in* and *feeds/day*, and positively related to *troop size*. The *no. of subs in* and *feeds/day* are positively related to one another, yet appear to affect resting behaviour in opposing directions. *Troop size* was included in the MR equation because it improved the predictive model by 5%, yet its correlation with resting behaviour was very weak (simple r^2, -0.076). Attempts to interpret this relationship are probably not statistically valid, given the weak relationship and the intercorrelation between IVs in the model (Martin & Bateson, 1996). The influence of *troop size* on resting behaviour is probably best interpreted as part of a combined affect together with the other IVs in the model and therefore the relationship between *feeds/day* and resting behaviour are explored further in section 3.3.1, without mention of the conflicting associations with *troop size*.

3.2.4 Foraging behaviour

Total floor area, *bark* (used as an inside flooring material), the *no. of subs in* and *no. of subs. out*, were included into the multiple regression model which significantly predicted 17% of the variation observed in foraging behaviour ($R^2 = 0.17$, $F_{4/84} = 4.26$, $p < 0.01$). Two of the IVs had significant β coefficients, *bark* and the *no. of subs. in*, which indicated that these two variables were useful independent predictors of foraging behaviour. Partial correlation coefficients indicated that foraging behaviour was positively related to *total floor area* and the *no. of subs. in* and negatively related to *bark* and the *no. of subs. out*. *Bark* and the *no. of subs. in* had the highest partial correlation coefficients with foraging behaviour and also contributed most to the predictive model ($sr_i^2 = 0.051$ and 0.053 respectively). Therefore we can tentatively suggest that foraging behaviour would increase with *total floor area* and *no. of subs. in*, but decline as the *no. of subs. out* increase and when *bark* was used as an inside flooring material. *Bark* and *no. of subs. in* are highly correlated, which is supported by their low tolerance values of 0.12 and 0.1 respectively. Therefore the independent influence of these two factors on the time spent foraging cannot be established.

3.2.5 Feeding behaviour

Two predictive models are presented for feeding behaviour to illustrate the complexities inherent in MR analyses. Results will be presented below and the implications discussed later (section 3.3).

In the first model (feeding 1), *troop size*, *area/individual* and *bark* significantly predicted 45% of the variation observed in feeding behaviour ($R^2 = 0.45$, $F_{3/85} = 23.22$, $p <$ 0.001). The β coefficients for all three IVs included in the model were significant, indicating that they were all useful independent predictors of feeding behaviour. Simple correlation coefficients indicate positive relationships between all the IVs in the model and feeding behaviour. However, partial correlation coefficients for the same pairs show a negative relationship between *area/individual* and feeding behaviour. Partial correlation coefficients provide a 'true' picture of the relationship between two variables, as the effects of other variables are eliminated (Martin & Bateson, 1996). The positive relationship between *area/individual* and feeding calculated through simple regression is probably a reflection of intercorrelation and overriding effects from other variables in the model. *Area/individual* was highly correlated with both *bark* and *troop size*, which were positively related to feeding, thus resulting in the false positive relationship between *area/individual* and feeding behaviour. Partial correlation coefficients indicate that all three IVs in the model were moderately related to feeding behaviour, the strongest relationship being between *bark* ($r^2 = 0.63$), *troop size* ($r^2 = 0.49$) and then *area/individual* ($r^2 = -0.39$). *Bark* accounted for the majority of the predictive power of the feeding behaviour model ($sr_i^2 =$ 0.28). Though *troop size* had a greater correlation with feeding behaviour relative to *area/individual*, it contributed less to the final predictive model, which indicates that both *troop size* and *bark* overlapped in their abilities to predict feeding behaviour. *Bark* was the first to enter the multiple regression equation so all of its predictive power entered the model, while *troop size's* contribution was reduced by the overlap it shared with *bark*. Thus the strength of the relationship between feeding and *troop size* was not reflected clearly in the multiple-regression equation. These results suggest that feeding behaviour increases with *troop size* and in the presence of *bark*, but decreases as the *area/individual* rises.

The second predictive model for feeding behaviour (feeding 2) attempted to reduce the level of intercorrelation between the IVs in the model, by removing *area/individual* as it was obviously related to *troop size,* which was also entered into the equation. *Total floor* *area* was therefore substituted for *area/individual,* thus IVs that represented enclosure size and group size were still entered into the equation. *Troop size*, *total floor area* and *bark* significantly predicted 44% of the variation observed in feeding behaviour ($R^2 = 0.44$, $F_{3/85} = 22.64$, $p < 0.001$). The *no. of substrates in* and *troop size* were highly correlated (r^2 0.93) and exceeded the default intercorrelation value imposed by the statistical package and therefore one had to be excluded (SPSS, 1997). As *troop size* entered the multiple regression equation first, it remained and *no. of subs. in* was excluded from further analyses. The β coefficients for all three IVs included in the model were significant, indicating that they were all useful independent variables in accounting for variation in feeding behaviour. *Bark* accounted for the majority of the predictive power of the model ($sr_i^2 = 0.35$), indicating that it had a large impact on feeding behaviour. All of the IVs in the feeding model were positively correlated with feeding, so we can loosely predict that the use of *bark* as an inside flooring substrates promotes feeding behaviour, as does an increase in *troop size* and *total floor area*. The tolerance values of the IVs in the model were closer to 0 than the tolerance values calculated for the first predictive model for feeding behaviour. Efforts to reduce intercorrelation were not successful, as *total floor area* (substituted for *area/individual*) was highly correlated to *bark* and *troop size*, producing a higher level of intercorrelation than in the previous model.

3.2.6 Intercorrelation

All the MR models show a degree of intercorrelation between the incorporated IVs (multicollinearity). The influence of individual IVs on behaviour are difficult to interpret with multicollinearity, as the independence of the IVs is questionable and therefore their affect on the expression of the behaviours is probably linked. When tolerance values are high for particular IVs, their influence on behaviour can be suggested with a little more certainty. The results from the MR analyses have established that captive environmental factors contributed significantly to the behavioural expression of the Sulawesi macaques, and have also revealed how some of these environmental factors work together to affect behaviour.

Table 3.2.1 The influence of captive environmental factors on SOCIAL behaviour: Summary results from a forward statistical multiple-regression analysis, weighted by sex-age class.

Variable	Simple r					Partial r	B	β	$sr^2{}_i$	Tolerance
	Social (DV)	Troop size	Feeds/ day	24 hr access	Enclosure area - out				sequential	
Troop size	-0.20*					-0.4	-1.11	-4.06***	0.041	0.36
Feeds/day	0.11	0.71***				0.38	2.46	3.67***	0.13	0.28
24 hr access	-0.12	0.01	0.47***			-0.16	-2.35	-0.19	0.02	0.57
Enclosure area - out	-0.15	0.74***	0.51***	-0.37***		Intercept = 27.32				
									R^2=	0.19
Means	19.31	11.74	2.8	0.59	814.34				Adjusted R^2=	0.16
Std. Dev	9.03	4.62	1.89	0.74	726.37				R=	0.44***

$*p<0.05, **p<0.01, ***p<0.001$

Table 3.2.2 The influence of captive environmental factors on MOVING behaviour: Summary results from a forward statistical multiple-regression analysis, weighted by sex-age class.

Variable	Simple r					Partial r	B	β	sr^2_i sequential	Tolerance
	Social (DV)	No. of subs out	Troop size	Area/ individ.	Useable area in					
No. of subs out	-0.35					-0.2	-0.76	-1.88	0.12	0.73
Troop size	-0.076	-.024				-0.4	-1.32	-4.051***	0.027	0.3
Area/ individ.	0.26	-0.46	0.52			0.37	0.24	3.62**	0.043	0.055
Useable area in	0.21	-0.35	0.18	0.9		-0.32	-0.029	-3.085**	0.082	0.078
						Intercept = 28.6			R^2=	0.28
Means	19.86	7.48	11.74	70.22	140.75				Adjusted R^2=	0.24
Std. Dev	8.85	2.39	4.62	53.96	311.04				R=	0.53***

*p<0.05, **p<0.01, ***p<0.001

Table 3.3.3 The influence of captive environmental factors on RESTING behaviour: Summary results from a forward statistical multiple-regression analysis, weighted by sex-age class.

Variable	Simple r				Partial r	B	β	sr_i^2 sequential	Tolerance
	Resting (DV)	No. of subs inside	No. of feeds/ day	Troop size					
No. of subs inside	-0.31				-0.34	-1.56	-3.39**	0.098	0.99
No. of feeds/ day	-0.13	-0.11			-0.27	-3.081	-2.68**	0.026	0.49
Troop size	0.05	-0.053	0.71		0.2	1.004	2.15*	0.045	0.49
						Intercept = 33.71		R^2=	0.17
Means	28.37	5.47	2.8	11.74				Adjusted R^2=	0.14
Std. Dev	15.33	3.33	1.89	4.62				R=	0.41**

*p<0.05, **p<0.01.

Table 3.3.4 The influence of captive environmental factors on FORAGING behaviour: Summary results from a forward statistical multiple-regression analysis, weighted by sex-age class.

Variable	Simple r					Partial r	B	β	sr_i^2 sequential	Tolerance value
	Foraging DV	Total floor area	Bark	No. subs in	No. subs out					
Total floor area	0.19*					0.061	6.24 E-04	0.56	0.034	0.52
Bark	-0.11	0.48***				-0.34	-9.26	-0.35**	0.051	0.12
No. subs in	0.025	0.61***	0.93***			0.26	1.51	2.51*	0.053	0.1
No. subs out	-0.15	-0.43***	-0.42***	-0.4***		-0.19	-0.55	-1.77	0.031	0.74
						Intercept = 9.03			R^2=	0.17
Means	11.21	871.1	0.27	5.5	7.5				Adjusted R^2=	0.13
Std. Dev	6.46	800.96	0.66	3.33	2.39				R=	0.41**

$*p<0.05$, $**p<0.01$, $***p<0.001$.

Table 3.3.5 The influence of captive environmental factors on FEEDING behaviour: Summary results from a forward statistical multiple-regression analysis, weighted by sex-age class.

Variable	Simple r				Partial r	B	β	sr_i^2 sequential	Tolerance
	Feeding DV	Bark	Troop size	Area/ individ					
Bark	0.53***				0.63	9.53	0.85***	0.28	0.51
Troop size	0.25**	-0.05			0.49	0.9	0.56***	0.076	0.55
Area/ Individ	0.26**	0.57***	0.52***		-0.39	-0.07	-0.52***	0.099	0.37
						Intercept = 11.38			
								R^2=	0.45
Means	19.5	0.27	11.74	70.22				Adjusted R^2=	0.43
Std. Dev	7.46	0.66	4.62	53.96				R=	0.67***

*$p<0.05$, **$p<0.01$, ***$p<0.001$.

Table 3.2.6 The influence of captive environmental factors on FEEDING (2) behaviour: Summary results from a forward statistical multiple-regression analysis, weighted by sex-age class.

Variable	Simple r^2					Partial r	B	β	sr_i^2 sequential	Tolerance
	Feeding DV	Bark	Troop size	Total floor area	No. of subs in					
Bark	0.53***					0.62	9.55	0.85*	0.28	0.49
Troop size	0.25**	-0.05				0.48	1.15	0.71*	0.08	0.33
Total Floor area	0.3**	0.48***	0.7***			-0.38	-0.0056	-0.61*	0.09	0.25
No. of subs in	0.4***	0.93***	-0.053	0.61***		(Intercept = 11.38)				
									R^2=	0.44
Means	19.5	0.27	11.74	871.1	5.47				Adjusted R^2=	0.42
Std. Dev	7.46	0.66	4.62	800.9	3.33				R=	0.67*

*$p<0.05$, **$p<0.01$, ***$p<0.001$.

3.3 Discussion

Multiple regression analyses significantly predicted 17% - 45% of the variation observed in captive Sulawesi macaque behaviour. Captive environmental variables that represent housing and husbandry regimes included in the predictive models were troop and enclosure size, enclosure complexity, the use of bark as an inside flooring material (bark) and the number of feeds provided daily (feeds/day). It was evident from these results that a degree of intercorrelation between environmental variables incorporated in the predictive models for behaviour was present. Intercorrelation reduces the accuracy of the predictive model and makes it difficult to distinguish between the contributions made to behavioural expression by different environmental variables. In situations where there is a high level of intercorrelation between variables, the influence of the variables should be viewed as collaborative, while interpretations of the individual influence of environmental factors on behaviour should be cautious.

Results from the multiple regression model that predicted feeding behaviour, indicated that larger enclosures held greater troop sizes and were more likely to use bark as inside flooring material. These types of interactions between environmental factors are not surprising, as larger enclosures are able to hold more animals and therefore paralleled increases in both should be expected. The use of bark can be explained in terms of the time required to maintain it, which seems to be inversely related to enclosure size. In smaller enclosures bark becomes quickly soiled, so requires more frequent renewal than when used in larger enclosures. In larger enclosures the soiled bark can degrade to produce a microclimate that kills bacteria and also appears to be cleaner due to its larger surface area, therefore it can be changed less frequently which translates into easier management (Chamove *et al.*, 1982).

The creation of naturalistic enclosures attempts to simulate a wild habitat, which loosely translated means a large, complex enclosure that is able to hold a large social group. Wild Sulawesi macaque troops can comprise 100 individuals and though captive social groups are far smaller, the inclusion of other 'naturalistic enclosure' features into the captive environment has been attempted by increasing enclosure complexity and using bark as an inside flooring material (Maple & Finlay, 1989; O'Brien & Kinnaird, 1997; Norcup, 2000). Modifications made to enclosures, so that they resemble 'naturalistic' habitats (large and complex), results in intercorrelation between these environmental factors. As the inclusion of one factor into the captive environment, is usually associated with the presence or absence of other environmental factors and so the problem with intercorrelation between environmental variables will persist.

It is interesting to note that the factors that resemble the wild habitat are indeed those that were found to be positively related to the expression of 'active' behaviours like feeding and foraging behaviour. The results of the multiple regression analyses support the idea that naturalistic enclosures promote 'active' behaviours, but whether this brings the activity budget of captive Sulawesi macaques into greater agreement with their wild conspecifics depends on the how we view and compare 'wild-type' behaviour (Hediger, 1955; Maple & Finlay, 1989; Redshaw & Mallinson, 1991; section 1.4.1). Understanding how these environmental variables, and their interaction together, affect captive Sulawesi macaque behaviour also provides zoo managers with the information necessary to manipulate behaviour through enclosure modifications.

Despite variable levels of intercorrelation between the environmental factors in the predictive models for behaviour, the process by which environmental factors influence behaviour can be considered separately and the final activity budget a result of the combined processes from all of the environmental factors. Therefore, the processes by which environmental factors influence behaviour are discussed separately.

3.3.1 Feeding frequency

Environmental enrichment programmes often involve the presentation of a variety of feeding methods to increase feeding and foraging levels and promote activity (reviewed by Reinhardt & Roberts, 1997). Captive Sulawesi macaques in this study were fed between once and five times per day, depending on the regime in place at the zoo. The results from the multiple regression analyses revealed that the number of feeds per day (feeds/day) received by the captive Sulawesi macaques significantly influenced the time spent in social and resting behaviour. Feeds/day was the greatest predictor of social behaviour, accounting for 13% of the variation observed, but contributed least to the prediction of resting behaviour, accounting for about 3% of the variation observed (Table 3.3.1 and 3.3.3). A positive correlation between feeds/day and social behaviour suggested that as feeds/day rose, so did the incidence of social behaviour. Feeding time in captivity is often associated with high levels of tension for social groups (Belzung & Anderson, 1986). Competition for food is further increased if food is provided in discrete patches, which can be easily monopolised by high-ranking individuals (Ettah, 1997). If macaques are fed more frequently, it follows that they will be exposed to a greater number of stressful events than those that get fed less frequently. According to de Waal (1989) primates are willing to put a lot of energy into preserving their long-term social relationships within a group, through the expression of reconciliation and affiliative behaviours. He proposed a model that suggested that changes in the environment that elevated stress levels would result in an increased expression of 'calming gestures' and affiliation with con-specifics. These positive social behaviours reduce the risk of aggression and conflict. Feeds/day appears to influence the time spent in social behaviours and not just event behaviours at the time of feeding, supporting de Waal's theory. As feeding time is distributed throughout the day and sometimes at random intervals, macaques may need to reaffirm social hierarchies to limit aggression and assert their consequent priority access to resources throughout the day rather than just at the time of feeding. Therefore, a rise in the time spent in social behaviours would be expected as the number of feeds/day increases.

Contrary to this hypothesis is the use of additional feeding to alleviate stress and reduce aggression. In Basel Zoo, long-tailed macaques were provided with an additional scatter feed daily, which was observed to reduce aggression (Angst, 1980, reported in de Waal, 1989). In the present study, the number of feeds/day was positively correlated with troop size, indicating that larger Sulawesi macaque troops get fed more frequently. Therefore, high levels of social behaviour may be a consequence of larger troop size rather than an increase in the number of feeds/day, which could be coincidental or as suggested by the observations at Basel Zoo, a measure undertaken to alleviate tension in larger troops. The influence of troop size on behaviour is considered in section 4.3.2.

These two hypotheses are similar in that the proximate effects upon behaviour, but the first considers feeding to be stressful and the second contends that feeding relieves stress. Certainly the style of food presentation, as discrete clumps or evenly distributed patches, would affect competition and the ability of high ranking individuals to dominate the food resource (Gore, 1993). However, to fully appreciate the effects of feeds/day, an experiment would need to be carried out where the troop size was held constant and the effects of changes in feeds/day alone were monitored (section 4.2).

3.3.2 Troop Size

Benefits attributed to group living in primates are balanced by the constraints that it also imposes, including increased competition between individuals and agonistic behaviour (Dunbar, 1988). Increased vigilance, improved protection from predators and enhanced foraging efficiency has also been proposed as benefits of group living in mammals (MacDonald, 1984; van Shaik & van Noordwijk, 1985; Scheel, 1993). However, it has been suggested that increased foraging efficiency is less applicable to primates than other mammal species (Dunbar, 1988). Many of the selection pressures that shape wild primate troop size do not exist in captivity and the size of captive primate troops is largely determined by the captive management regime, which aims to provide ample resources relative to troop size. In captive situations where these conditions are met, troop size should not be expected to influence the activity budget of Sulawesi macaques, as competition should be minimal, ample space should be provided to suit the troop size *etcetera*. However, troop size influenced more of the behaviours in the captive Sulawesi macaque activity budget than any other environmental factor. Troop size was incorporated into the multiple regression models that significantly predicted social, moving, resting and feeding behaviour. Troop size was not the greatest influence on any of the behaviours, but did account for about 4% of the time spent social, 3% of moving, 5% of resting and 8% of feeding (Table 3.2.1, 3.2.2, 3.2.3 and 3.2.5). This may reveal that the conditions provided in the captive environment do not provide ample resources for the troop, or that there are behavioural implications of troop size regardless of the resources available.

A study by Caine & Marra (1988) revealed that as social groups become larger, there is a greater need to co-ordinate individual behaviours to reduce aggression and promote affiliation. However, the results of the multiple regression analyses in this present study suggested that as Sulawesi macaque troop size increased, the time spent in social behaviour declined. These results also indicated that troop size was positively correlated to enclosure size and feeds/day, which suggests that a rise in social behaviour may have resulted from increases in enclosure size or feeds/day, rather than a consequence of troop size (Table 3.3.1). The frequency of social behaviour recorded for wild troops of Sulawesi macaque also decreased as troop size rose, which could have been a consequence of troop size, but could be the result of a corresponding increase in home range as troop sizes rose (O'Brien & Kinnaird, 1997). The increase in home range enabled additional food to be found, which was essential to feed the extra macaques and may be linked to the decrease in social behaviour observed in captive macaques when larger enclosures or more feed/day were provided.

Extensive investigations into the effects of crowding (the inter-relationship between troop size and enclosure size) have shown that troop size influences behaviour more than the area/individual (Chamove, 1989). It has been suggested that as quarters become more confined, there is an increased risk of aggression (de Waal, 1989). In small enclosures, primates have little control over their proximity to neighbours and are prevented from dispersing. De Waal (1989) predicted that as the risk of aggression rose, so to would the level of social behaviour. This prediction was supported by a study, which revealed that chimpanzees (*Pan troglodytes*) in smaller areas would express elevated levels of social grooming and submissive greeting behaviours, compared to when they were housed in larger enclosures (Nieuwenhuijsen & de Waal, 1982). The results in this study, in which Sulawesi macaques in smaller enclosures express elevated levels of social behaviour, further supports de Waal's theory (1989). Some primate social systems may not include sufficient placatory behaviours, to alleviate the increased risk of aggression resulting from smaller enclosure sizes. The social behaviour of gorillas is considered to lack the effusive placatory behaviours exhibited by other primate species like macaques, and so it has been suggested that subtle eye contact may serve to reduce social tension (Yamagiwa, 1987). In the absence of placatory behaviours when there is a close proximity between individuals, the rate of aggression would be expected to rise. In a study by Hoff *et al*. (1997) lowland gorillas were observed in two enclosure areas that differed in size and complexity: one was large and complex, while the other was small and less complex. The level of aggression recorded increased when the gorillas were maintained in the smaller of two enclosure areas, which Hoff *et al*. (1997) considered a demonstration that enclosure complexity was a greater determinant on social behaviour than crowding. This is a confusing conclusion, as the increased level of aggression was also a consequence of crowding, as the gorillas were in closer proximity in the smaller enclosure. Due to the experimental design it is not possible to attribute the elevation in aggression to either crowding (enclosure size) or enclosure complexity alone, but as a result of them both.

