

Designing habitats to meet the mental and physical needs of captive primates

ABSTRACT

It is inevitable that the lives of primates in captivity will be different to those of wild conspecifics. However, if animal welfare is to be maintained, it is important that consideration is given to providing a captive environment which meets the behavioural and physical needs of the inhabitants. Environmental enrichment constitutes modifications to an environment to improve the biological functioning of the animals within it, and thus has the potential to allow the fulfilment of behavioural needs and reduce the development of abnormal behaviour. Careful consideration of the behaviour and anatomy of non-human primates, with particular reference to locomotion, food acquisition, resting, social interaction and lifestage should be used to guide the design of captive environments in order to maximise the welfare of the animals living in them.

KEYWORDS

Primates, behaviour, environmental enrichment, stereotypic behaviour, adaptations

INTRODUCTION

When animals are maintained in captivity it is important to consider the environment in which they are kept. The captive environment includes the design of the enclosure; the furnishings within it; the sensory inputs from outside the enclosure; the provision of food; and the other animals within the enclosure and surrounding areas.

The captive environment inevitably differs from the wild. A wild animal is required to spend much of its time trying simply to survive - avoiding predation and hunting or foraging for enough food to meet energy requirements. In the captive environment,

protection from predators and adequate nutrition is typically provided. As a result, a great deal of energy is 'leftover' without a useful outlet (Hediger, 1964). In addition the environment is generally less complex. This has the potential to lead to the development of 'boredom', abnormal behaviours and obesity (Herbert & Bard, 2000).

The provision of an inappropriate environment for captive animals can result in a number of problems including compromised animal welfare, a reduction in breeding success and compromised safety of both animals and human caregivers/visitors.

Environmental enrichment can be defined as 'an improvement in the biological functioning of captive animals resulting from modifications to their environment' (Newberry, 1995). These changes can vary in magnitude – from small-scale modifications like a change in substrate or the addition of a foraging device, to completely redesigning the environment in which the animals are housed. It should be remembered, however, that whilst environmental enrichment is of fundamental importance, it should not be used in order to compensate for a poorly designed and built enclosure (Law & Reid, 2010).

If changes to the environment are going to improve the biological functioning of animals – this is most likely to be via an increase in the expression of species-typical behaviour – then one must consider the adaptations of the species in question before undertaking any changes. It could be argued that these considerations are particularly important in primate species, which often have complex behavioural and physical needs. The design of primate enclosures is further complicated by the need to take into account the cognitive abilities, strength and manual dexterity of many primate species.

This review will consider the relationship between behavioural 'needs' and stereotypic behaviour, with particular reference to the use of environmental enrichment to allow the

former to be met; and to ameliorate the latter. This is followed by a discussion of the aspects of the environment which should be evaluated when designing a captive habitat, with special reference to the specific anatomical and behavioural characteristics of primates.

Behavioural 'Needs', Stereotypic Behaviour and Enrichment

Behavioural 'Needs'

Survival in the wild is dependent upon the performance of specific goal-directed behaviours. Thus it seems evident that evolution would favour the selection of individuals for whom the performance of such behaviours is self-rewarding (Dawkins, 1990). The chance to perform behaviours such as foraging or hunting may then be an important component of welfare. The concept of behavioural 'needs' was suggested by Hughes and Duncan (1988) as a powerful potential explanation as to why captive animals perform certain behaviours in the absence of positive reinforcement for the behaviour. The suggestion is that the underlying motivation to perform such behaviours (for example nest building in sows) is so strong that to deny the opportunity to perform them constitutes an animal welfare problem. The denial of behavioural 'needs' is one theory behind the development of so-called 'stereotypic' behaviours (Broom, 1983).