The results of the multiple regression analyses revealed that troop size influenced the time captive Sulawesi macaques spent feeding and foraging, as larger troops foraged for longer periods, but fed less than smaller troop sizes (Table 3.3.4 and 3.3.5). It seems sensible that in the presence of food (after provisioning) macaques will eat and in the absence of food macaques will forage, so an inverse relationship between the two behaviours would be expected to match food availability. In the wild, troop size has been shown to vary according to food distribution and abundance (Clutton-Brock & Harvey, 1977). Food availability in captivity is viewed as very different from the wild, as captive primates are provisioned and receive more food as their numbers increase, and therefore competition for food would not be expected. However, competition for food was observed in a captive troop of Sulawesi macaques, where the dominant individuals gained priority access to the food provided (Ettah, 1997). In captivity provisioned food is usually distributed in either a couple of clumps (food bowls), or patches in close proximity (scatter feeding). Both of these situations would allow the food to be monopolised by high-ranking individuals. As troop size increases the competition for food rises and macaques can be observed to eat (or store food in their food pouches) as quickly as possible, probably in an attempt gain food before the temporal source is depleted, or before conflict with dominant individuals ensues. In this study, vegetation present in the outside enclosures provided an unrestricted additional food source whose supply was not limited to the time of day provisioning occurred. This vegetation allowed animals to forage and possibly make up for a shortfall in nutritional content that may have resulted from competition for food during provisioning. Therefore, elevated competition for food experienced by macaques in larger troops could have lead to them foraging for longer. Alternatively, as enclosure size was positively related to troop size, a higher incidence of foraging in larger troops may have resulted from a greater availability of vegetation.

3.3.3 Enclosure size and complexity

Results from multiple regression analyses revealed that enclosure size significantly affected the time spent feeding, forging and moving. Enclosure size was positively related to the time spent foraging and moving, but negatively related the feeding (Table 3.2.2, 3.2.4 and 3.2.5). The influence of enclosure size on foraging behaviour was mentioned previously (section 3.3.2). It seems sensible that as the space available to captive macaques increases, a consequent elevation in moving behaviour would result and indeed the results in this study support this. Many studies have previously sought to investigate the effect of increasing space on primate behaviour but have failed to be conclusive, due to either confounding variables like social composition, novelty and/or troop size, or because the variation was too small (Erwin, 1979; Nash & Chilton, 1986). As discussed previously the effects of crowding on primate behaviour are far-reaching and a consequence of both troop and enclosure sizes (section 3.3.2).

It is interesting that the time spent feeding declined as enclosure size increased. However, this is possibly due to the methodology used to record behaviour, where feeding was the second to last in a hierarchy of behaviours to be noted. Therefore, if foraging and feeding occurred simultaneously, only foraging behaviour would be recorded and so the time spent feeding would be artificially reduced. As previously discussed, larger enclosures had a greater abundance of vegetation and therefore probably stimulated higher levels of foraging, and any feeding behaviour that occurred at this time would have been excluded, so a negative relationship between enclosure size and feeding may have resulted.

The importance of enclosure size in providing the opportunities for primate behavioural expression is keenly debated against the need to provide complex enclosures (de Waal, 1989). Special emphasis has been placed on the effects of enclosure size on laboratory-housed primates and especially those housed singly where space restrictions are greatest (Reinhardt & Reinhardt, 2000). Reinhardt *et al.* (1996) asserted that studies that investigate the influence of more or less 'barren' space on primate behaviour and welfare were worthless, as 'furnished' space is more important to primate species as they have adapted to live in a three-dimensional world. Chamove (1988) avoided debating whether enclosure space or complexity should be promoted, by suggesting that both physical and psychological space be provided, where 'psychological space' was a term coined to represent how captive primates perceived their environment and could be promoted through enclosure complexity. Chamove (1989) suggested that increasing the usable area of an enclosure would promote enclosure complexity as it increased psychological space. Such useable area could be interpreted as a measure of both enclosure complexity and enclosure size. In this study, useable area appeared to be more closely related to measurements of enclosure size than enclosure complexity and as such, it was considered to be a measure of enclosure size. The promotion of psychological space is associated with an increase in activity and reduction in resting behaviours (Chamove, 1989). Therefore the results revealed in this study were unexpected, though useable space was shown to be the greatest determinant of moving behaviour in captive Sulawesi macaques the relationship between the two factors was negative (Table 3.2.2).

The number of substrates present in the enclosures was used as a measurement of enclosure complexity. Results from the multiple regression analyses indicate that enclosure complexity significantly affects captive Sulawesi macaque behaviour. More interestingly, behaviour differs markedly between cases when the complexity exists as part of the inside enclosure compared to when it is part of the outside enclosure. This suggests that the function of different areas within the enclosure varies. Inside enclosure areas are sheltered and usually relatively small, so resting would be expected in this area, compared with the larger exposed outside area where there were greater opportunities for moving. Enclosure complexity was revealed to significantly affect foraging, moving and resting behaviour, and contributed most to the predictive models for resting and moving behaviour, accounting for almost 10% and 12% of the variation observed in each of these behaviours. The enclosure complexity inside reduced the time spent resting and increased foraging, while enclosure complexity outside reduced both moving and foraging.

These results suggest that complexity can be used either to increase or reduce moving according to the area supplemented with substrates. Exploration and interaction with the substrates inside may reduce the time spent resting and exploration and interaction with the outside substrates may reduce moving in the outside areas, as the macaques move smaller distances between objects rather than generally moving around their enclosure. It is not suggested that resting and moving behaviours are diametrically opposed, so despite a reduction in moving and foraging behaviours in complex outside areas, other active behaviours may be occurring for example, social or feeding behaviours.

In the predictive models for resting and moving behaviour, the number of substrates in and out demonstrated very low levels of intercorrelation with the other IVs in the model, as they both scored very high tolerance levels of 0.99 and 0.73. Therefore, the influence of the number of substrates on the expression of moving and resting behaviours, as discussed above, can be made with a high degree of confidence.

3.3.4 The use of bark as an inside flooring material

The results from the multiple-regression analyses indicate that the use of bark as an inside flooring material promoted the time spent feeding, while inhibiting foraging behaviour (Table 3.3.4 and 3.3.5). Bark accounted for 28% of the variation observed in feeding behaviour, and therefore contributed the most to its expression. The impact of the bark on feeding behaviour was expected, as previous studies have demonstrated that certain flooring materials can significantly affect primate behaviour (Anderson & Chamove, 1984; Lutz & Novak, 1995; Reinhardt & Roberts, 1997). These studies generally advocate using a deep litter system, where a thick layer of bark or a similar material is used to cover the inside flooring area and serves as a forage medium (McKenzie *et al.*, 1986; Ludes & Anderson, 1996). Flooring materials that have been associated with increased foraging and a concurrent reduction in behavioural pathologies have included straw, woodchips and wood-wool (Anderson & Chamove, 1984; Baker, 1997). The results of this present study conflict with previous work as they showed that foraging in the presence of bark significantly declined, whereas previous studies have shown foraging behaviour to increase with deep litter systems e.g. bark. The data from some of these studies do not reflect the desirability of the substrate alone, as some provision the litter with small amounts of nuts, seeds or biscuits, which undoubtedly results in increased foraging behaviour (Reinhardt & Roberts, 1997). Britt (1993) carried out an investigation into the influence of flooring material on feeding and foraging behaviour in captive Sulawesi macaques, but unfortunately conflicting variables led to ambiguous results. As the results from the multiple-regression analyses suggest that there is a link between flooring substrate and the time spent feeding and foraging, two further experiments were conducted to investigate captive Sulawesi macaques' preferences for flooring materials and their consequential effect on activity budgets (Chapter 4).

3.3.5 24 hr access between inside and outside areas of the enclosure

Captive management routines include numerous factors that are frequently variable between zoos therefore the influence of many of these factors on behaviour have not been identified or studied. The access provided between inside and outside areas of the enclosure is one such variable. Of the seven zoos visited in this study, the access between enclosure areas varied from: 24 hr access, with concurrent access to both areas; semi-restricted access, with concurrent access to both areas during the day and then locked in at night; and finally restricted access, where macaques were either locked in or locked out and had virtually no concurrent access. The results from the multiple regression analyses indicated that providing 24 hr concurrent access between inside and outside areas was associated with a reduction in the time spent in social behaviours (Table 3.2.1). Twenty four hour access accounts for 2% of the variation observed in social behaviour and does not significantly contribute to the predictive model for social behaviour ($\beta = -0.19$; Table 4.2.1). Therefore the statistical influence of access on social behaviour appears to be very small. Practically, providing access between enclosure areas increases the space available in which macaques can distribute themselves and therefore could alleviate social tension related to crowding and the pressures that ensue when the proximity between individuals decreases (discussed in section 3.3.2).

3.4 SUMMARY OF RESULTS

Multiple-regression analyses proved to be a successful method of identifying captive environmental factors that affected Sulawesi macaque behaviour. All aspects of the physical housing and husbandry routine were found to affect the behaviour of captive Sulawesi crested black macaques significantly. In all the predictive models, with the exception of moving behaviour, one environmental variable accounted for the majority of the variation observed and was responsible for over 58% of the coefficient of determination. In the case of moving behaviour, enclosure size (sr_i^2 = 0.12) and complexity (sr_i^2 = 0.125) were equally influential. Environmental variables that contributed most to the predictive models were measurements of enclosure size (inside useable area, area per individual), enclosure complexity (number of substrates in and out), inside flooring material (bark) and husbandry (number of feeds/day). Troop size influenced most of the behaviours and was incorporated into four of the five predictive models for behaviour, relating negatively to social and moving behaviours and positively to resting and feeding behaviours.

Due to the intercorrelation between the environmental variables, the relationships between them and behaviour frequently overlapped. As many zoos now aim to supply naturalistic enclosures the overlap between environmental variables and their effects on behaviour were inevitable. This did restrict the interpretation of how individual environmental variables affected behaviour. However, it provided a systematic basis on which further hypotheses could be formulated and tested by further experiments.

The results of the predictive models demonstrate that current captive management routines vary between zoos and have significant implications for captive Sulawesi macaque behaviour. The next chapter in this thesis is dedicated to testing the following hypotheses:

4.1) Using bark as an inside flooring substrate significantly increases feeding behaviour, while significantly reducing foraging behaviour.

4.2) As the number of feeds per day increases so does the time spent in social behaviour, while the incidence of resting behaviour declines.

4.3) An increase in useable area (in the inside area of the enclosure) lead to an expected rise in the time spent moving.

4.4) Social and moving behaviours are expected to increase and feeding and resting behaviours decline if troop size is reduced.

Chapter 4

ENVIRONMENTAL MODIFICATIONS

4.1 FLOORING MATERIAL

Many zoos use inside flooring materials as part of their captive management regime, primarily to ease cleaning and provide bedding. Research on laboratory-housed primates has found that these flooring materials, and notably deep litter systems also provide additional complexity to the environment and stimulation for the animals housed there (Chamove & Anderson, 1979; Chamove *et al.*, 1982). On the basis of these findings, further research was initiated to explore whether laboratory-housed primates had preferences for different flooring materials (Ludes-Fraulob & Anderson, 1999). There are differences between laboratory conditions and zoo enclosures provided for primates: the latter are usually larger, more complex and provide access to outside areas and a diversity of substrates. Therefore we should not expect inside flooring materials at zoos to have the same impact as when they are used in laboratories.

The results of the multiple-regression analyses, predicted that the use of bark as an inside flooring material would lead to significant increases in the time spent feeding and a significant reduction in the time spent foraging. To investigate whether the current flooring materials used by zoos influence the behaviour of Sulawesi crested black macaques, two studies were carried out which established whether daily activity budgets were significantly affected by different flooring materials, and then the use of each flooring material was compared when they were provided simultaneously.

4.1.1 Effect of different flooring materials on activity budgets

Bark (woodchip), straw and sawdust (wood shavings) were frequently used as inside flooring materials in the zoos visited in this project, though some zoos did not provide any flooring material. At Paignton Zoo, a light scattering of straw was normally used as a flooring material, but to explore the effect of using different inside flooring materials on the activity budget of captive Sulawesi macaques, bark, sawdust and no flooring material (nothing) were incorporated into the captive management regime.

4.1.1.a Methodology

The macaques at Paignton Zoo were exposed to four treatments, each for eight consecutive days. Two days were left between treatments, during which the usual management of the macaques recommenced, so a couple of sections of straw (each section approximately 450 mm x 300 mm x 150 mm) were provided for flooring. The treatments were bark, straw (barley), sawdust and nothing used as inside flooring materials. Enough flooring material was used to cover the floor completely; bark was provided at a depth of about 100 mm, several sections of straw were loosely scattered; and an even covering of sawdust was provided. The enclosure was cleaned daily as per routine, with the exception that bark remained unchanged throughout the 8 day trial as bark is usually left unchanged for long periods in zoos.

Behaviour, location and substrate use were recorded daily for each of the macaques in the troop (N = 7), using instantaneous scan sampling every 30 min between 8am-4pm as described in section 2.1.1.b.

4.1.1.b Statistical analyses

Data collected on the first day of each treatment were excluded from analyses, to control for any temporary and immediate changes in behaviour caused by the novelty of the treatments. Consequently, 7 days of behavioural observations were used in the statistical analyses. Activity budgets were generated from the behavioural data for each treatment; the mean percentage time spent performing each of the behaviours was calculated from the mean daily totals of behaviour for each individual, which were divided by 16 (number of scans/day) and multiplied by 100.

As the data met the requirements necessary for parametric statistical analyses, a doubly repeated measures ANOVA was performed to compare the mean percentage time spent performing each of the behaviours, between treatments. Repeated measures ANOVA requires that the assumption of sphericity is met, which can be tested for using the SPSS Mauchly's Test of Sphericity (SPSS, 1999c). With the exception of moving behaviour, this assumption was met by the behavioural data recorded. In the case of moving behaviour adjustments were made to the numerator and denominator degrees of freedom, used in the determination of the significance level (SPSS, 1999a). Adjustments were made using the Huynh-Feldt Epsilon, as it is sensitive to small sample sizes (SPSS, 1999c). Post-hoc multiple pair-wise comparisons were carried out and the significance levels adjusted for the multiple comparisons made, using Bonferroni adjustments (SPSS, 1999b).

4.1.1.c Results

As illustrated in figure 4.1.1, the inside flooring material had a significant effect on captive Sulawesi macaque behaviour and the amount of time spent inside (Wilk's $\lambda = 0.01$, df = 21, $p < 0.001$). Univariate tests revealed that the time spent moving and inside were both significantly affected by inside flooring material (moving, F = 9.5, df = 2.5, $p = 0.001$; inside, F = 94.0, df = 3, $p < 0.001$). Results from post-hoc analyses reported in table 4.1.1, reveal that moving was significantly greater when sawdust was present on the floor, rather than bark. When nothing was provided on the floor moving was also higher than on bark, though the relationship was not quite significant ($p = 0.075$). The macaques spent significantly more time inside when bark was used as an inside flooring material, followed by straw, then sawdust and finally when nothing was provided as an inside flooring material the macaques spent the least time inside.

Figure 4.1.1 Mean ± SE percentage time spent inside and performing behaviours by the Sulawesi macaques at Paignton Zoo when provided with different flooring materials (N = 7).

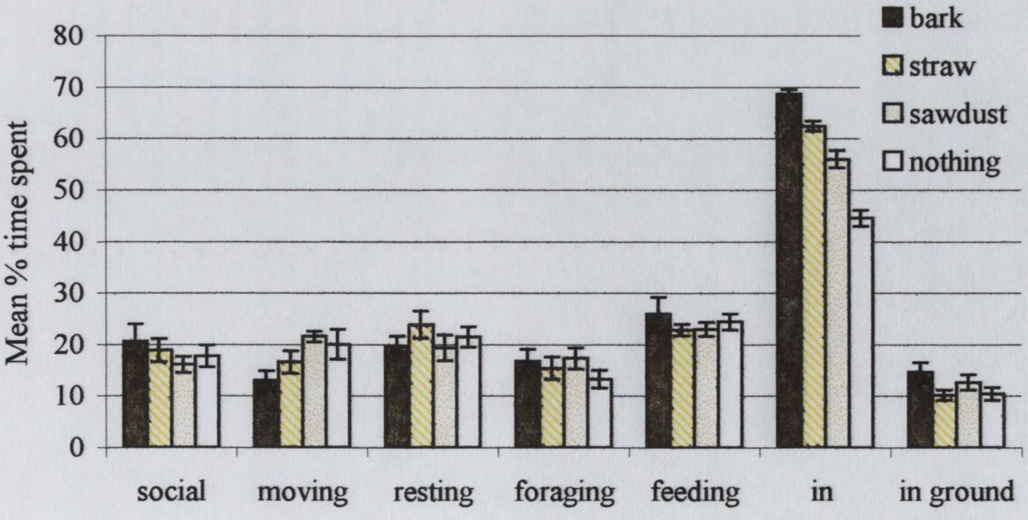


Table 4.1.1. Post-hoc analyses results revealing the significant relationships between the mean percentage time spent performing behaviour and inside, and flooring material.

Behaviour	Paired comparisons (flooring material)		Mean Difference
Moving	Bark	Sawdust	-8.5**
		Nothing	-6.95 $^{(p = 0.075)}$
In	Bark	Straw	6.25*
		Sawdust	12.63***
		Noting	24.12***
	Straw	Sawdust	6.38*
		Nothing	17.87**
	Sawdust	Nothing	11.5**

**p<0.05, **p<0.01, ***p<0.001

4.1.2 Preference test

The previous study (section 5.1.1) revealed that the time spent inside by Sulawesi macaques at Paignton Zoo differed significantly according to the type of inside flooring material used, suggesting a preference for interaction with one type of flooring material over another. To establish the existence of this preference, the following study was set up to quantify how long the macaques would interact with each flooring material when they were provided simultaneously.

4.1.2.a Methodology

Four flooring materials (bark, straw, sawdust and nothing) were presented to the macaques simultaneously, so they occupied the corners of the inside enclosure with a gap of about 100 mm separating them. The position of each flooring material was rotated daily to ensure that it occupied different corners within the enclosure and that its neighbouring materials were also rotated (Table 4.1.2). Bark remained in the same corner for 6 days, while other flooring materials were rotated around it. Bark was exempt from daily rotations, in an attempt to simulate its usual management in zoos which is, that is it left unchanged for long periods unlike the daily removal and replenishment of other flooring materials. To observe the macaques' reactions to bark in each of the corners, and the accompanying rotation of other flooring material around it, observations were made for 24 days.

Behavioural observations were made using one-zero scan sampling (see below) (Martin & Bateson 1996). Behavioural observations were conducted in the first two hours after the enclosure was cleaned and the flooring materials were presented to the macaques (novel, 1200-0100 hr) and about 20 hrs later in the final two hours before the enclosure was cleaned and the flooring materials were replenished (long-term, 0800-0900 hr). Observations of each macaque in the troop (N = 7) were restricted to when they came to the ground, when the flooring material the macaque came into contact with and their behaviour was noted every 60 sec (60 scans/hr). The behaviours recorded were limited to feeding, foraging, feeding/foraging (when performed simultaneously) and object manipulation, as these were the only behaviours found to be significantly affected by inside flooring material (section 3.3.4) and were also most frequently performed by macaques when on the ground. In section 4.1.1 a significant relationship was revealed between the time spent moving and different flooring materials; however, the macaques routinely moved on each of the flooring materials during each scan and so it was thought that due to the limitations inherent in one-zero sampling (see below), a difference in the level of moving between flooring materials would not be detected.

The usefulness of data collected using one-zero sampling has been masked by assertions that it does not accurately represent behavioural frequencies or durations (Martin & Bateson, 1996). In one-zero sampling, behaviours are recorded if they have been observed in a sampling period, irrespective of how often they were performed in that period. In this study the macaques spent little time on the ground inside and so their interaction with the inside flooring materials was equally brief, though at times repetitive. Continuous sampling would have provided an ideal method of recording how an individual macaque behaved in the presence of several different flooring materials, however, data from each macaque in the troop was required. One-zero sampling was chosen as it ensured that behaviours of short duration were recorded and it could easily be adapted to enable scans of multiple individuals. Instantaneous scan sampling can also be used to record observations of several individuals, but runs the risk of missing short-lived behaviours between sampling points. Unfortunately, one-zero sampling does not provide real frequencies or durations, as the behaviour may be expressed more than once in a time period and only be recorded once. In addition, the performance of a behaviour expressed for 3 s and 40 s would be recorded as equal. To minimise these limitations, 'a short sampling interval relative to the average duration of the behaviour pattern' is recommended by Martin & Bateson (1996), as it brings the sampling approximations closer to those found if using instantaneous sampling. A short scan interval was therefore used.

Table 4.1.2 An illustration of how the flooring materials were rotated inside the Paignton Zoo enclosure (SD = Sawdust, N = No flooring material).

DAY	WEEK							
	1		2		3		4	
1	Bark	Straw	SD	Bark	N	SD	Straw	N
	SD	N	N	Straw	Straw	Bark	Bark	SD
2	Bark	N	N	Bark	Straw	SD	SD	N
	SD	Straw	Straw	SD	N	Bark	Bark	Straw
3	Bark	SD	Straw	Bark	N	Straw	N	SD
	Straw	N	SD	N	Bark	SD	Bark	Straw
4	Bark	Straw	SD	Bark	Straw	SD	Straw	N
	N	SD	Straw	N	Bark	N	SD	Bark
5	Bark	N	Straw	Bark	SD	Straw	SD	N
	Straw	SD	N	SD	Bark	N	Straw	Bark
6	Bark	SD	N	Bark	N	Straw	SD	Straw
	N	Straw	Straw	SD	Bark	SD	N	Bark

4.1.2.b Statistical analyses

As data were recorded using one-zero scan sampling, non-parametric statistical analyses were used. G-tests calculate whether the observed frequencies differ significantly from those expected, using the natural logarithm in the calculation of the expected values

(Fowler & Cohen, 1990). The total observations recorded for each individual on each flooring material were pooled and averaged by sex-age class (adult female = 3, big juveniles = 2 and small juveniles = 2). These means and their corresponding standard errors (Figure 4.1.3) revealed that the behaviour of the sex-age classes overlapped considerably and therefore these data were considered to be from the same population and so pooled for further analyses. G-tests were employed to compare the mean observations /hour for each behaviour on each flooring material and thus the effect of flooring material over time was obtained. Repeated measures Friedman tests were then undertaken to investigate if the mean observations recorded for each of the behaviours were significantly different between flooring materials or over time. Table 4.1.3 and 4.1.4 present the results of the non-parametric post-hoc multiple pair-wise comparisons carried out by substrate and by hour, using the mean rank calculated in the Friedman tests.

4.1.2.c Results

The difference in response to flooring materials by different sex-age classes was analysed visually and considered to be negligible as the standard error bars for the mean observations recorded for each of the sex-age categories overlapped substantially (Figure 4.1.2). There was a significant difference in the total behavioural observations recorded between flooring materials and over time (Figure 4.1.2 and 4.1.3) (G = 287505.0, df = 9, critical value = 27.9, $p < 0.001$). Flooring material and the amount of time it had been present in the enclosure significantly affected foraging, feeding, feeding/foraging and object manipulation (df = 9, critical value = 27.9, $p < 0.001$, G values for foraging = 8416.04; feeding = 6032.24; feeding/foraging = 19092.98; object manipulation = 1100.48). Significantly more behavioural observations occurred on straw and were highest in the first hour that the material was made available to the macaques (Figure 4.1.2). Results of the post-hoc multiple pair-wise comparisons (Table 4.1.3 and 4.1.4) revealed that the levels of total behavioural observations, foraging and feeding were similar in the first couple of hours for sawdust and nothing, and in the last couple of hours for bark and sawdust, and bark and nothing. Levels of feeding/foraging were similar on bark, sawdust and nothing for all hours except the first. Object manipulation was observed at higher frequencies on bark compared to the other flooring materials, however, these differences were not significant. There was a significant increase in the use of nothing and sawdust in hours 18 and 19, when behavioural observations were greatly increased.

Figure 4.1.2 Mean ± SE number of observations recorded for different sex-age class categorises of Sulawesi macaques, when provided with various flooring materials at Paignton Zoo (adult female = 3, big juvenile = 2 and small juvenile =2).

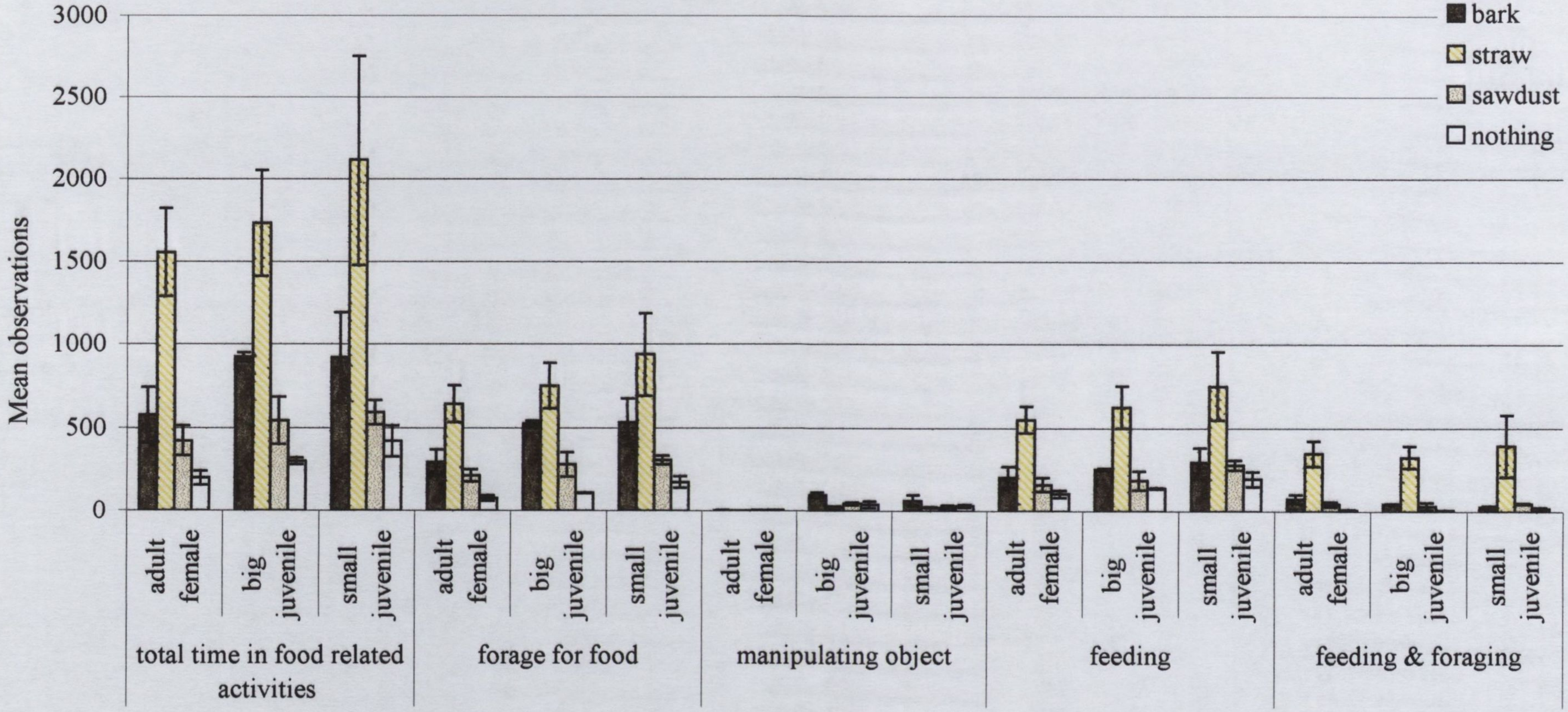


Figure 4.1.3 Mean ± SE behavioural observations of Sulawesi macaques at Paignton Zoo (N = 7), when provided with various flooring materials and how this behaviour changes over time (novel, hrs 1 & 2; long-term, hrs 18 & 19).

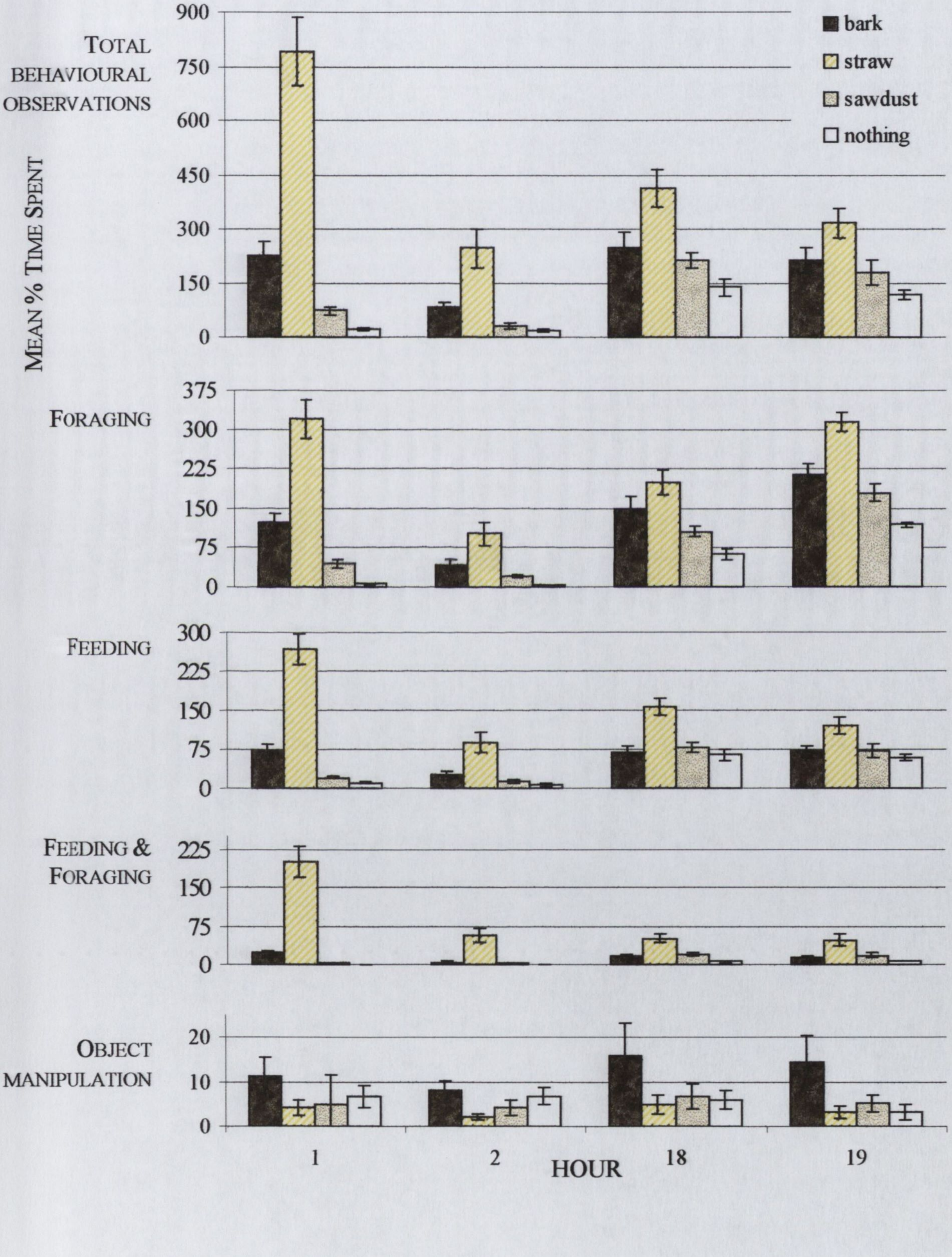


Table 4.1.3 Non-parametric repeated measures Friedman test results, which investigated how Sulawesi macaque behaviour varied between different flooring materials and over time (N = 7, df = 3).

Friedman results	Substrate χ^2				Hour χ^2			
Behaviour	Bark	Straw	Sawdust	Nothing	1 (1200)	2 (0100)	3 (0800)	4 (0900)
Total observations	11.86**	15.34**	17.9***	18.26***	21***	21***	17.4***	11.74**
Foraging	11.48**	18.26***	17.9***	19***	21***	21***	17.61***	12.6**
Feed	11.86**	16.2***	18.3***	18.26***	19.97***	19.97***	13.1**	10.03*
Feed/forage	15.4**	13.29**	13.5**	18.47***	20.74***	18.3***	12.77**	11.06*
Object manipulation	1.1	2.08	3.16	10.62*	6.27	9.34*	2.7	9.56*

*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$

Table 4.1.4 Post-hoc analyses results for the comparisons between the mean observations recorded on each flooring material over time (N = 7, 7; critical value = 11.6). Blue denotes significant differences.

Behaviour	Pair-wise comparisons (hour)		Mean difference (flooring material)			
			Bark	Straw	Sawdust	Nothing
Total Behavioural observations	1	2	144.29	546	41.29	6.43 ns
		3	20	379.28	138.84	115.43
		4	11.43 ns	476.14	107.14	94.43
	2	3	164.29	166.72	180.13	121.86
		4	132.86	69.86	148.43	100.86
	3	4	31.43	96.86	31.7	21
Foraging	1	2	80.14	220.42	23.14	1.85 ns
		3	26	121	60.86	56.86
		4	93	4.71 ns	135.43	112.43
	2	3	106.14	99.42	84.86	58.71
		4	173.14	215.71	159.43	114.28
	3	4	67	116.29	74.57	55.57
Feeding	1	2	43.88	179.58	8.28 ns	4.86 ns
		3	4.14 ns	110.73	57.43	52.85
		4	0.57 ns	146.86	50.29	46.42
	2	3	39.71	68.75	65.71	57.71
		4	43.28	32.72	59	51.28
	3	4	3.57 ns	36.13	7.14 ns	6.43 ns
Foraging/ feeding	1	2	16.86	144	0.28 ns	0.14 ns
		3	6.29 ns	148.43	19	6.57 ns
		4	9 ns	151.71	15.86	6.86 ns
	2	3	10.57 ns	4.43 ns	19.28	6.43 ns
		4	7.86	7.71 ns	16.14	6.72
	3	4	2.71 ns	3.28 ns	3.14 ns	0.29 ns
Object manipulation	1	2	3.43 ns	2 ns	0.71 ns	0.15 ns
		3	4.43 ns	0.86 ns	1.57 ns	0.85 ns
		4	2.86 ns	1 ns	0.14 ns	3.57 ns
	2	3	7.86 ns	2.86 ns	2.28 ns	1 ns
		4	6.29 ns	1 ns	0.85 ns	3.72 ns
	3	4	1.57 ns	1.86 ns	1.43 ns	2.72 ns

Table 4.1.5 Post-hoc analyses results of the comparison between the mean observations, recorded each hour, on the different flooring materials (N = 7, 7; critical value = 11.6). Blue denotes significant differences.

Behaviour	Pair-wise comparisons (flooring material)		Mean difference (hour)			
			1	2	18	19
Total Behavioural observations	Bark	Straw	556.14	164.43	166.86	101.43
		Sawdust	153.57	50.57	34.73	35
		Nothing	202.86	65	107.43	97
	Straw	Sawdust	719.71	215	201.59	136.43
		Nothing	769	229.43	274.29	198.43
	Sawdust	Nothing	49.29	14.43	73	62
Foraging	Bark	Straw	199.14	58.86	52.14	101.43
		Sawdust	77.43	21.29	42.57	35
		Nothing	116.43	38.14	85.57	97
	Straw	Sawdust	276.57	80.15	94.71	136.43
		Nothing	315.57	97	137.71	198.43
	Sawdust	Nothing	39	16.85	43	62
Feeding	Bark	Straw	196.15	60.42	89.56	49.86
		Sawdust	50	14.43	11.57 ns	0.86 ns
		Nothing	60.12	20.86	2.86 ns	12.86
	Straw	Sawdust	246.15	74.85	77.99	49
		Nothing	256	81.28	92.42	62.72
	Sawdust	Nothing	9.85 ns	6.43 ns	14.43	13.72
Foraging/feeding	Bark	Straw	178.14	51	36	35.43
		Sawdust	19.72	3.14 ns	5.57 ns	5.14 ns
		Nothing	21.86	4.86 ns	9 ns	6 ns
	Straw	Sawdust	197.86	54.14	30.43	30.29
		Nothing	200	55.86	45	41.43
	Sawdust	Nothing	2.14 ns	1.72 ns	14.57	11.14 ns
Object manipulation	Bark	Straw	7.29 ns	5.86 ns	10.86 ns	11.15 ns
		Sawdust	6.43 ns	3.71 ns	9.29 ns	9.15 ns
		Nothing	4.72 ns	1.14 ns	10 ns	11.15 ns
	Straw	Sawdust	0.86 ns	2.15 ns	1.57 ns	2 ns
		Nothing	2.57 ns	4.72 ns	0.86 ns	0 ns
	Sawdust	Nothing	1.71 ns	2.57 ns	0.71 ns	2 ns

4.1.3 Discussion

The use of different inside flooring materials clearly affects the behaviour of captive Sulawesi macaques. The time spent moving was significantly higher when sawdust was provided as an inside flooring material compared to bark and straw. There are two possible mechanisms that may explain these differences. First, the macaques may move less on flooring materials they found to be more interesting, as they would spend more time in concentrated interaction with them; for example, foraging for edible items or manipulating parts of the flooring material. According to this explanation of flooring material use, we would suggest that the macaques were most interested in bark, as they moved at significantly lower levels on bark than any other flooring material provided. Secondly, it is possible that some flooring materials enhanced moving. When no flooring material or sawdust was provided, the macaques were observed to slide 'enthusiastically' and easily over the floor, which appeared to be incorporated into their play behaviours.

The time spent inside also differed significantly between flooring materials. Macaques spent significantly more time inside when bark was present compared to straw, sawdust and nothing. Strangely, this pattern of behaviour was not duplicated in the time spent inside on the ground, which would be expected if the time spent inside was determined by a preference for one of the flooring materials. The disparity between these observations could be a product of the methodology used to record behaviour, as it was limited to observations every 30 min. An observation interval of 30 min is adequate to record broad state behaviours, but is likely to miss or underestimate brief events (Martin & Bateson, 1996; Melfi, 1997). The macaques predominately used a frame and other 'off-ground' apparatus when they were inside, suggesting a preference to be 'off-ground' (see section 2.4). As the periods spent on the ground were brief, observations taken every 30 min may have missed and/or underrepresented the use of different flooring materials by the macaques. The time spent inside corresponded very well with changes in the flooring material, which suggests that their level of interest in the different flooring materials determined how frequently they used them.

To assess whether the time spent inside was a reflection of their preference for bark over other flooring materials, the different flooring materials (bark, straw, sawdust and nothing) were presented simultaneously and the macaques' behavioural response was recorded. These observations revealed that the macaques interacted with straw significantly more than the other flooring materials, suggesting that when alternatives were available macaques preferred straw. On the basis of the previous study, it was expected that macaques would interact most with bark, then straw, sawdust and finally the area with no flooring material, and thereby reveal that macaques prefer bark as an inside flooring material. During this experiment it was noted that the straw quality was especially good with a lot of ears of corn (barley) present which the macaques ate. The level of foodstuffs available in the other flooring materials was low, though bark harboured some insects and left over food from previous days, whereas no foodstuffs were available in the sawdust or the area left vacant (nothing). The bias observed for the straw in feeding, foraging and feeding/foraging behaviour is therefore not unexpected and probably reflects the disproportionate abundance of foodstuffs present in the flooring material. Previous studies designed to investigate how primates use different flooring materials, have scattered food (raisins or seeds) on the flooring material prior to behavioural observations, to promote interactions with the flooring material (Anderson & Chamove, 1984; Ludes & Anderson, 1996). Another quality of the flooring material that appears to affect behaviour is the abundance of objects, which the macaques perceive suitable for manipulation. Although observed incidences of object manipulation were very low, they were higher on bark than any other flooring material. Although the difference was not quite significant, due to a low number of observations, it does suggest that bark was preferred for object manipulation.