Stereotypic Behaviours

'Stereotypic behaviours' is a term used to describe a range of behaviours which share the common characteristics of being repetitive and apparently functionless (Mason et al., 2007). It has been suggested that some such behaviours may be indicative of a dysfunction of the Central Nervous System (CNS), evidence of frustration or a physical manifestation of a coping mechanism (Mason, 2006). There is evidence to suggest that

stereotypic behaviour may be indicative of underlying poor welfare, having been shown to co-vary with other signs of poor welfare such as elevated cortisol or poor reproductive performance (Wielebnowski et al., 2002). However, studies in some species have shown opposite results – for example farmed mink with high levels of stereotypic behaviour have lower levels of baseline plasma cortisol than mink with low levels of stereotypic behaviour (Bilsoe et al., 1991).

The reduction of the performance of stereotypic behaviour is one of the most common aims of environmental enrichment programmes implemented by zoos (Young, 2003). There are a number of reasons why the development of stereotypic behaviour in captive wild animals should be monitored, controlled and prevented. If education is an important function of zoos, it is important to display animals in a habitat which resembles their natural habitat and for individuals to display species-typical behaviour. Secondly, if individuals are to be released or bred for release into the wild, it is important that they are able to function in a manner which will promote survival in the wild. This is also true of animals undergoing rehabilitation with a view to eventual release. Thirdly, as caregivers for animals it is ethically important to consider the welfare of the animals being maintained in captivity.

A successful enrichment strategy is likely to reduce stereotypic behaviour by one or more of three mechanisms - creating an opportunity to perform alternative behaviour which is more rewarding than the stereotypic behaviour; by reducing the motivation driving the stereotypic behaviour (e.g. frustration or stress) or by offering an increase in control over the environment (Mason et al., 2007).

Enrichment

The aims of environmental enrichment vary according to the situation in which it is to

be implemented. However, two commonly cited objectives are to promote 'natural' behaviour and to 'improve' animal welfare. Chamove and Moodie (1990) describe some features of 'normal' behaviour which are desirable. These include a reduction in abnormal behaviours; an increase in the range or number of 'wild' behaviour patterns; performance of behaviours at a more natural time of day and a more natural response to environmental or social challenges. However, the quantification of success in these objectives is problematic (Newberry, 1995). In particular, one must be clear on two factors – firstly, what constitutes 'natural' behaviour? Secondly, what are the benefits of the performance of 'natural' behaviours over 'unnatural' or 'abnormal' behaviour?

For an enrichment strategy to be successful the aim should be for it to provide interest and stimulation to the recipient(s) beyond initial exploration and for it to be able to motivate desired changes in behaviour over a continued period of time (Tarou & Bashaw, 2007): i.e. the recipient should not become habituated to its effects.

The Physical Environment

A good enclosure will allow animals to demonstrate their preferences for different aspects of the captive environment (Dawkins, 1983). In order to facilitate this choice, careful consideration of the design of the enclosure is essential. Designing an appropriate captive environment can be a challenging task. Much debate has taken place throughout the history of modern animal keeping as to the merits of functional vs. naturalistic enclosures and enrichment. 'Behavioural engineering', was pioneered by Markowitz (1982) and utilises enrichment devices which reward animals with food when a task is performed correctly. This form of enrichment does not require a naturalistic enclosure, provided the furniture available allows the performance of natural

behaviour. There are two main potential difficulties with this approach. Firstly, the features of the natural environment which are important, or indeed essential, to the animals may not be immediately apparent to the observer. To the untrained eye, a rigid climbing frame built from scaffolding poles may appear to fulfill the same role as a tree in the captive environment. However, when considered from the animal perspective, the practical characteristics are very different – the tree is much more likely to elicit species-typical behaviours such as brachiation and increases usage of spatial learning and memory (Young, 2003), due to its complexity and flexibility/mobility of branches. The second difficulty is reconciling a ‘functional’, non-naturalistic enclosure with the modern zoo’s educational role. A non-naturalistic enclosure is likely to be less useful in educating the public about wild habitats and the interdependence of ecosystems. An alternative to this is a ‘naturalistic’ approach, whereby the environment is engineered to resemble the ‘natural’ environment as closely as possible (e.g. Hancocks, 1980). A number of studies have shown that visitors spend longer viewing naturalistic enclosures (e.g. Bitgood et al., 1988). Used properly, this approach may be more successful in encouraging species-typical behaviours in a captive environment. Recent research has suggested that naturalistic enclosures are more likely than non-naturalistic enclosures to appropriately meet the biological requirements of their inhabitants (Fabregas et al., 2011). Naturalistic enclosures have been associated with a decrease in the incidence of stereotypic behaviour and aggression and an increase in affiliative behaviour (Clarke et al., 1982; Hoff et al., 1997). However, the creation of a naturalistic enclosure may not be without pitfalls. Young (2003) describes two examples of this. In one zoo a specially-designed fiberglass tree provided for orang-utans (*Pongo pygmaeus*) did not provide enough grip to be climbed. Similarly, trees provided for anteaters had bark too smooth to facilitate climbing.