Interactions with the flooring materials changed significantly over time. In the first hour after cleaning, when the flooring materials had been replenished or renewed, behavioural observations reached a peak, which dramatically declined in the second hour. The decline in behavioural observations could reflect the exhaustion of foodstuffs present in the flooring material, satiation from eating in the first hour, or a lapse in the macaques' attention span which resulted in them leaving the inside flooring area. The macaques' attention could have been piqued by the activities of other macaques outside, the public, or other substrates and materials within their enclosure. It is unlikely that the foodstuffs in the flooring materials were all consumed in the first hour, as 18 hours later (0800, hr 18) observations revealed that feeding levels were still significantly higher on straw. This suggests that some aspect of the straw was still more appealing than the other flooring materials, and that ears of corn were still probably present in the straw and were not depleted in the first hour. It is possible that the macaques were satiated temporarily and moved on to other areas of the enclosure, however, the motivation to feed six hours later was enough, that the macaques could be enticed inside with food, which was consistent with their husbandry routine. The behaviour of the macaques could also reflect an immediate interest in the new flooring materials, which was surpassed by more interesting events in time e.g. by end of the first hour.

Resurgence in the behavioural observations occurred between 0800 and 1000 hr (hours 18 and 19). The macaques had been locked inside all night and were probably highly motivated to find food, as it was morning. Food provided the previous day was distributed evenly throughout the inside enclosure to entice the macaques in, whereupon they were locked in over night. Food left over from the previous day's feed led to exaggerated behavioural observations from 0800 – 1000 hr, however as the food was evenly distributed throughout the enclosure there was an expectation that the behavioural observations would be similar for the different flooring materials. Observations recorded where no flooring material was provided (nothing), served as a control providing an indication of the level of behaviours expected as a result of the leftover food alone. Using this control it appears that with the exception of object manipulation, behavioural observations recorded remained highest on straw, though there was little difference in the observations of foraging on straw and bark.

The interpretation of these results are limited to evaluating which flooring materials are used during feeding and foraging behaviours, but as these behaviours predominated on the ground it seems sensible to consider straw a preferred inside flooring material for captive Sulawesi macaques. As the macaques do not build nests from the flooring material, its only other function would be to provide objects for manipulation, which was achieved using bark. The quality and quantity of the flooring material given to the macaques will almost certainly influence how much time the macaques spend using it. More straw was provided in this study to the macaques, than would be usual for most captive management routines, which may be responsible for the extreme difference in behaviours observed on the flooring materials. In general husbandry routines, with the exception of bark, flooring materials are usually provided at such low densities that they receive little or no attention from the macaques. Finally, the preference displayed for straw relative to the alternative flooring materials, does not suggest that straw, even in large quantities, is the best flooring material, but that of the currently used materials straw may provide the greatest foodstuffs and therefore receive most attention. The information available from preference testing is limited by the number of alternative materials presented and in this study many flooring materials were not tested which have been used in studies with laboratory housed primates, for example, wood wool and peat (Fraser & Matthews, 1997).

4.2 FEEDING REGIME

Sulawesi macaques in the UK and Ireland are fed between one and five feeds per day. Many believe that primates in zoos rest too much and move too little, therefore any action taken to promote activity is considered beneficial (Morris, 1964; Chamove, 1988). Intuitively, some believe that giving primates frequent small feeds throughout the day leads to increased activity. Although no quantitative studies support this belief, the results of the multiple-regression analysis in section 3.3.1, predicted that social behaviour would rise and resting behaviour decline, if the number of feeds/day were increased. To explore this issue more fully, the number of feeds/day was manipulated at Dublin Zoo, enabling a direct quantification of the effects of feeding frequency on the activity budget of captive Sulawesi macaques.

4.2.1 Methodology

Feeding frequency was manipulated so that a troop of macaques received 1, 2, 3 or 4 feeds/day (4 treatments). The amount of food presented daily remained constant, by dividing the macaques' standard feed into appropriate portions. Each treatment was provided for ten consecutive days, with at least two days between treatments, in which the macaques were fed 1 to 2 feeds day, as was their usual routine.

Two methods of behavioural observations were employed; the first used instantaneous scan sampling (as described in section 2.1.1.b), between 8am – 4 pm daily. These data were used to construct activity budgets for each macaque in the troop for each feeding treatment (described in section 2.1.1.c; N = 8). The second method recorded behaviour and food intake immediately after food presentation, using instantaneous scan sampling every 3 min, of each individual in the group. The behaviours recorded are described in table 3.1.3. Allogrooming which was usually recorded as part of social behaviour was recorded separately and defined as slowly searching the hair or skin of another macaque with fingers or teeth whilst stationary and was recorded as present irrespective of whether attention was being given or received. Sampling ended after 30 min or until fewer than four macaques were feeding for three consecutive scans (9 min), whichever was longer.

4.2.2 Statistical analyses

To investigate how feeding frequency affected the daily activity budget of the macaques the following was undertaken: The mean percentage time spent performing behaviours was calculated from the behavioural data recorded from 8am – 4pm, as described in section 2.1.1.c. (number of scans = 16). The data met the requirements for parametric statistical analyses, with the exception of allogrooming and miscellaneous/not seen behaviours as they did not have normal distributions or homogenous variances and so were excluded from analyses. Doubly repeated measures ANOVA were used to compare the mean percentage time spent performing behaviours between feeding regimes (social, moving, resting, foraging and feeding). These data met the assumption of sphericity required for repeated measures analyses (SPSS, 1999a; see section 4.1.1.c).

Data collected every 3 min post-feeding were explored in two ways; 1) 'Group feeding' was defined as the time spent feeding by four or more macaques, which was considered to have ended when three or fewer macaques were left feeding. The time the group spent feeding was recorded from initial food presentation until the first of the three scan observations that recorded that three or fewer macaques were feeding. The mean time spent feeding by the group was calculated for each feed (number of feeds; N = 10) and treatment (feeding frequency; N = 4), by averaging the total observations for each feed and the total daily observations for each treatment (over the 10-day trial). The effect of feeding frequency on the time spent feeding by the group was explored using a two-way ANOVA, which compared the mean scores per feed and treatment. Post-hoc analyses with Bonferroni adjustments for multiple pair-wise comparisons were then carried out. 2) To explore the impact of feeding frequency on all observed behaviours, the following approach was adopted: the mean time spent performing behaviour immediately post-feeding (30 min) was calculated for each of the individuals per feed (10 feeds). The time spent performing each of the behaviours per treatment was calculated to provide information on the total behaviours recorded by day, a) by adding together the mean time spent performing the behaviour for each feed in that treatment/individual (mean daily time spent performing behaviour/individual); and to provide information on the mean time spent performing behaviour in 30 min, b) by averaging the mean time spent performing behaviour for each feed/individual per treatment for example, averaging feeds 1, 2 and 3 for treatment 3 feeds/day (mean time spent performing behaviour/30 min). This latter calculation of the time spent performing behaviour per treatment (b) controlled for the different number of observations recorded daily. A one-way ANOVA and Bonferroni post-hoc analyses was employed to establish if the time spent performing behaviours significantly differed between treatments.

4.2.3 Results

The time spent moving, resting, foraging and feeding observed every 30 min for 8hr/day, was not significantly affected by feeding frequency (Figure 4.2.1; df = 3, moving, F = 2.1, $p = 0.12$; resting, F = 0.96, $p = 0.43$; foraging, F = 0.75, $p = 0.5$; feeding, F = 1.3, $p = 0.3$). The time spent performing social behaviour was revealed to be significantly different between feeding regimes (F = 3.4, df = 3. $p = 0.04$); however, post-hoc pair-wise comparisons with Bonferroni adjustments for multiple comparisons did not indicate any pairs which were significantly different from each other.

Group feeding/feed was significantly affected by the frequency of provisioning (F = 4.1, df = 3, $p < 0.001$), as was group feeding/day (F = 13.1, df = 3, $p < 0.001$). The mean time spent feeding by the group of macaques was lower during each feed as feeding frequency increased, but the total time spent feeding per day increased with feeding frequency (Figure 4.2.2; post-hoc analyses results table 4.2.1).

Data collected in the 30min after food presentation revealed that the time spent feeding and resting were affected by feeding frequency (Figure 4.2.3 & 4.2.4). The mean daily time spent performing most of the behaviours increased with an increase of feeds/day, which was expected as the number of observations and therefore opportunities for recording each of the behaviours were greater as feeding frequency increased (1 feed/day = 10 observations, 4 feeds/day = 40 observations) (Figure 4.2.3). To correct for this, the mean time spent performing each of the behaviours/30 min was calculated and it too, was significantly different between treatments (df = 3, allogrooming, F = 4.4, $p = 0.01$; resting, F = 3.1, $p < 0.05$; feeding, F = 13.8, $p < 0.001$). Results from post-hoc analyses (Table 4.2.2) revealed that the macaques at Dublin Zoo performed allogrooming behaviours significantly less often when feed once a day compared to conditions when 2 or 4 feeds/day were provided. The mean time spent feeding/30 min was greater when fed once a day, compared to when three and four feeds/day were provided, feeding was also higher when two feeds/day were provided compared to four. The mean time spent resting was significantly greater when fed four times a day, compared to twice a day.

Figure 4.2.1 Mean ± SE daily observations of Sulawesi macaque behaviour at Dublin Zoo, in response to different feeding frequencies (1, 2, 3 and 4 feeds/day) (N = 8).

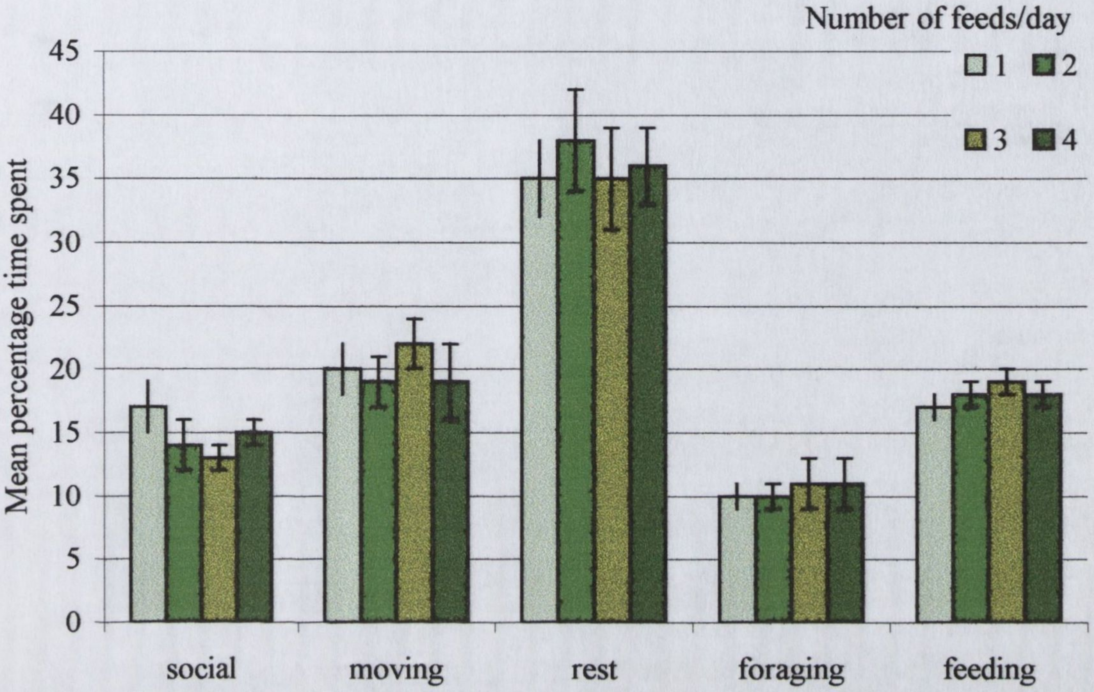


Figure 4.2.2 Mean ± SE time spent feeding as a group by the macaque troop at Dublin Zoo during 4 treatments (1, 2, 3 and 4 feeds/day) (N = 8).

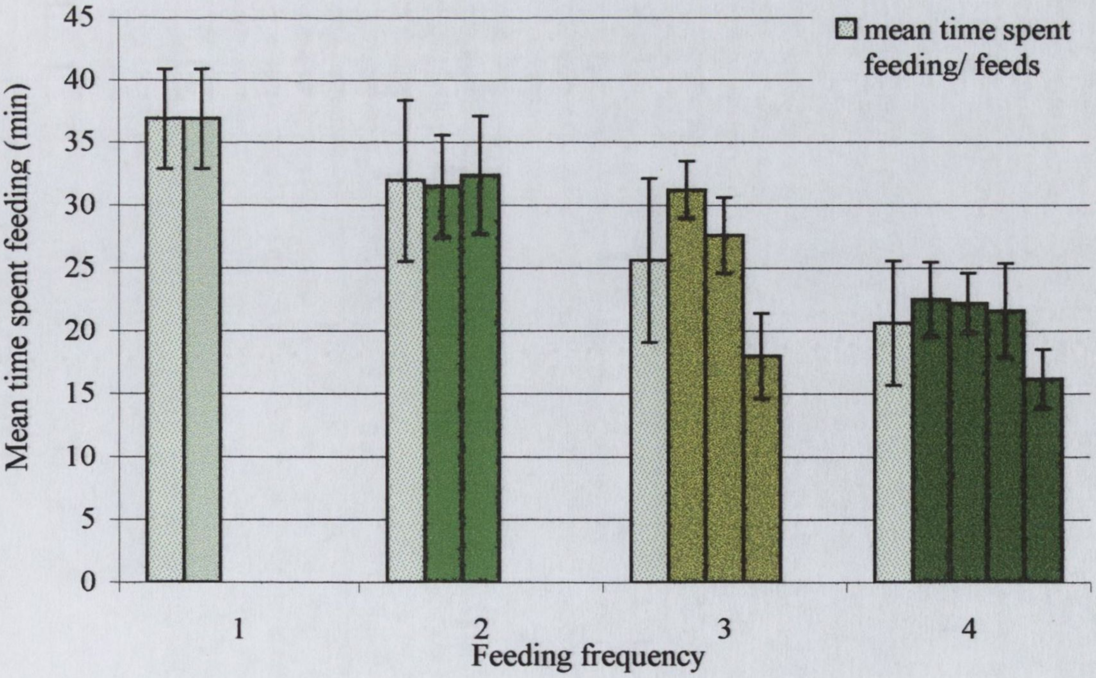


Figure 4.2.3 Mean ± SE total time spent performing behaviour in 30 min/day after provisioning, between feeding frequencies (1, 2, 3 and 4 feeds/day) (N = 8).

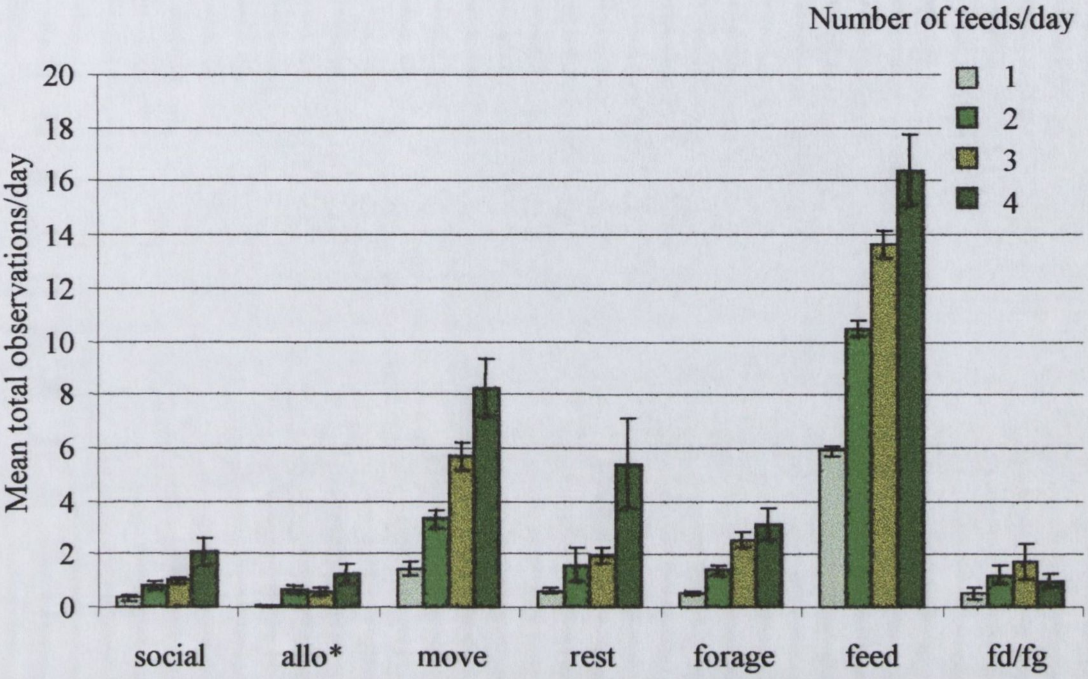
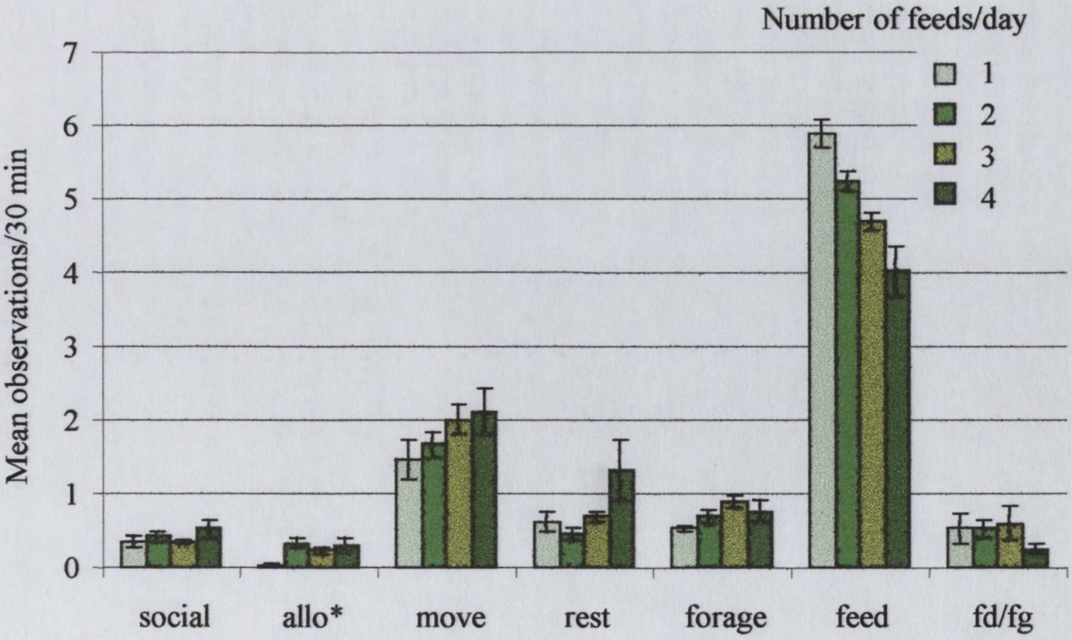


Figure 4.2.4 Mean ± SE time spent performing behaviour in 30 min after provisioning for each feeding regime (1, 2, 3 and 4 feeds/day) (N = 8).



*allo = allogrooming

fd/fg = feeding and foraging simultaneously

Table 4.2.1 Post-hoc analyses results of the significant relationships between group feeding time and feeding frequency, at Dublin Zoo (N = 8).

Pair-wise comparisons		Mean difference
Feed		
1	6	18.9**
	10	20.7**
3	10	16.2*
Treatment		
1	2	-27.0**
	3	-39.9***
	4	-45.2***2

*$p<0.05$, **$p<0.01$, ***$p<0.001$ value of significance.

Table 4.2.2 Post-hoc analyses results of the significant relationship between feeding frequency and the mean time spent performing the behaviours in the 30 min after provisioning, in a troop of Sulawesi macaques at Dublin Zoo (N = 8).

Pair-wise comparisons		Mean difference
Allogrooming		
1	2	-0.29*
	4	-0.27*
Resting		
2	4	-0.87*
Feeding		
1	3	1.21**
	4	1.88***
2	4	1.23**

*$p<0.05$, **$p<0.01$, ***$p<0.001$ value of significance.

4.2.4 Discussion

The use of small frequent meals as enrichment has not been previously studied. Multiple-regression analyses (MR) identified feeding frequency as a factor that positively affected the social behaviour of captive Sulawesi macaques and negatively affected resting behaviour (Chapter 3). The behavioural observations recorded in this study were collected and analysed in three ways through the exploration of: daily activity budgets which used the same data collection methodology as used in the MR; group feeding time, the time the group spent feeding together; and the behaviour observed in the thirty minutes immediately after provisioning. The results from these analyses indicated that social, resting and feeding behaviour were significantly affected by feeding frequency.

There were some discrepancies between the results of the MR and those obtained from the daily activity budget data. The MR results indicated that feeding frequency significantly affected social and resting behaviour, while the daily activity budget data recorded during this study revealed that only social behaviour differed significantly between feeding regimes. These discrepancies may have arisen because the MR included data from eight different zoos, whereas the feeding experiment was conducted at only one zoo. It is possible that the relationships identified in the MR between behaviour and feeding frequency varied between zoos, therefore if these relationships were not strongest at Dublin Zoo (the site of this study) then we might not expect the relationships to be significant. At Dublin Zoo there was an abundance of vegetation on the island that made up the macaques' outside enclosure area that supplied the macaques with an alternative food supply, which may have detracted from the influence feeding frequency had on the behaviour of the macaques. A further discrepancy occurred when the daily activity budgets were analysed. The results of the analysis of variance that compared behaviour between feeding regimes, found that social behaviour was significantly different between treatments, however, post-hoc pair-wise comparisons did not support this. The most likely explanation is that a type II error, the hasty rejection of the null hypothesis, occurred during the post-hoc analyses. When performing multiple comparisons, type II errors are more likely to occur (Siegal & Castallan, 1988). To reduce the likelihood of type II errors, a Bonferroni adjustment was made to the significance levels of the post-hoc results, which thereby increased the risk of a type I error occurring and the hasty acceptance of the null hypothesis (SPSS, 1999b). In this situation, the results of the ANOVA revealed that social behaviour was performed at significantly different levels between feeding frequencies and therefore the null hypothesis that social behaviour was equal between treatments should be rejected. In addition, data collected immediately after provisioning indicated that social behaviour did change significantly with feeding regime. In the light of these finding it would seem that the non-significant post-hoc analyses results were too strict.

Observations immediately after provisioning revealed that the daily time spent feeding increased with feeding frequency, but declined per feed. The amount of food did not vary with feeding frequency, so intuitively a reduction in the time spent feeding per feed would be expected as meal size becomes smaller with increased feeding frequency and so less time is required to eat the food provided. Despite a decrease in the time spent feeding/feed, the daily time spent feeding increased with feeding frequency, suggesting that in addition to the time required to eat the food presented, another factor is affecting how long the macaques feed for. At the end of each meal there was usually some food left, so it is not known how long the macaques took to eat all the provisioned food, beyond that observed during sampling. It is possible that when the food was presented more frequently in smaller portions, the macaques ate more of the food in the time observed, whereas when the food was presented in one large portion, more food was left over and eaten later when observations were finished. More extensive sampling or matched-control observations, so that irrespective of the feeding frequency four sampling periods a day were observed, could have made that relationship between the time spent feeding and feeding regime easier to decipher.

These observations also revealed that feeding regime was positively related to allogrooming (part of social behaviour) and negatively related to resting behaviour, which was compatible with the results of the MR (Table 3.2.3). In section 3.3.1, it was suggested that feeding could be stressful, so as feeding frequency increased so too would the level of stress. According to a coping mechanism suggested by de Waal (1989), the expression of social behaviour (primarily reassurance and calming gestures) increases with stress in an attempt to prevent aggression and maintain long-term social relations with con-specifics. The observations in this study do support this theory, as allogrooming was significantly lower during one feed/day relative to two and four feeds/day. The pattern of social behaviour elevation with feeding frequency was not consistent, as there was a fall in the level of social behaviour observed when the macaques were fed three times, relative to twice and four times a day. An alternative explanation for the change in social behaviour is that the activity budget is fixed, and that if one of the behaviours changes e.g. feeding, due to presentation of food, then another 'elastic' behaviour would need to change accordingly to compensate e.g. allogrooming and resting (Bubier, 1996). This second hypothesis is further supported by the observations that resting behaviour was significantly higher during the four feeds/day regime compared to when two feeds/day were presented, whereas the converse was true for feeding behaviour, which was significantly less during four feeds/day relative to two feeds/day. Similarly, there is a significant drop in allogrooming and significant increase in feeding behaviour when the macaques receive four rather than one feed/day. In this situation, the change in provisioning may alter the time spent feeding, which is compensated for by changes in resting and social behaviour. Another consideration that may affect the time spent feeding is enclosure complexity, especially in a situation where food is not scarce and so the decision to stop feeding is less likely to be based on energetic demands (Collier *et al.*, 1999). As the captive Sulawesi macaques in this study lived in a complex social environment with a guaranteed supply of food, it would seem likely that additional factors affected the time spent feeding.

The daily activity budget which was generated from observations taken every thirty minutes attempted to evaluate how much feeding the macaques performed during the day, as a result of provisioning and did not account for the vegetation available in the outside enclosure area. Data recorded immediately post-feeding revealed that the daily activity budgets were not very sensitive to fluctuations in the time spent performing behaviours between feeding regimes and unfortunately these observations did not control for the time spent feeding on the leftovers from a meal or the vegetation on the island which made up their outside enclosure. Despite these limitations, it would appear that feeding frequency does affect the behaviour of captive Sulawesi macaques. Further investigation is required to explore fully the extent to which variations in feeding frequency can be used as a method of enrichment. To fit the criteria of enrichment, a technique or device should lead to physical or psychological stimulation, which many consider to be analogous to increased levels of activity (Chamove, 1989; discussed section 1.4.2.d). A lot of studies have contrasted the time spent feeding by wild and captive primates. Although these comparisons are based on limited representations of both wild and captive populations, they reveal that levels of feeding and foraging are lower in captivity, though the difference is not always significant (Anderson & Chamove, 1984; Melfi, 1997; Reinhardt & Roberts, 1997; Boccia & Hijazi, 1998). An increase in feeding behaviour is therefore considered to be beneficial, especially if it is associated with a reduction in resting behaviour. As both these behavioural changes occurred with small frequent feeds, it may be appropriate to consider it as another form of 'feeding' enrichment.

4.3 USEABLE AREA

The concept of useable space, the area within an enclosure that captive primates can use and/or manipulate, envelops aspects of enclosure space and complexity that are interrelated. An increase in useable space can be achieved through the implementation of environmental enrichment, or structural changes to the enclosure (Carlstead & Shepherdson, 1994). Chamove (1989) considered that any non-social change to the environment of captive primates would affect their perception of their surroundings, which he termed their 'psychological space'. An increase in 'psychological space', which could be achieved by maximising useable space, is thought to promote welfare through psychological and physical stimulation (Chamove, 1988; Chamove, 1989).

The results of the multiple-regression analyses in chapter 3 revealed that the impact of enclosure complexity on Sulawesi macaque behaviour varies according to where in the enclosure the complexity exists. When inside enclosure areas are complex, the time spent moving is expected to rise. In this experiment, the effect of increasing useable space in a Dublin Zoo enclosure was investigated.

4.3.1 Methodology

Behaviour, location and substrate use were recorded for 8 macaques at Dublin Zoo, from 8am – 4pm, as described in section 2.1.1.b (N = 8). Observations were carried out for 10 consecutive days, before and after changes to the enclosure. The useable area of the inside enclosure was increased by replacing simple rope/branch structures with four rope cargo nets (each measuring approximately 320cm 240cm). Originally, two ropes were suspended from four points distributed evenly across the ceiling, and a log and some browse was suspended between the ground and a metre above it. The rope/branch fixtures were defined as the sections where the rope and branches were interconnected, otherwise rope and branch were categorised individually. Three new cargo nets were hung from the ceiling by two corners so that they covered the length of the largest wall in the enclosure (10m x 2.2m), thus providing a 'useable' wall. Another cargo net was suspended from the ceiling by all four corners and so provided a horizontal climbing area in the middle of the enclosure. Before changes to the enclosure, useable space was calculated at approximately 26m^2, which included the floor area and the wire around the enclosure. After changes to the enclosure, useable space was calculated at approximately 56.7m^2, with the cargo nets accounting for 30.7m^2. The cargo nets provided dramatically more horizontal and vertical climbing opportunities. At Zoo Köln, Germany, cargo nets were used to increase the useable space of an enclosure with tiled walls (Maple & Finlay, 1989).

4.3.2 Statistical analyses

Mean time spent performing behaviours was calculated for each individual/treatment (as described in section 2.1.1.c, scan = 16). As the data met the requirements necessary for parametric statistical analyses, the mean time spent performing each of the behaviours by each individual was directly compared between treatments, using a matched t-test.

Substrate use within the inside enclosure area was evaluated, by calculating the total number of observations in which the macaque was in contact with each of the substrates, recorded every 30 min from 8am to 4pm. Mean substrate use was then calculated by averaging the total substrate use for all the macaques in the troop. Mean substrate use is illustrated in figure 4.3.2, and non-parametric matched Wilcoxen signed ranks tests were employed to compare the use of each substrate before and after changes to the useable area. As cargo nets replaced the rope/branch fixtures, the use of these materials were compared between treatments by using the matched Wilcoxen signed ranks test to assess how rope/branch use before differed from cargo net use after changes to the useable space.

4.3.3 Results

Figure 5.3.1 illustrates how changes in useable area did not significantly affect the mean percentage time spent performing behaviours by captive Sulawesi macaques (df = 7; $p > 0.05$; social, t = -0.11; moving, t = -0.295; resting, t = 0.41; foraging, t = -0.77; feeding, t = 1.0; miscellaneous/not seen, t = -1.53). The spatial use of the inside enclosure did however, change between treatments as illustrated in figure 4.3.2. Of the substrates available within the inside enclosure, logs, branch/rope fixtures and the ground were used most in the first treatment, and then the cargo nets were used most frequently in the second treatment. A decline in the branch/rope fixtures was expected in the second treatment, as they were not present. The predominant use of the cargo nets, lead to a significant decline in the use of wire and the ground (Wilcoxen signed rank tests, N = 8, 8; wire, Z = -2.37, $p = 0.018$; ground, Z = -2.52, $p = 0.012$). The time spent inside also rose from 108.5 mean observations to 112.25, after the useable area was increased (Z = -1.9; N = 8, 8; $p = 0.055$).

Figure 4.3.1 Mean ± SE percentage time spent performing behaviour before and after changes to the useable area of the inside enclosure at Dublin Zoo (N = 8).

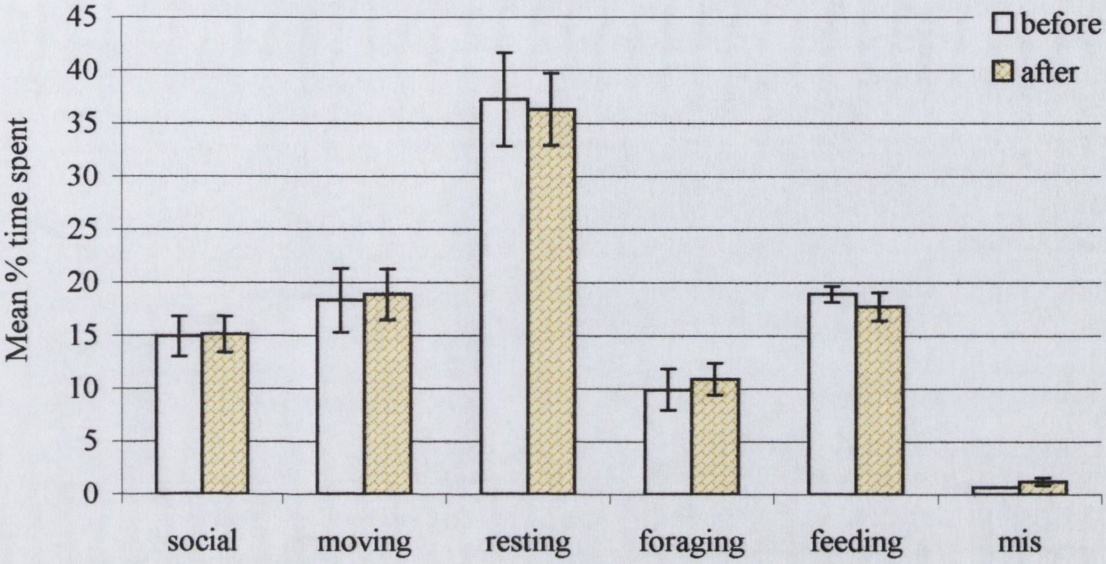
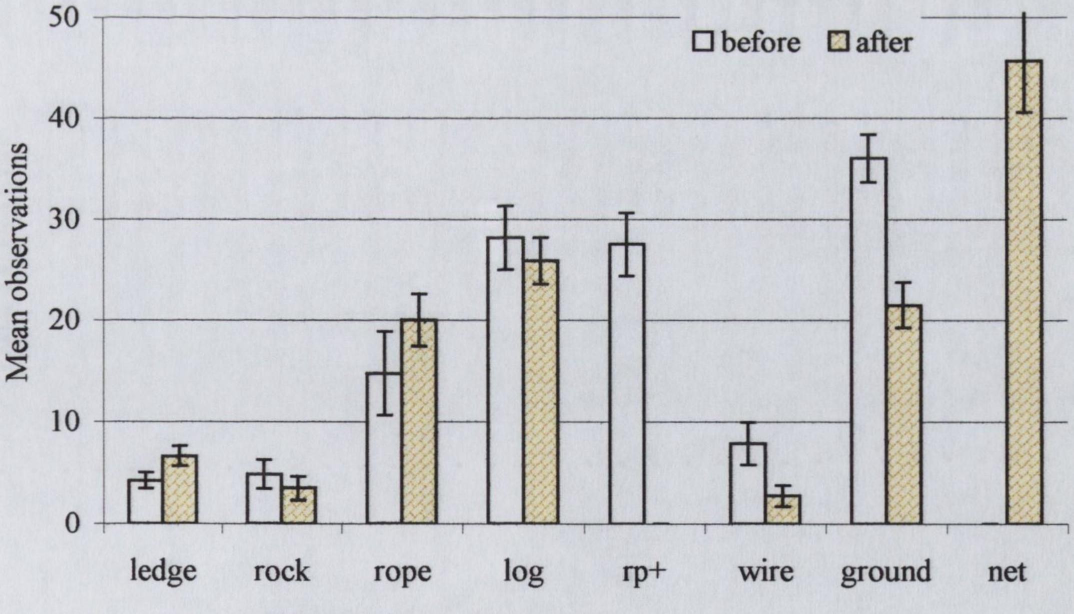


Figure 4.3.2 Mean ± SE observations of substrate use before and after changes to the useable area of the inside enclosure at Dublin Zoo (N = 8).



rp+ = rope and branch internal structure

Two factors that may have affected the use of the cargo nets were that they were novel, and covered a large horizontal and vertical area, so the macaques would be expected to use them more extensively than other less abundant substrates or those which were no longer 'interesting'.

4.3.4 Discussion

Increasing the useable area available to captive primates can be achieved by simply making better use of the existing space (Chamove, 1989). Chamove (1989) suggested that non-social modifications to the captive environment of primates increased their 'psychological space', a concept which encapsulates how captive primates perceive their surroundings, and which can be achieved through environmental enrichment: for example, visual barriers, flooring materials, and the incorporation of fixtures and furniture within the enclosure. Carlstead & Shepherdson (1984) noted that a lot of the techniques employed to increase useable area make the lives of captive primates more demanding as more energy is required to gain commodities in their enclosure - for example, food from deep litter, or moving on small flexible branches that require more balance than usual perching. The results of the present study revealed that changes in the useable area available to a troop of Sulawesi macaques at Dublin Zoo did not significantly affect their daily activity budget, but did significantly affect their spatial use of the enclosure. Environmental enrichment is frequently reported to have significant effects on the expression of behaviour, however, as the techniques implemented under this heading are so broad it is not surprising that they may have different functional implications to the lives of captive primates, which are expressed as different changes in behaviour.

Studies have compared the behaviour of captive primates in a barren space relative to an enriched area, which is considered to have more useable space, and found that there were significant changes in behavioural expression including a decline in the level of stereotypical behaviour (Bayne *et al.*, 1991; Leu *et al.*, 1993). In these studies an extreme variation in the useable area available to the captive primates was compared. In Bayne's study (1991) individually housed capuchin monkeys were transferred from small metal cages to a large, complex enclosure where they were integrated into a social group. In Leu's study (1993) the behaviour of long-tailed macaques was compared between empty cages and those with some enrichment, and so an extreme behavioural response should be expected in both studies to match the extreme change in environment. It is possible that a behavioural response is proportional in size to the changes made to the environment. In the present study, the environmental change could be considered quite minor, given that the enclosure was large and fairly complex. Studies which have increased useable area in association with food presentation have also lead to significant changes in behaviour. In a study carried out by Lutz and Novak (1995) employed foraging racks and feeding in deep litter (shavings) both of which lead to significant changes in behaviour and spatial use of the enclosure. Behavioural changes have also been observed in circumstances when modifications to useable area have been targeted at social interactions (visual barriers). In this study, increased useable area was not associated with food, did not provide visual barriers and was not extreme, as the macaque enclosure had been relatively enriched prior to the incorporation of cargo nets into the enclosure, all of which may have reduced the influence of the environmental change on the daily activity budget of the Sulawesi macaques.

In a similar study, several baboon troops were each provided with a ladder/drum fixture suspended in the middle of their enclosure to increase useable space (Kessel & Brent, 1996). Kessel & Brent (1996) found that all the baboons used the new ladder/drum fixture, but use was significantly different between sex-age class categories, with females and infants using the fixture at significantly higher levels than males. They concluded that difference in body size, dominance and activity levels probably contributed to the differential use of the fixture, and drew from the data of several other studies that older primates prefer stationary objects compared to the more mobile fixtures (swings and perches preferred by the younger primates). Increasing the useable area available to the Sulawesi macaques did significantly affect their spatial utilisation of the inside enclosure and all the macaques in the troop used the newly incorporated cargo nets. The provision of the cargo nets took two forms, which may explain its appeal to all the sex-age classes in the troop. Depending on how the cargo net was suspended in the enclosure it provided a flexible (horizontally suspended from the ceiling) and stationary (vertically hung down the wall covering the length and height of the back wall of the enclosure) surface. In fact, the macaques used the cargo nets to the exclusion of other materials in the enclosure and more thoroughly than the pre-existing branch/rope fixtures which had been favoured. Fundamental to the extensive use of the cargo nets was probably choice of opportunities, the area covered by the cargo nets was greater than that provided by the ground and allowed the macaques to position themselves at a variety of heights along the length of the enclosure, on either stationary or more flexible cargo nets. The cargo nets also enable the macaques to move and rest off of the ground, which they appear to prefer, compared to being on the ground (section 2.3). It is the element of control and choice within their enclosure that was possibly the most effective and beneficial repercussion of the incorporation of the cargo nets. The ability of captive animals to retain some control over their lives has been identified as vital in the promotion of animal welfare (Weipkema &

Koolhaas, 1993). Chamove (1988) suggested that captive primate environments are restrictive, and when they attempt to hide from the public and/or work for resources in their environment that are freely available (contrafreeloading, Osborne, 1977), they are attempting to gain some control over this restrictive environment. In a newly constructed enclosure for orang-utans, the provision of areas which were just out of public view offered privacy to the orang-utans and was frequently used (Herbert & Bard, 2000).

In conclusion, change or addition to the useable space of an enclosure may not necessarily modify behaviour but it may deliver some control to the captive residents and thus aid in the promotion of animal welfare. Building on the knowledge of how captive primates use space allows further steps to be made that could enhance their lives, for example, the creation of mixed-species exhibits that provide dynamic and unpredictable enrichment (Chamove, 1988; Thomas & Maruska, 1996; Pullen & Buchan, 2001).

4.4 SOCIAL COMPOSITION

Social composition and group size have been reported to affect behaviour, however, investigations along this theme are hard to implement in zoos as practically group size and composition can rarely be manipulated for the purpose of research (Visalberghi & Anderson, 1993; Hawkins, 1999). Troop size was predicted to negatively affect the social and moving behaviours, and positively affect resting and feeding behaviours of captive Sulawesi macaques (section 3.1). Conducting quantitative studies to test these predictions are difficult, but changes do occur in accordance with captive management protocol that result in major social composition and troop size changes. During this project two such changes were implemented at Jersey and Paignton Zoos. Behavioural observations were undertaken before and after these changes were made, so that the behaviour of the Sulawesi macaques could be compared and an indication of some of the effects of different social structures could be gained.

4.4.1 Methodology

The social structures of the troops observed are described in table 4.4.1. At Paignton Zoo the behaviour of six macaques was compared before and after changes to the social structure. Data were recorded while the macaques were part of a multi-male group and a no male group (after the removal of 7 macaques, 3 adult males, 2 adult females including dominant females and 2 big juveniles). The no male group were observed twice, approximately $2^1/_2$ weeks after the change in social structure, and then 16 weeks later. At Jersey Zoo the social structure changed from a multi-male to a single-male group, with the removal of several adult males and the introduction of one new male. Data collected during a previous study of all the individuals in the multi-male group, was compared with behavioural data recorded of all the individuals in the single-male group. There was a gap of 2 years between the two data collection periods.