A sensible initial question is: ‘where in the physical environment is the species found?’. Eisenberg (1981) proposed an assessment of the substrate in which the animal lives in order to answer this question. In the case of primates, the answer is usually either terrestrial: (adapted to live on land); scansorial (adapted for climbing); arboreal (adapted to live in the trees) or, commonly, some combination of the three. Consideration of how a primate species may move through these habitats can facilitate appropriate enclosure design and selection of cage furniture.

Variation in Locomotor Styles

Primates exhibit a high diversity of morphology and behaviour (Cant, 1992) and this is particularly evident when one examines variation in locomotion. Aspects of the physical environment may obstruct straightforward locomotion and so features which enable

Table 1: Anatomical adaptations to locomotor styles in primates (Adapted from Fleagle, 1999)

Anatomical Feature	Terrestrial Quadruped	Arboreal Quadruped	Leaper	Suspensory
Digits	Short	Elongated/grasping	Elongated/grasping	Elongated/curved
Forelimbs	Robust radius	Deep ulna	Short, slender	Elongated; Rotary wrist
Elbow (Figure 1)	Posterior extension of olecranon; extensors predominate	Elongated olecranon; extensors predominate	-	Shortened olecranon; flexors predominate; supinators>pronators ¹
Shoulder	Restricted to anterior-posterior motion	Scapula laterally placed	-	Scapula dorsally placed
Thorax	Narrow	Narrow	-	Broad
Hindlimbs	Robust; retractors predominate	Long cf. forelimb	Elongated; narrow tibia; deep femoral condyle; short femoral neck (Figure 2)	Mobile joints
Tail	Reduced	Long	-	Often absent

¹ Supinators: muscles rotating the limb so palm is up and thumbs are away from body
Pronators: muscles rotating the limb so palm is down and thumbs are away from body

these obstacles to be overcome are important components of natural selection (Cant, 1992). Most species are capable of several types of locomotion, but show particular adaptations to a preferred method (Table 1).



Figure 1: Radiographic anatomy of the primate elbow

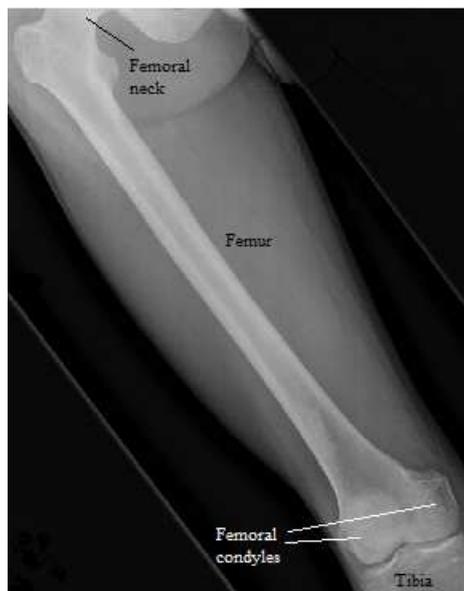


Figure 2: Radiographic anatomy of the primate femur

Consideration of normal locomotion in the wild provides guidance as to the structural requirements of the enclosure for a species. Closely related species with superficially similar external morphology may in fact have anatomical adaptations for particular styles of locomotion (e.g. *Presbytis* spp.; *Macaca* spp., discussed below). By considering observed behaviour alongside anatomical adaptations for locomotion, one

can make predictions about enclosure features which may be important for natural behaviour and hence animal welfare.

Body size is one feature which plays a role in the mechanism by which arboreal primates will choose to cross a gap between trees. The relatively small, gracile gibbon for example is able to leap or swing between branches due to the development of powerful muscles in the shoulder, carpal flexor region and in particular elbow flexor region (Michilsens et al., 2009), features which are consistent with the anatomy of other arboreal, brachiating species. The larger, heavier orang-utan is also capable of brachiation, but due to its size is more likely to utilise a ‘tree-swinging’ technique to cross a gap across which the gibbon would perform a ‘brachiating leap’ (Hunt et al., 1996) or swing (Napier, 1967). Consequently, gibbons are more likely to occupy the highest levels of the canopy, where the less dense structure favours the latter method of locomotion (Napier, 1967); whereas the orang-utan is more likely to remain lower in the canopy where sturdier tree limbs are able to support its larger weight.

However, size is not the only morphological feature which affects method of locomotion, as can be seen when similarly sized and even sometimes closely related species are compared.

Ateles sp. (spider monkey) and *Alouatta* sp. (howler monkey) are sympatric, prehensile-tailed New World monkeys which provide a useful comparison of the anatomical features which enable two different forms of locomotion. The spider monkey uses two-handed suspension and climbing as the predominant locomotor pattern. The muscle masses of the elbow flexors and supinators¹ are relatively large. This allows for the production of greater force in suspensory locomotion. In contrast, the howler monkey

moves through the forest using arboreal quadrupedal locomotion. The extensor muscles of the elbow predominate, resulting in more powerful forward motion during quadrupedal movement (Turnquist, 1983).

Similar relative adaptations can be seen if the anatomy of two closely related species of leaf monkey (*Presbytis obscura* and *P. melanophos*) is examined. Examples of these adaptations include relative enlargement of the retractors of the hind limb and extensors of the elbow in the more quadrupedal *P. obscura*, and relative enlargement of the flexors of the elbow in *P. melanophos*, which tends towards forelimb suspension and brachiation for forward movement (Fleagle, 1977).

Thus whilst initially it might be expected that these four species of arboreal monkey would have similar furnishing requirements for a captive environment, in reality their specific requirements are somewhat different. The quadrupedal species will require more attention to be paid to the provision of broad, horizontal or slightly angled supports, raised above the ground, along which they can move and between which they can jump. The brachiating species have a requirement for narrower branches which can be gripped by powerful hands and which have adequate space beneath them through which the body can be pulled by the forelimbs.

Arboreal locomotion in wild marmosets (*Callitrichidae*) is characterized by quadrupedal travel along moderate-large branches (Garber et al., 1996). Marmosets show reluctance to spend time on the ground except when absolutely necessary to cross clearings in the forest, or for occasional foraging expeditions (Stevenson & Rylands, 1988). This reluctance also applies in captivity, with common marmosets spending only 1-10% of their time on the floor of their cage (Mackenzie et al., 1986). In addition tree

trunks or other vertically orientated cage furnishings which are narrower than 15cm tend to be avoided (Hamrick, 1998). This preference for an arboreal lifestyle is reflected by several anatomical adaptations in marmosets. The digits end with small apical pads and claw-like nails, in contrast to the flattened true nails of most primates (Garber et al., 1996) which improve traction during clinging to vertical supports (Hamrick, 1998). By examining the relative extent of these adaptations one can make predictions about how much time the species is likely to spend foraging amongst the smallest branches of the canopy (diameter <3cm) (Hamrick, 1998). This information about the physical and behavioural characteristics of these species is essential in planning a suitable enclosure. Broad (>15cm diameter) vertically-orientated tree trunk-like structures are important features of the marmoset environment, as are a variety of elevated branch or perch-like structures which enable locomotion to take place high above the terrestrial substrate.