Behavioural data were collected as described in section 2.1.1.b. Data were gathered for 10 hrs between 7am and 7 pm for the multi-male group at Jersey and all other data were recorded for 12 hr from 7am to 7pm. Ten days of data were collected for each treatment (before and after social change) at Jersey Zoo and the 'before' treatment at Paignton Zoo, while five days of data were collected for each post-social change treatment at Paignton Zoo.

4.4.2 Statistical analyses

The mean percentage time spent performing behaviours by each individual observed was calculated as described in section 2.1.1.c. Behavioural data recorded met the requirements necessary for parametric statistical analyses (normal distribution and homogeneity of variances). Doubly repeated measures ANOVA was used to compare the mean time spent performing behaviours between treatments (Jersey Zoo, multi-male to single male; Paignton Zoo, multi-male to no male novel and no male long-term) and was followed by post-hoc analyses, the significance of which were adjusted for the multiple pair-wise comparisons by using the Bonferroni adjustment. With the exception of feeding behaviour, all other behavioural data collected at Paignton Zoo met the assumption of sphericity required to perform repeated measures ANOVA, which was indicated by the Mauchly's test of Sphericity (feeding, Mauchly's W = 0.19, df = 2, $p < 0.05$; SPSS, 1999a). As the sphericity assumption was violated for the time spent feeding, an adjustment to the numerator and denominator degrees of freedom was made using the Huynh-Feldt epsilon, which is multiplied with the numerator and denominator degrees of freedom and the adjusted degrees of freedom used in the computation of the observed significance level. The Huynh-Feldt epsilon was chosen over others, as it is was more suitable for small sample sizes (SPSS, 1999a; SPSS, 1999c).

As the behavioural observations recorded at Jersey Zoo were separated by a couple of years, the ageing of some individuals had resulted in their age classification being changed. Matched pairs analyses were therefore used to analyse the effects of different social structure on the behaviour of macaques at Jersey Zoo, rather than using repeated measures (N = 13, 13; multi-male and single male group). This would avoid confounding behavioural changes in behaviour that resulted from maturation, with behavioural changes that had arisen from changes in social structure. A paired sample T-test was used to compare the mean time spent performing behaviours between treatments, as part of a multi-male and single-male troop.

4.4.3 Results

Social composition changes at Paignton Zoo significantly affected the mean time spent performing each of the behaviours (Figure 4.4.1; Wilks' $\lambda = 0.008$, df = 12, $p = 0.001$). Univariate tests revealed that social, resting and foraging behaviours were significantly affected by changes in the social composition (df = 2; social, F = 7.02, $p = 0.012$; resting, F = 32.11, $p < 0.001$; foraging, F = 8.08, $p < 0.01$). Results from the post-hoc analyses (Table 4.4.2) revealed that the macaques rested significantly more when they were part of multi-male group, compared to observations immediately and sixteen weeks after the removal of the other macaques. The macaques' behaviour changed significantly sixteen weeks after the change in social composition, compared to immediately after the change as social behaviour declined and foraging behaviour increased. Paired sample T-tests indicated that the behaviour of Sulawesi macaques at Jersey Zoo significantly altered when social composition changed from a multi-male to a single-male group (df = 12; moving, t = -5.4, p <0.001; resting, t = 3.67, p < 0.01, feeding, t = 3.94, p < 0.01). The time spent moving increased, while resting and feeding decreased.

Table 4.4.1 Information about the social structure of the troops observed at Jersey and Paignton Zoos, and the timetable used for behavioural sampling, carried out before and after changes to the social structure.

Zoo	Date of observations	Troop size *(number used in comparison, if different)*	Sex-age composition					Age range
			Adult		Juvenile		Infant	
			♂	♀	Big	Small		
Jersey I	1 - 11/6/97	16 (13)	3	6	3	4	0	2 - 25 yr
Jersey II	6 -15/8/99	15 (13)	1	6	4	3	1	1 wk – 13 yr
Paignton I	23/11-6/12/99	13 (6)	3	4	3	3	0	1 – 16 yr
Paignton II	29/12/99-4/1/00	6	0	2	1	3	0	1 – 11 yr
Paignton III	22 - 30/4/00	7 (6)	0	2	1	3	1	3 mth – 11 yr

Table 4.4.2 Post-hoc analyses results, revealing the significant differences observed in the behaviour of macaques at Paignton Zoo when social composition changed from a multi-male group (1) to a no male group (immediately after change = 2, 16 weeks after change = 3).

Behaviour	Pair-wise comparison		Mean difference
Social	2	3	7.29*
Resting	1	2	10.83**
		3	11.67**
Foraging	2	3	-7.5*

Figure 4.4.1 Mean ± SE percentage time spent inside and performing behaviours by Sulawesi macaques at Paignton Zoo, when they were part of a multi-male group, immediately after the males were removed (no male, novel) and then 16 weeks later (no male, long-term) (N = 6; * $p < 0.05$, ** $p < 0.01$, ***$p < 0.001$).

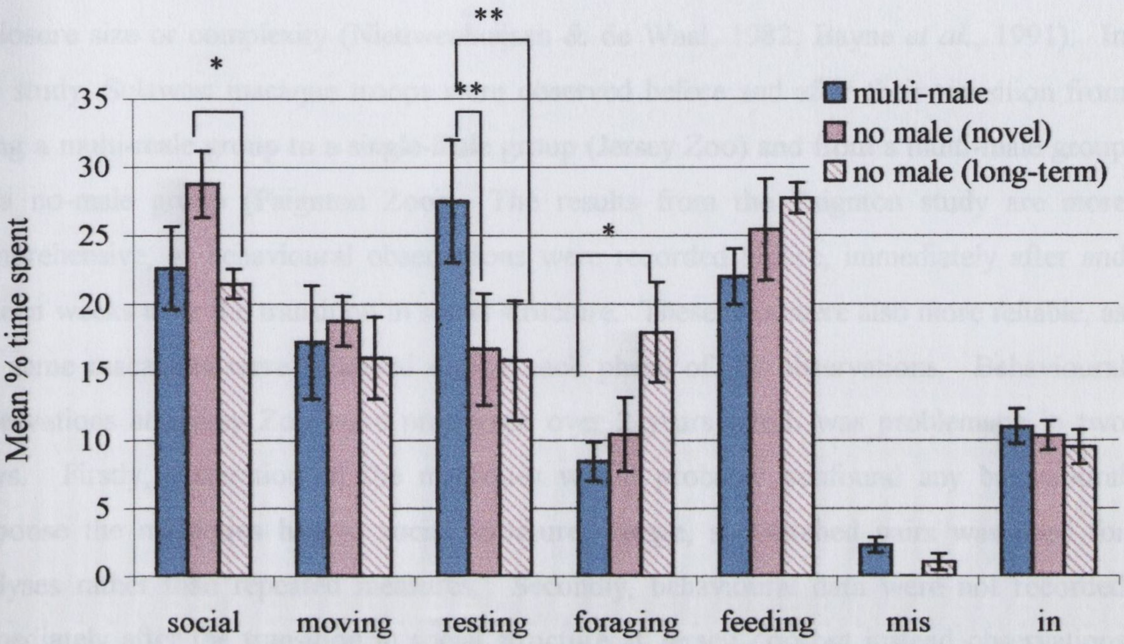
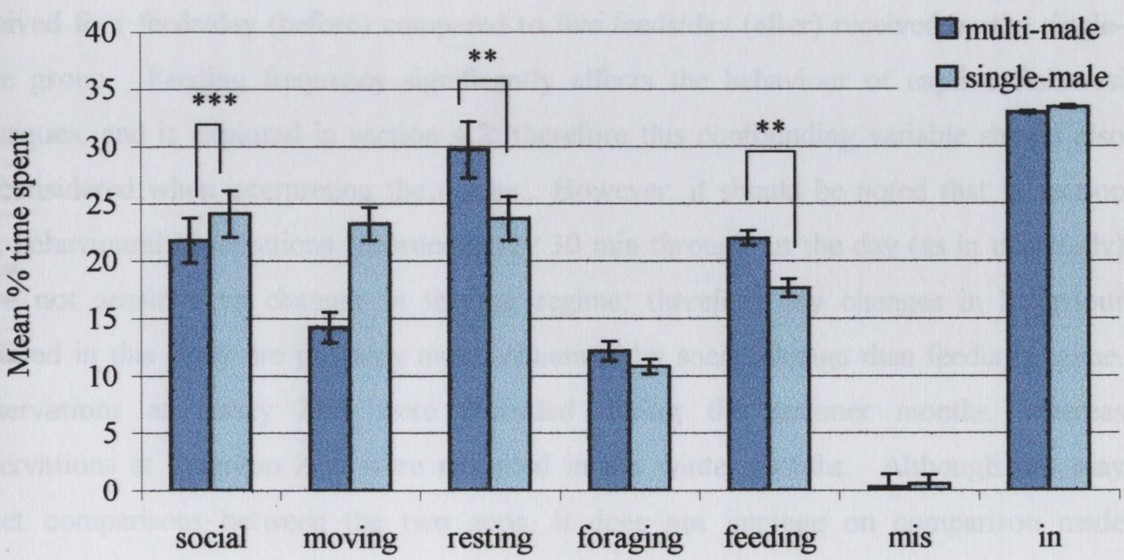


Figure 4.4.2 Mean ± SE percentage time spent inside and performing behaviour by matched pairs of Sulawesi macaques at Jersey Zoo, when they were part of a multi-male and single-male social group (N = 13; * $p < 0.05$, ** $p < 0.01$, ***$p < 0.001$).



4.4.4 Discussion

In zoos, the manipulation of social groups for research is not practical and so studies are limited to events dictated by captive management. There are many problems inherent in studying the effect of social structure or group size on captive primate behaviour, not least that there are usually many confounding variables for example, enclosure size or complexity (Nieuwenhuijsen & de Waal, 1982; Bayne *et al.*, 1991). In this study, Sulawesi macaque troops were observed before and after their transition from being a multi-male group to a single-male group (Jersey Zoo) and from a multi-male group to a no-male group (Paignton Zoo). The results from the Paignton study are more comprehensive, as behavioural observations were recorded before, immediately after and sixteen weeks after the transition in social structure. These data were also more reliable, as the same macaques were followed during each phase of the observations. Behavioural observations at Jersey Zoo were protracted over 2 years which was problematic in two ways. Firstly, maturation of the macaques would probably confound any behavioural response the macaques had to social structure change, so matched pairs was used for analyses rather than repeated measures. Secondly, behavioural data were not recorded immediately after the transition in social structure at Jersey Zoo but instead observations were made before and about two years after. The immediate response to the transition in social structure at Jersey Zoo was followed in a study conducted by Matthews (1998), but as the methodology varied from that used in this present study, comparisons were limited. A final complication when interpreting the behaviour observed at Jersey Zoo was that the feeding regime had also changed alongside social structure, so that the multi-male group received four feeds/day (before) compared to five feeds/day (after) received by the single-male group. Feeding frequency significantly affects the behaviour of captive Sulawesi macaques, and is explored in section 4.2; therefore this confounding variable should also be considered when interpreting the results. However, it should be noted that in section 4.2, behavioural observations recorded every 30 min throughout the day (as in this study) were not sensitive to changes in feeding regime; therefore any changes in behaviour revealed in this study are probably more influenced by social change than feeding regime. Observations at Jersey Zoo were recorded during the summer months, whereas observations at Paignton Zoo were recorded in the winter months. Although this may affect comparisons between the two zoos, it does not impinge on comparison made between social structures at each zoo.

There were significant differences in macaque behaviour over the short (immediate observations) and long-term (after 16 weeks), when the composition of their social group was changed. Analyses of the results revealed that groups with fewer adult males (one or none) spent significantly less time resting. Adult males have been described as more sedentary than other sex-age classes, a characteristic that may be exacerbated in captivity (section 2.1). As macaques are very social and frequently in close proximity to one another, the tendency of other individuals to aggregate around the dominant individuals may bias the activity budget of troops with adult males toward more resting behaviour, mimicking the adult males. In the Jersey group there was also a significant increase in the time spent moving, when one adult male replaced five, supporting the suggestion that more adult males may reduce the activity of a group.

In the Paignton group there was a short-term rise in the time spent performing social behaviours, immediately after the adult males and dominant adult females were removed from the group. The fall in social behaviour after sixteen weeks was significant, although its immediate rise after social change was not, as the time spent in social behaviours was more variable in the multi-male group compared to the no-male group. Intuitively a rise in social behaviour is not unexpected, as the group had undergone a surprising and traumatic event. For example, the eldest remaining macaque (a female) was instantly promoted from the third highest-ranking female to the most dominant macaque in the group, an infant lost her mother and the whole group lost the security of adult males. In a study by Matthews (1998) the social behaviour of the macaques at Jersey group, was revealed to decline after the transition of the multi-male group to a single-male group., and was interpreted as the dominant females and the new adult male asserting themselves in the group, thus not actively interacting with one another.

There was a steady rise in the level of foraging behaviour observed at Paignton Zoo, which was significantly greater sixteen weeks after the transition in social structure. It is most likely that the time spent foraging reflected the abundance of vegetation available to the macaques, which increased from the first series of observations in December, to the final observations that were carried out in April. Feeding and foraging levels may also have risen, due to a lack of adult males and dominant females in the group to monopolise the food sources. By contrast the time spent feeding at Jersey Zoo declined after the social transition from multi to single-male group. The feeding regime at Jersey Zoo changed at the same time as the social composition, but the level of feeding declined, whereas data suggests that feeding levels increase with a rise in feeding frequency (section 4.2). It is possible that as the number of feeds rose and the feed size became smaller, that the macaques spent less time feeding/feed, which would have been easily missed by the behavioural observations. When only one or two feeds/day were provided, as at Paignton Zoo, the feeds were larger in size and the macaques took longer to eat them, so feeding behaviour was more readily observed under the conditions of the methodology used in this study. It is possible that there is a threshold level above which feeding frequency no longer increases the time spent feeding, especially if the size of the feeds are getting proportionately smaller and the animals eat what is available ever more quickly. Alternatively, the elevation in moving levels in response to the change in social structure may have left less time to feed and rest.

The interpretation of these results is limited by confounding variables, however, it appears that social structure does significantly affect the activity budgets of captive Sulawesi macaques, and that the sedentary behaviour of adult males is reflected in the behaviour of other sex-age classes, through elevated levels of resting and lower levels of moving behaviour.

Chapter 5

CONCLUDING DISCUSSION

5.1 KEY RESULTS

This thesis was successful in its attempt to identify captive environmental factors that affected the behaviour of Sulawesi macaques. Differences in the environmental conditions between zoos significantly affected Sulawesi macaque behaviour, as did their sex-age class. Equally, the behaviour of wild Sulawesi macaque troops was reported to vary according to different environmental factors (O'Brien & Kinnaird, 1997). No significant difference was found between the behaviour observed in wild and captive troops, which was probably the result of the variation that existed between troops in each data set. The pattern of behavioural expression observed in captive macaques of different sex-age class, closely mimicked that recorded for wild con-specifics. However, conditions in captivity were thought to further increase the frequency of resting behaviour in adult males. Enclosure and substrate use did not reflect the area available or abundance; instead, macaques displayed convincing preferences for sites and substrates within their enclosure. Inside enclosure areas made up a very small fraction of the overall enclosure space, however macaques spent about 50% of a 12hr day inside (where access allows). The interpretation of substrate use was considered biased against those which macaques would use fleetingly, for example, the swing or tyre. The incorporation of many substrates into the enclosure was concluded to be beneficial, as it provided the macaques with a choice of opportunities, even if they were not fully utilised (section 1.4.3.b).

The results of the multiple regression analyses identified five key features of the housing and husbandry regime that significantly affected captive Sulawesi macaque behaviour: enclosure size and complexity; troop size; the use of bark as an inside flooring material; and feeding frequency. Social behaviour was significantly predicted by troop size and feeds/day. Contrary to previous literature, social behaviour reduced with troop size, however troop size was positively related to enclosure area and so macaques could disperse further in larger enclosures, which possibly lead to fewer social interactions. Feeds/day was positively correlation with social behaviour, but confounded by troop size as larger troops generally received more feeds/day. Both variables could explain the rise in social behaviour (section 4.2).

Feeding and foraging behaviours were predicted to increase with a large enclosure, troop size, the use of bark as an inside flooring material and many substrates distributed within the enclosure to manipulate. These environmental factors are similar to those in the Sulawesi macaque's native habitat, which supports the long-held hypotheses that 'naturalistic' enclosures are conducive to the promotion of feeding and foraging behaviours (Hutchings *et al*., 1978b; O'Brien & Kinnaird, 1997; section 1.4.3.b). The effect of enclosure complexity was dependent on its situation in the enclosure and to an extent on the behaviours that predominated there. Negative relationships were calculated between moving behaviour and enclosure complexity (outside), and between resting behaviour and enclosure complexity (inside). The amount of time spent resting was higher in large enclosures and lower in more complex enclosures, or when the troop size was large. These data support previous findings that increasing social or structural complexity within captive primates housing, promotes active behaviours (Carlstead & Shepherdson, 1994). Resting behaviour declined as feeds/day rose, which was probably an artefact of larger troop size stimulating feeding, foraging and social behaviours (section 3.3.2)

Practicalities influenced which environmental factors would be tested quantitatively, resulting in tests of enclosure complexity (useable area); flooring material; feeding frequency; and social composition. Appropriate modifications were made to the captive environment of one Sulawesi macaque troop, to quantify the effects of these environmental factors on behaviour. All the factors tested did significantly affect captive Sulawesi macaque behaviour and/or enclosure use. The inconsistencies between these results and those revealed by the multiple regression analyses are discussed in chapter 5, though the underlying cause of these differences appeared to result from the inter-relationships between environmental factors. Behavioural expression is frequently noted for its multi-factorial origins and so it not unexpected that this study established that many environmental factors acted together as a single unit in the stimulation of behaviour and therefore, changing simple elements of this unit did not always lead to quantitative differences in behaviour (Manning & Dawkins, 1998).

Different inside flooring materials significantly affected Sulawesi macaque behaviour and enclosure use, as also seen in laboratory housed macaques (Chamove, 1986; section 3.3.4). Straw was clearly preferred by the macaques, but the quality and quantity provided in the experiment almost certainly affected this choice. There was a distinction between the macaques' use of bark or straw and their use of sawdust or nothing. The former stimulated more behavioural interactions and was associated with the macaques spending more time inside. The flooring material appeared to have a short-lived effect immediately after its presentation into the enclosure. The effect may have worn off so quickly because of the complexity of the captive enclosure and the alternative sources of interest it held. Previous studies in this area have been based on laboratory-housed primates, which may be assumed to be in less complex environments than those in this study which were zoo-housed primates (section 4.1). In these previous studies, flooring materials have been demonstrated to have significant effects on primate behaviour, but unfortunately details have not been reported on whether this effect was prolonged or just after the presentation of the flooring materials (section 4.1).

As feeds became more frequent, macaques spent less time feeding per feed, which was expected because meal size became smaller. The accumulation of this time feeding lead to an increase in the overall daily total time spent feeding. Increasing feeds per day lead to a reduction in resting behaviour, while stimulating feeding and social behaviours. These changes in behaviour conform to the concept of enrichment, however, the proximal cause of social behaviour change is unclear, and may reflect increased levels of stress within the group and as such would probably not be considered beneficial (section 1.4.2.a and 4.2). Further study in this area is necessary.

The amount of useable area in the enclosure reflects its size and complexity. Despite the general assumptions that prescribe large and complex enclosures to remedy the restrictions of captive enclosures, no significant change in the time apportioned to the observed behaviours was recorded after increases to the useable area (section 1.4.3). However, enclosure use was significantly affected by changes in useable area. A preference for the new substrate (cargo nets) was evident, with macaques using all aspects of the cargo nets, however it should be noted that its relative abundance was great and it was novel (section 4.3).

Opportune changes in social structure revealed that adult males significantly affected the behaviour of other sex-age classes. Adult males rested predominantly, which appeared to suppress the activity of other individuals in the group, as the absence of males or a reduction to their number was associated with an increased level of moving and foraging behaviours.

5.2 EVALUATION OF THE METHODOLOGY

Two principle methodologies were used in this thesis; activity budget comparisons and work based on multiple-regression analyses. Activity budgets provide an indication of the level at which broad state behaviours are performed. A scan sampling method was used, sampling at fixed intervals. As the sampling interval becomes larger there is a greater possibility that behaviours will become misrepresented (Martin & Bateson, 1996). Due to the size and topography of enclosures included in this study, a sampling interval of 30 min was used between scan observations. An interval of this length may appear long and, therefore, result in a misrepresentation of the time spent performing behaviours. However, a study was carried out to assess the strength of this effect, and no significant difference was found between Sulawesi macaque activity budgets generated from data collected every 10 min or every 30 min (Melfi, 1997). Thus there was no suggestion that data collected at shorter intervals would have provided a more accurate representation of the captive Sulawesi macaque behaviour.