The pig-tailed macaque (*Macaca nemestrina*) and long-tailed macaque (*M. fascicularis*) are two species of macaque which occupy the same habitat when parts of their range overlap (Groves, 2001). Both species are quadrupedal, however, they tend to utilise different levels of the habitat during locomotion and foraging. Pig-tailed macaques tend to travel terrestrially over long distances, and thus one would expect to find anatomical adaptations for efficient ground travel, whereas long-tailed macaques require adaptations, particularly in the forelimbs, to enable leaping and climbing (Rodman, 1979). When startled, long-tailed macaques exhibit a primate-typical flight response and escapes upwards into the tree canopy. In contrast pig-tailed macaques show an atypical response, dropping to the ground and making an escape through terrestrial undergrowth (Rodman, 1979). Pig-tailed macaques feed primarily in the middle canopy, despite a preference for terrestrial locomotion. Wild long-tailed macaques feed almost

exclusively in the upper canopy, descending to the ground for only about 2% of their time (Wheatley, 1978).

Adaptations to differing locomotion are found in macaque anatomy. The pig-tailed macaque has elongated distal forelimbs which improve the efficiency with which ground is covered for each protraction of the shoulder joint. Conversely the long-tailed macaque shows elongation of the distal hind limb, as an adaptation for arboreal leaping (Rodman, 1979). More subtle anatomical differences include lengthening of the olecranon (Figure 1) in long-tailed macaques, allowing greater transmission of power in the elbow. This increased forelimb power aids efficient climbing. Relative shortening of the olecranon in pig-tailed macaques allows the elbow to extend fully during each stride, thus elongating stride length (Rodman, 1979). At every joint the pig-tailed macaque displays anatomical changes which appear to encourage efficient terrestrial travel by providing greater stride length for a given energy expenditure. Conversely, the more arboreal long-tailed macaque has an anatomical structure which appears to increase the transmission of power at each joint, allowing for more explosive leaping during locomotion (Rodman, 1979).

Another obvious morphological difference between these two macaque species is in the length of the tail – indeed this difference has resulted in the common names used for these species. Although their tails are not prehensile, they are nonetheless important for arboreal primates, aiding balance and acting as a counterbalance when at rest. This may help to explain the much longer tail length in *M. fascicularis* vs. *M. nemestrina* (Rodman, 1979).

Considering the anatomy of these two species together with their behaviour in the wild,

a number of differences in their environmental requirements become apparent. Both require arboreal elements to their enclosure; however this is likely to be more important to the long-tailed macaque. It is important that particular attention is played to the terrestrial substrate provided for pig-tailed macaques. This substrate may be used for ground foraging, resting and in particular locomotion and thus consideration should be given to the depth, texture and insulating capacities of the substrate.

Cage furnishings for arboreal animals should be of material and dimensions that are appropriate and the structure should feel suitably stable when in use (Redshaw & Mallinson, 1991). Primates are only seen to make use of cage structures if they are of an appropriate height and position for the individuals concerned (Ely et al., 1998). The position of visual barriers is also important. Long-tailed macaques and pig-tailed macaques, for example, require species-typical retreats at arboreal and ground levels respectively.

However it must also be remembered that natural habitats are dynamic. This may be particularly true of arboreal habitats – trees grow, branches break, seasonal changes result in differing foliage densities. This provides a constant challenge both to primate physical features but also to mental capabilities. New routes must be found and remembered, challenging cognitive mapping abilities. A static captive environment runs the risk of failing to challenge primate minds (Young, 2003). It is therefore important that cage furnishings are mobile and flexible, and that consideration is given to how the environment will be manipulated and updated.

Food Acquisition and Feeding

Primates also exhibit significant diversity in the methods by which they obtain food in the wild. As with locomotion, one can use evidence from morphology in combination with behaviour observations to guide the design of the captive environment.