The multiple-regression analyses provided a systematic approach to the investigation and provided a sound basis for further hypothesis creation. As noted by Mellen (1994) this approach is very demanding in terms of time and finances, however the results gained could not have been achieved using an alternative method e.g. single-site comparisons or surveys. Multiple regression analyses are central to this project, and call for the use of complex statistics not frequently used in behavioural science. The methods employed draw usefully on information cited in Tabachnick & Fidell (1996) and in the few pioneering papers that have followed this approach (Wilson, 1982; Mellen, 1991; Perkins, 1992).

5.3 FUTURE WORK

I believe that the methodology used in this project provides a new insight into the effect of captive environmental factors on behaviour. However, this study also highlighted areas that require further study:

1) One of the limitations of this study was that the quantitative experiments that tested the relationships between behavioural expression and environmental variables could only be conducted at one zoo. These relationships could be better interpreted, if experiments were conducted at other zoos, preferably five more, to enable the statistical testing between zoos.

2) It is important to investigate whether modifications to housing and husbandry factors are affected by the prior condition of the enclosure, i.e. what are the implications of changing environmental variables in a complex enclosure compared to a 'barren' one? There are two

main points to this study, 1) as enrichment is costly in time and money, we want to be sure that the enrichment is necessary and providing stimulation above that gained from the enclosure and 2) animals may become accustomed to complex environments and therefore require more from enrichment compared to those that are housed in relatively 'barren' enclosures.

3) It would be enlightening to investigate whether environmental changes that provide an additional function to the enclosure, lead to more substantial changes in behaviour compared to those that may replicate function that is already present in the enclosure.

4) The data in this study provided information regarding the time apportioned to behaviours. Carlstead (1996) suggested that any behavioural divergence between wild and captive animals was probably reflected in the variation of expressed behaviours, rather than the time apportioned to them. To test this proposition, the behavioural diversity of wild and captive Sulawesi macaques could be compared; as could the behavioural diversity of macaques between zoos, to investigate the impact of different environmental factors on behavioural diversity.

5) Analyses of the macaques' enclosure and substrate use were limited in this study (section 2.3.2), so it would be interesting to expand this aspect of the study, to investigate the relationship between area use and the number or types of substrates it holds. This could probably be achieved using multivariate log-linear analyses (Ogden *et al.*, 1993). If the macaque's use of the enclosure was shown to be affected by certain types of substrate or their abundance; the position of these substrates in the enclosure could be manipulated, to see if the macaque's use of the enclosure could be maximised.

5.4 IMPLICATIONS FOR THE CAPTIVE MANAGEMENT OF SULAWESI CRESTED BLACK MACAQUES

The detailed nature of this project provides a rare indication of how captive environmental factors affect the behaviour of Sulawesi macaques. As the environmental factors studied were not exhaustive, other factors may also affect the macaques' behaviour. However, the experiments in this project do demonstrate that changes to those environmental factors studied will alter their behaviour.

Not surprisingly the factors that affected captive Sulawesi macaque behaviour were integral to housing and husbandry regimes (enclosure size and complexity, troop size, feeding frequency and the inside flooring material). The complexity of behavioural expression makes it difficult to identify how single environmental factors affect discrete behaviours, though in some circumstances this was achieved. Social composition, feeding frequency, useable area and the flooring material used were all shown to affect captive Sulawesi macaque behaviour significantly and therefore changes to these factors would modify their behaviour.

This project identifies environmental factors that modify captive Sulawesi macaque behaviour and, therefore, provides zoo managers with information that would make it possible to manipulate exhibits and the behaviour of their macaques. As discussed in section 1.4.1, 'wild-type' behaviour is usually desired by institutions that hold captive wild animals and taken to represent conditions of good welfare. The validity of this concept has long been debated, but it could be used in addition to other measures of animal welfare. For example, it could be used in conjunction with behavioural diversity, expression of 'abnormal' behaviours (self-destructive or behaviours without function) or analyses of 'stress' hormones, to provide information about how the captive environment has affected behaviour.

There was a large variation between the housing and husbandry regimes implemented at the zoos visited in this study. This lead to significant differences between the behaviour observed between the zoos. The variability observed in the captive macaque behaviour was similar to that observed in wild Sulawesi macaque troops, which were also subject to different environmental factors (O'Brien & Kinnaird, 1997). Due to the high level of behavioural variability both in the wild and in the captive troops, no significant difference was found between the two groups. However, a visual comparison of the mean rank of behaviour showed that captive troops rested more and wild troops moved and fed more. In addition, with the exception of a couple of adult female macaques that groomed their offspring excessively, no 'abnormal' behaviours were observed in the course of this study. This would suggest that the macaques' behavioural repertoire was greater than the environmental differences they experienced in captivity. So the captive environments (or influential elements of them) fell within a spectrum of environmental change that the macaques were able to adapt to. This would suggest that the captive environments provided for the eight troops of macaque in this study were adequate, though the ability to modify single factors in the environment which lead to significant changes in behaviour may indicate a lack of complexity. In a complex environment we might expect that a change to a single variable would not significantly affect behaviour. In the wild, environmental variation was considered a causal factor that determined the Sulawesi macaques' activity budget, although environmental variations were multifarious. For instance, the type of forest (pristine or secondary rainforest) was thought to affect the time Sulawesi macaques spent moving and feeding, due to changes in food availability and other factors, which resulted in difference troop size (O'Brien & Kinnaird, 1997). Similar complex relationships between environmental factors in captivity were visible in the results of the multi-regression analyses, which indicate interaction between the captive environmental factors in their influence on macaque behaviour. The captive environment is probably less dynamic than the wild, with fewer environmental variables that are able to change over time and therefore modifications to any one of these variables would probably have a greater influence on behaviour than we might expect.

This project has identified a couple of issues that are directly relevant to the maintenance and promotion of good welfare for captive Sulawesi macaques. Firstly, the inside enclosure area appears to be used a disproportionate amount for its size and the facilities it provides for the macaques. Large, complex inside areas with an interesting flooring material (straw or bark) would be desirable both for the macaques which use this area frequently and for the public, which are able to observe active macaques if these conditions are met. Feeding and foraging behaviours are also promoted in large, complex enclosures that hold large number of macaques (this study included troop sizes between 7 – 17). The influence of troop size on behaviour was based on the results of multiple-regression analyses, as it would be difficult to modify troop size both practically and experimentally (as other factors also change). There was a positive correlation between troop size and feeding and foraging behaviour, which suggests that large troops would perform these behaviours at higher levels. Therefore enclosures should be designed that are able to hold large numbers of macaques. The social structure and size of the troop also significantly affected the time spent resting. Large troops rested less and it appeared that the high level of resting behaviour observed in the adult males suppressed activity in the other members of the troop; this latter observation requires further study to investigate the costs and benefits of holding a 'natural' multi-male troop versus elevated activity in a troop with one adult male.

5.5 CONCLUSIONS

- Season significantly affected Sulawesi macaque behaviour, with social behaviour rising and foraging behaviour declining in the winter compared to the summer.
- Behavioural activity budgets and enclosure and substrate use were significantly different between zoos.
- Enclosure and substrate use did not reflect their abundance in the enclosure and the macaques showed clear preferences for some areas (they spent 50% of their time inside) and substrates (preferred substrates included frame and log) although the substrate analysis may have been biased against substrates they moved quickly on e.g. rope.
- Multiple regression analyses identified the following captive environmental factors as important in the determination of macaque behaviour: - enclosure size and complexity (measured by the number of substrates in the enclosure), troop size, the use of bark as an inside flooring material and feeding frequency.
  - Social behaviour was lowest in large troops, which also frequently had large enclosures.
  - Resting behaviour decreased with an increase in feeding frequency.
  - Feeding and foraging behaviour was highest in large complex enclosures, that used bark as an inside flooring material and maintained a large troop size.
- Frequently these captive environmental factors acted together to affect behaviour.
- Experiments were carried out to test the relationship between these environmental factors and the macaques' behaviour empirically.
  - Changes in useable area (a measure of enclosure size and complexity) did not affect the macaques' activity budget, though enclosure use changed significantly to incorporate the additional area.
  - As feeding frequency rose meal size decreased, which resulted in significant increases in feeding per day (though the time spent feeding per feed declined); social behaviour also rose, and resting behaviour declined.
  - The type of flooring material provided inside significantly affected the macaques' behaviour and enclosure use; they displayed a clear preference for straw, though it is suspected this is highly dependant on its quality and quantity. The time spent inside and behavioural interactions on the floor were greatest with bark and straw compared to sawdust and when no flooring material was present.

- The behaviour of wild and the captive Sulawesi macaques in this study was not statistically different.
- Behavioural expression of the macaques was significantly different between the sex-age classes. These differences were similar to observations recorded of wild macaques (O'Brien & Kinnaird, 1997).

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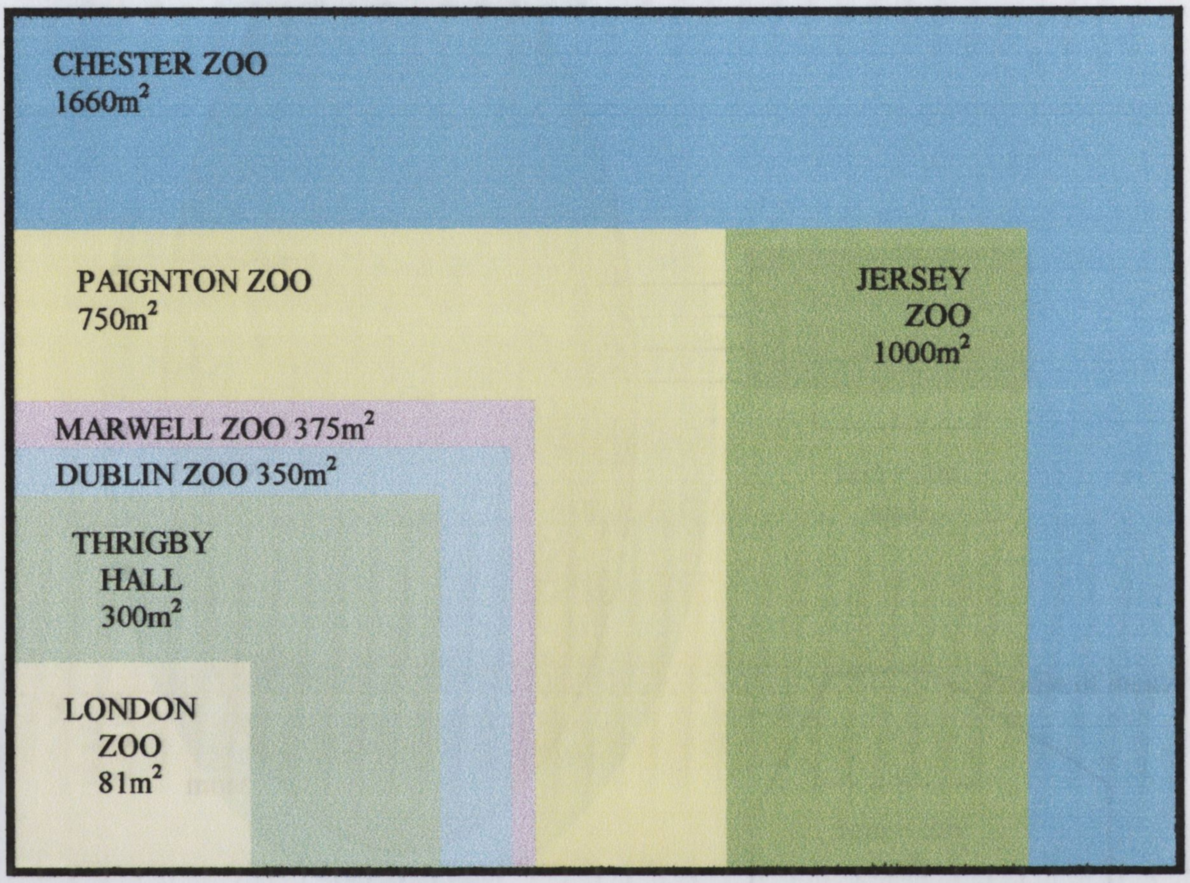
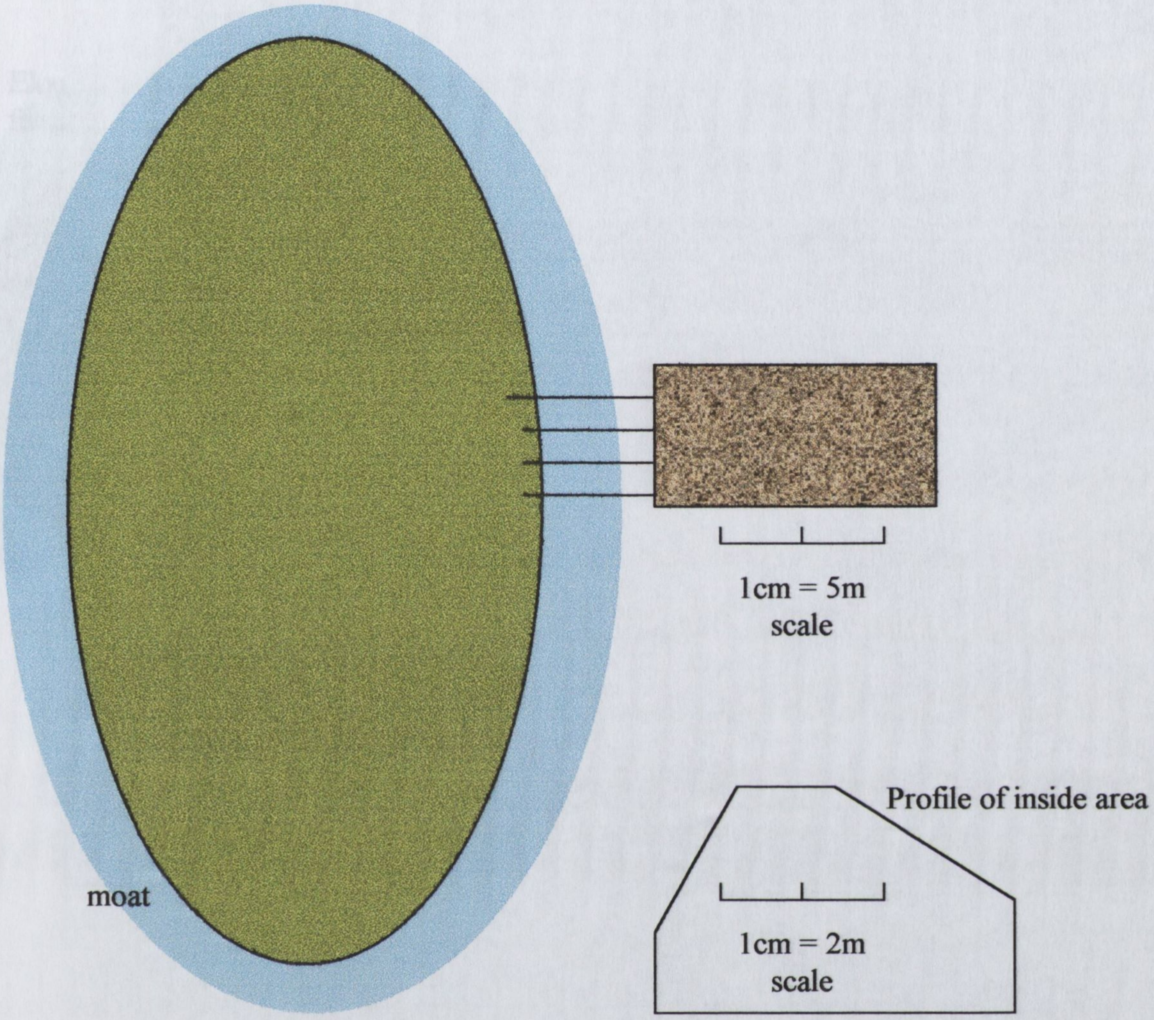
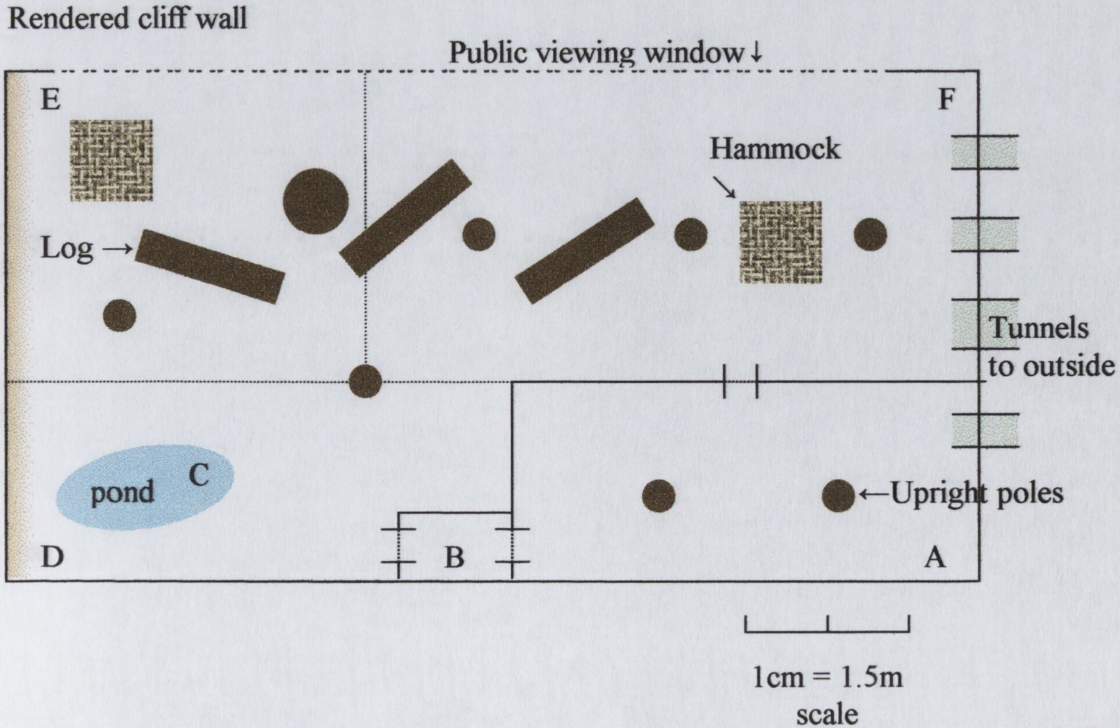
APPENDICES

Appendix 1 Relative Size of Sulawesi macaque enclosures.

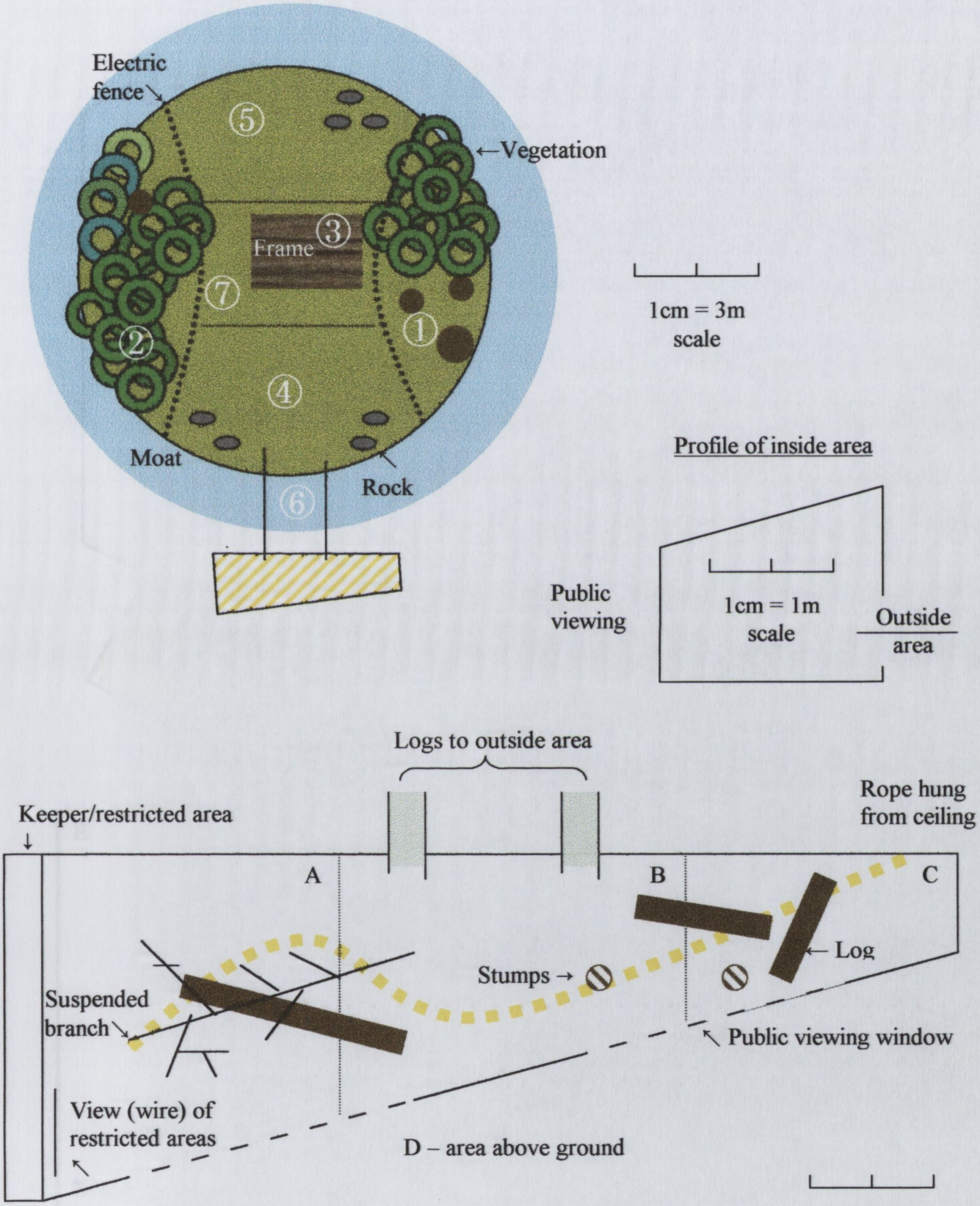


Appendix 2 Diagram of the Chester Zoo Sulawesi macaque enclosure.