Under natural conditions many primate species spend the greater part of their day searching for and manipulating food (Table 2). Captive primates tend to spend less time foraging than their wild counterparts (e.g. Kerridge, 2005); food is regularly provisioned and easier to consume. In addition feeding often follows a predictable schedule which can cause anticipatory anxiety, leading to negative changes in behaviour (Waite & Buchanan-Smith, 2001).

Table 2: Time spent engaged in feeding behaviour in some example primate species

Primary Feeding Pattern	Example Species	Percentage Time Spent Feeding	Reference
Folivorous	Gorilla <i>Gorilla gorilla</i>	54.2	Lehmann et al., 2008
Folivorous	Gelada <i>Theropithecus gelada</i>	47.7	Iwamoto & Dunbar, 1983
Gummivorous	Black tufted-ear marmoset <i>Callithrix jacchus penicillata</i>	35.2	da Fonseca & Lacher, 1984
Frugivorous	Night monkey <i>Aotus azarae</i>	31.7	Garcia & Braza, 1987
Frugivorous	Squirrel monkey <i>Saimiri sciureus</i>	11.0	Terborgh, 1983

Primate feeding patterns are typically classified as leaf-eating (folivorous); fruit-eating (frugivorous); insect-eating (insectivorous); animal-eating (carnivorous) or gum-eating

(gummivorous). However, this is a simplified interpretation of the reality of the complexity of primate diets - most primates will consume a mixture of these in varying proportions.

A major problem in feeding plant matter to captive primates is the nutritional difference between roots, fruits, vegetables and browse available in the wild vs. captivity (Kawata, 2008). Fruit and vegetables provided by zoos and rescue centres tend to be more nutritionally dense and lower in fibre than those consumed in the wild (Schwitzer & Kaumanns, 2001). In addition, the provision of sufficient browse in a zoo environment can be extremely difficult. As a consequence, more concentrated food may be provided, thus reducing feeding and foraging time compared to wild counterparts (e.g. Blois-Heulin & Jubin, 2004).

Even within one category – the folivores - the digestive anatomy can show substantial variation. Consideration of this anatomy provides information which can guide the formulation of appropriate diets and monitoring for the various potential health problems which may arise as a consequence of imperfect feeding regimes. Langurs (Genera *Trachypithecus*, *Presbytis*, *Semnopithecus*) are examples of foregut-fermenting species; the digestive system of these colobines is akin to that of cattle. When fed inappropriate diet such as those containing high proportions of fruit, coloured vegetables, grain and dairy products, they are prone to disturbances of the gut microflora and thus fermentation; this can lead to potentially fatal metabolic disease similar to rumen acidosis seen in cattle (Kay & Davies, 1994). Lower level disturbances often lead to chronic soft faeces and diarrhoea (van Nijboer et al., 2007). Folivorous lemurs (Families *Indriidae*, *Lemuridae*, *Lepilemuridae*) have a different anatomy as hindgut-fermenting species. This means that when fed similarly inappropriate diets

there is another nutritional problem - an over-production of energy from easily digestible carbohydrates. This is associated with the development of obesity in a large proportion of captive lemurs (Schwitzer & Kaumanns, 2001).

True carnivory is not a feeding pattern typically described in primates (tarsiers *Tarsius spp.* the only extant exception: Niemitz, 1984), however, many species show adaptations to an omnivorous feeding pattern, which may include aspects of predatory behaviour; Butynski (1982) describes the hunting of vertebrates by non-human primates as 'widespread but infrequent'. Adaptations to predatory behaviour may be anatomical (e.g. shortened gastro-intestinal tract; piercing dentition), behavioural or nutritional.

The slender loris (*Loris tardigradus*, *L. lydekkerianus*) exhibits specialised anatomical adaptations for the acquisition of mobile food. These species are almost exclusively (96-100%) faunivorous (Nekaris, 2005). Specialisations for hunting invertebrate prey on middle and terminal branches include small hands and a specialised blood supply to the distal limb which allows for extended grasping while awaiting the right moment to perform a one-handed or two-handed grab of prey. Slender loris are rarely seen on any support which is not narrow enough in diameter for them to grasp fully (Nekaris, 2001). Thus the provision of suitably narrow branches to allow this species-typical behaviour is crucial in the design of a captive environment for this species. This is in contrast to the related slow loris (*Nycticebus spp.*) which show a preference for larger, more stable branches (Dykyj, 1980) where they are more specialised for the consumption of plant exudates (Wiens, 2002) than live prey, which is of lesser importance in the diet. The acrobatic nature of the loris hunting posture and the specialised two-handed prey grab suggest that the opportunity to perform this hunting behaviour may be important to

these animals. A lack of opportunity to hunt moving prey may pose a welfare challenge to these animals and thus consideration should be given to ways in which hunting scenarios can be replicated in captivity.

Vitamin B12 is usually obtained by non-carnivorous animals via gut bacteria. An example of a nutritional adaptation to predatory behaviour is the requirement of baboons (*Papio spp.*) for an exogenous source of vitamin B12 (Hausfater, 1976). Another example is the chimpanzee, *Pan troglodytes* where hunting behaviour is relatively rare and regionally variable (Whiten et al., 2001), and as a rule only very few adult males appear to have a strong motivational drive for predatory behaviour (Gilby et al., 2008). However, small amounts of meat seem to be beneficial to these primarily vegetarian primates, and hunting behaviour is sometimes observed amongst wild troops. Thus the provision of animal protein in captivity may be more important than the provision of opportunities to perform predatory behaviour. Nutritional requirements for animal-derived food sources may be more easily dealt with in the captive situation than behavioural needs to express predatory behaviour – food supplements and/or prepared meat may be more easily obtainable and more aesthetically and ethically acceptable to the visiting public than the provision of live prey.

The provision of live foods to captive animals is a source of much ethical debate. In the United Kingdom the feeding of live vertebrate prey is illegal under the Animal Protection Act 1911. However, in many other countries the practice is legal and thus the ethical debate over the feeding of live prey must be considered. The central question is: which animal's welfare is more severely compromised – the predator not able to exhibit species-typical hunting behaviour, or the prey subjected to a hunt from which it is very unlikely to escape? The often-held view is that visitors find the practice of live feedings

distasteful. However, a study at San Francisco Zoo in California (Markowitz & Aday, 1998) found that visitors were in fact very interested in watching the species-typical hunting behaviour exhibited by North American river otters (*Lontra canadensis*) when they were provided with live fish; no negative comments from the public were elicited in response to this practice.

Marmosets and tamarins exhibit a number of adaptations for the acquisition and consumption of tree exudates or 'gum'. These exudates are an important source of energy and calcium, for which they may have a particular requirement (Power et al., 1999).

Evidence suggests that an ability to cling to large (>15cm) diameter vertical tree trunks to access gum is an important adaptation in marmosets (Garber, 1992); particularly visible morphological features of this adaptation are clawed fingers (Rylands & Faria, 1993). This adaptation would seem useful in maintaining an appropriate posture for the performance of exudativory behaviours. Oro-facial adaptations to gummivory are also found in these species, including adaptations to the jaw muscles (Taylor et al., 1999); incisiform canines (Rylands & Faria, 1993); sharpening of the upper incisors and a decrease in enamel on the lingual aspect of the lower incisors (Coimbra-Filho & Mittermier, 1978). Marmosets exhibit a strong behavioural drive to perform exudativory behaviours – captive individuals will even continue to gouge holes in cage furniture in the absence of a food reward (Kelly, 1993). Appropriate gum supplementation enables marmosets to perform species-typical behaviours (McGrew et al., 1986). This may result in improved animal welfare and a potential decrease in the performance of stereotypical behaviours related to frustration (Roberts et al., 1999; Pupe et al., 2011).