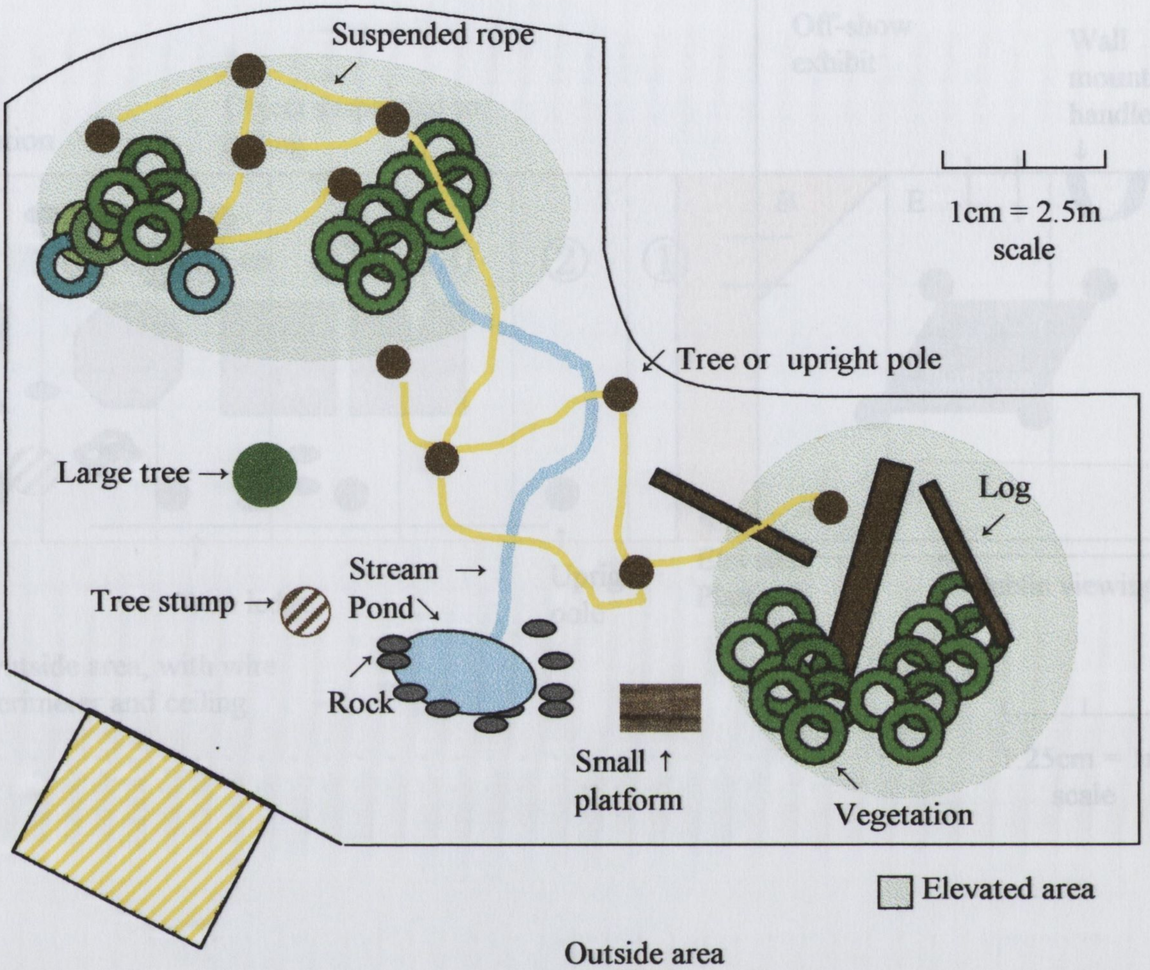


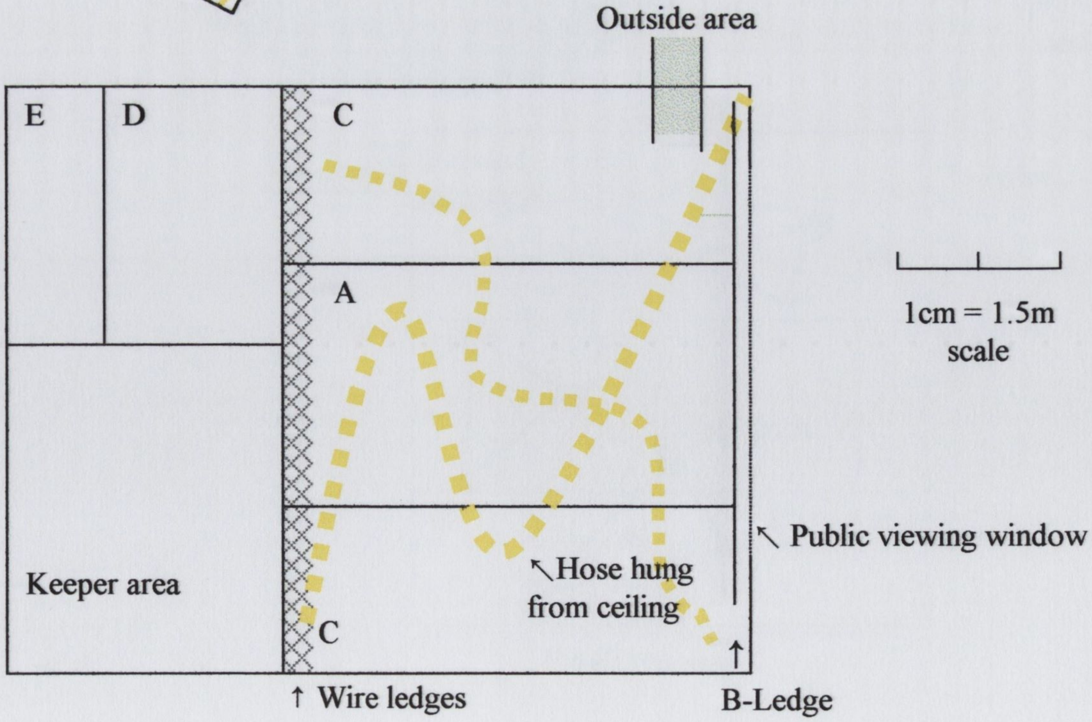


Appendix 3 Diagram of the Dublin Zoo Sulawesi macaque enclosure.

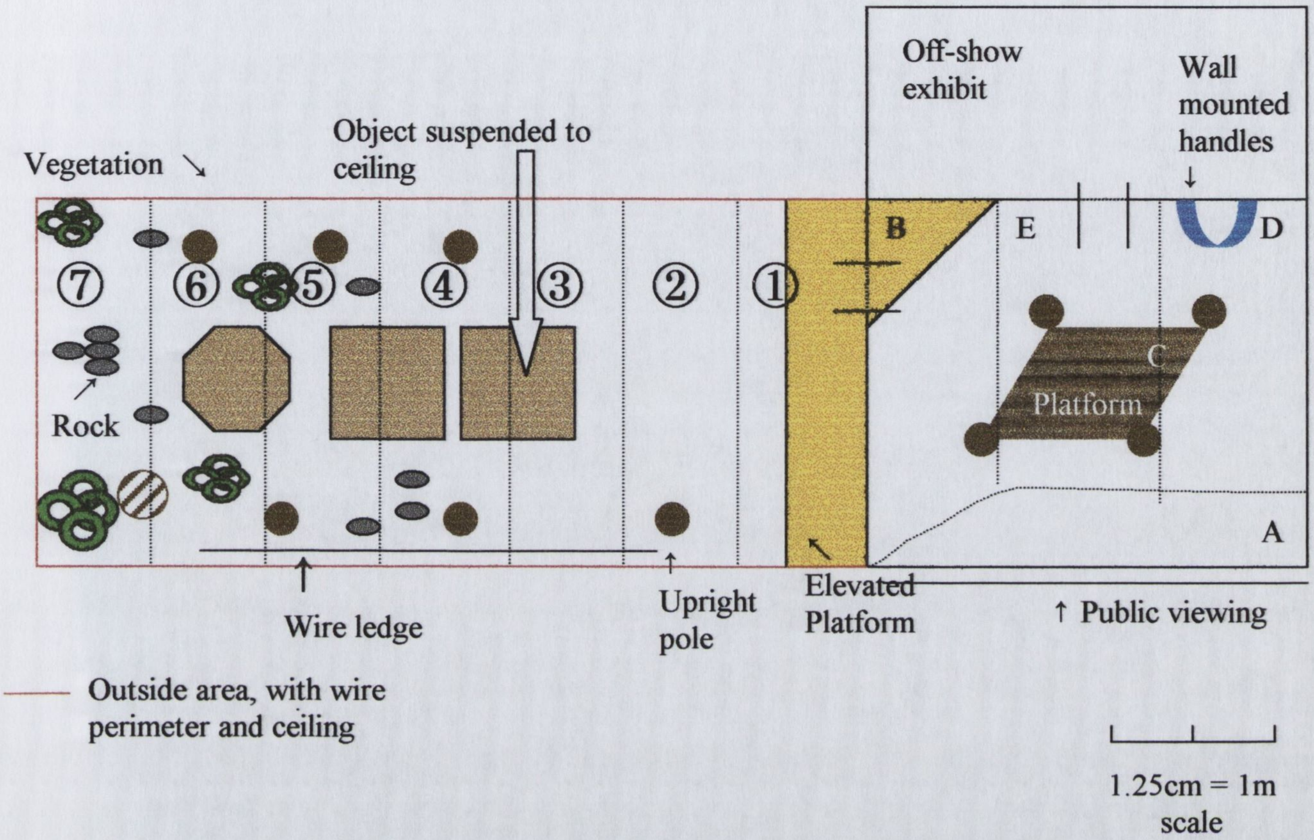


Appendix 4 Diagram of the Jersey Zoo Sulawesi macaque enclosure.

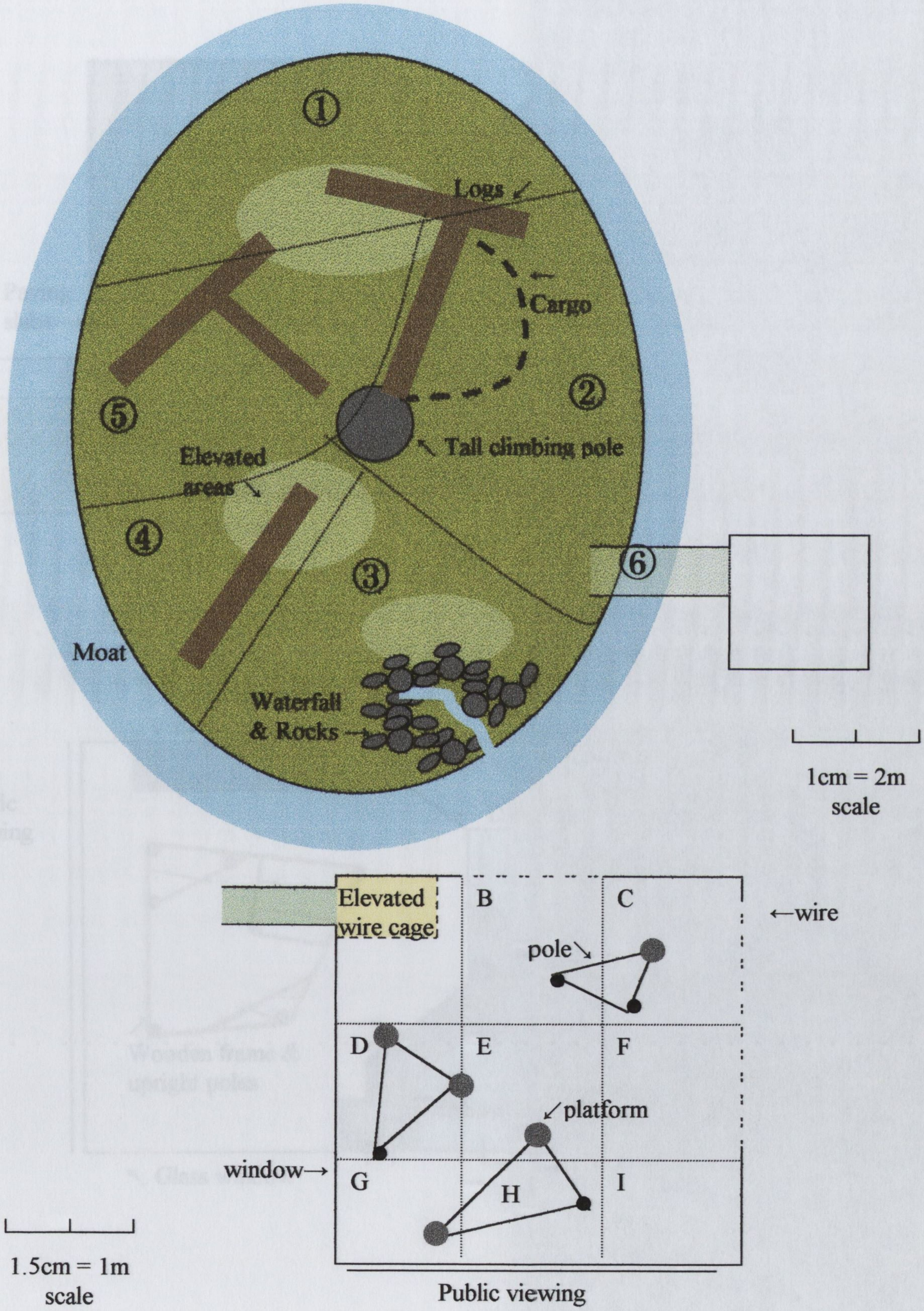




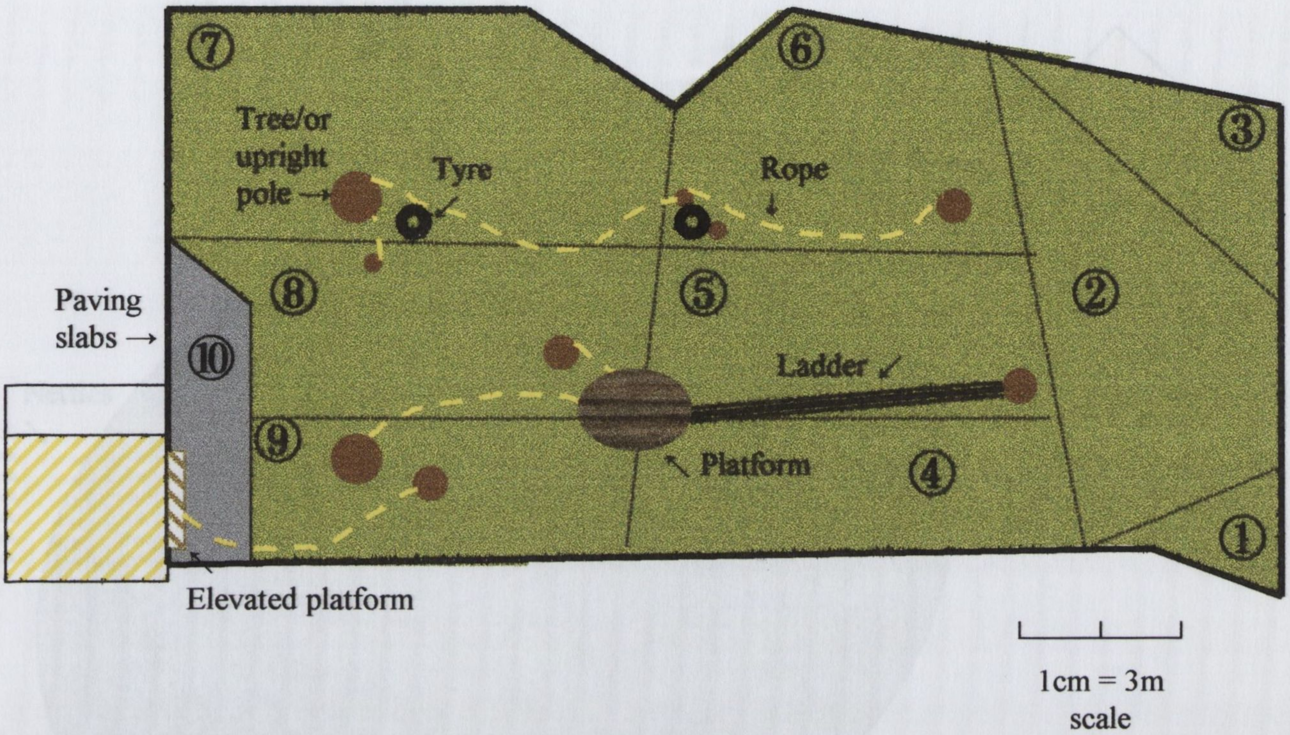
Appendix 5 Diagram of the London Zoo Sulawesi macaque enclosure.

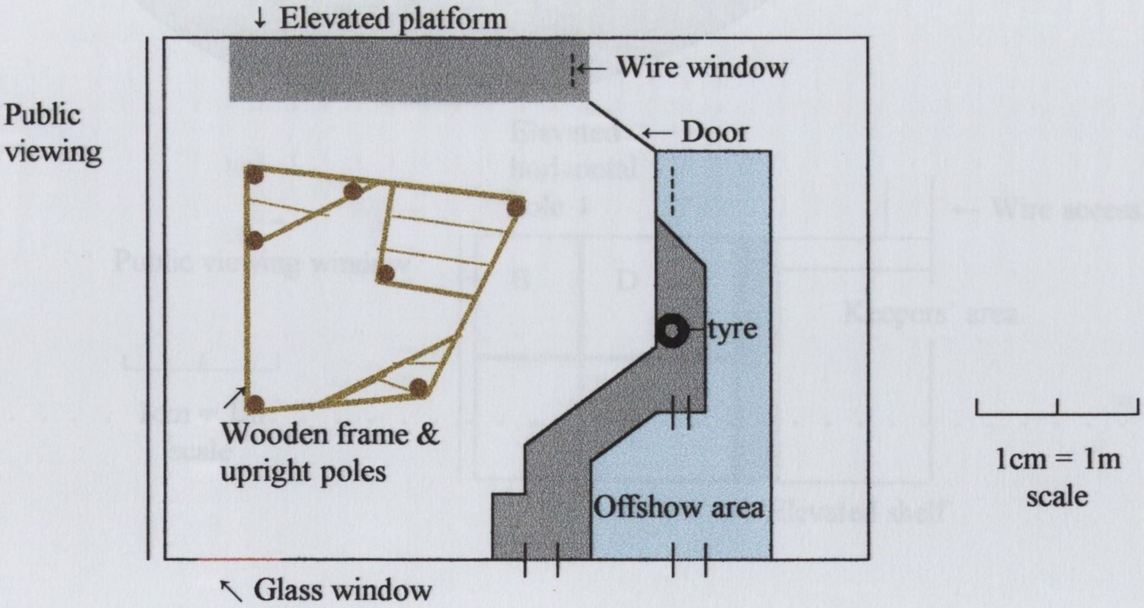


Appendix 6 Diagram of the Marwell Zoo Sulawesi macaque enclosure.



Appendix 7 Diagram of the Paignton Zoo Sulawesi macaque enclosure.





Appendix 8 Diagram of the Thrigby Hall Sulawesi macaque enclosure.