Resting and Comfort

Consideration should always be given to the provision of appropriate locations for sleeping and rest. Most species, even those which are semi-terrestrial, sleep in elevated locations at night (Anderson, 2000). The selection of a safe resting place may be considered a behavioural 'need' as many species will continue to select 'safe' sleeping locations even in the absence of predators (Anderson, 2000). Some primate species are known to build nests as sleeping areas (e.g. apes; Anderson, 2000). It is important that these species are provided with adequate quantities of an appropriate material in order to perform this species-typical behaviour. The opportunity to perform species-typical sleep-related behaviours may be particularly important when re-release is an option for animals or their offspring. Sleep behaviour may be learnt from the mother and thus social transmission could be lost when no appropriate sleeping locations are provided (Bernstein, 1962).

The new-world monkeys lack ischial calluses (hardened skin pads on the rump) and thus perch using their feet (Washburn, 1957). The provision of sleeping/resting perches which are rounded rather than flat is thus important in the prevention of sores.

Primates may be prone to thermoregulatory issues if they are housed in zoos or other captive situations in regions where the climate is cooler than their typical habitat. Many primate species huddle together as a thermoregulatory mechanism. Research has shown that the social behaviour of monkeys may be affected by the microclimate in which the animals are kept, for example a reduction in inter-individual distance in cool (13-24°C) temperatures (Schino & Troisi, 1990). There are two important consequences of this. Firstly, animals which are kept alone, in very small groups or with inappropriate

furniture which does not facilitate huddling behaviour may not be able to utilize this form of thermoregulation. Secondly, the keeping of social primates in very cold conditions may have a profound effect on their social behaviour. This could be partially controlled by using appropriately-located heat lamps, thermoneutral materials such as wood or plastic (Wolfensohn & Honess, 2005) and the selection of insulating substrates such as wood shavings, straw or bark (Waite et al., 2010).

Social Groupings

Two main theories have been suggested to explain the group-living social structure found in many non-human primate species. The first suggests that group living is advantageous as it allows primates to locate and defend high-quality food resources more efficiently (Wrangham, 1980). An alternative theory is that group-living confers an advantage in the form of predator avoidance (van Schaik et al., 1983). A meta-analysis by van Schaik (1983) suggests that the latter theory has played a greater role in the evolution of group living in diurnal primates. In captivity, food resources are generally sufficient, even abundant. Protection against predators is provided in almost every case. Therefore, what benefit is there to the captive-living primate to be housed with others of its own or other species?

Studies have shown that social isolation of normally social species results in severe behavioural abnormalities. Some extreme work by Harlow et al. (e.g. 1965) for example, showed that social competence in macaques was particularly compromised by prolonged isolation during formative months. Social isolation has been shown to have profoundly negative effects on the immune system and survival (Lewis et al., 2000). Other effects including increased incidence of stereotypic behaviours have also been

described (Roy, 1981). These findings would suggest that normal social interaction is important in order to learn about appropriate behaviour and to decrease stress levels. Allo-grooming, the grooming of others, is a particularly important social behaviour in primates (Dunbar, 2010), associated with physiological indicators of reduced stress: decreased heart rate (Boccia et al., 1989) and increased opioid levels (Graves et al., 2002). Appropriate social groupings are also essential for the reproductive success of many species.

In general non-human primates are motivated to seek social contact; this suggests that the company of conspecifics is of value to them. A large variety of choice tests have been performed in various primate species. Bonnet macaques (*Macaca radiata*) trained to use a joystick to perform simple tasks will choose a social reward as often as they choose a food reward (Andrews et al., 1995). Macaques of many species will also press a lever (Fujita, 1987) in order to obtain social stimuli; rhesus macaques (*Macaca mulatta*) sacrifice fluid intake in order to view the faces of high-ranking conspecifics or the perinea of oestrus females (Deaner et al., 2005). Thus it seems likely that the provision of appropriate social contact is important for animal welfare; indeed, of all forms of enrichment, social enrichment has the greatest potential to positively impact upon quality of life (Reinhardt, 2004). Vogt et al. (1981) demonstrated a reduction in the stress response of individuals following an aversive event (presentation of a caged snake), when conspecifics were present vs. the same event when isolated from conspecifics, a phenomenon termed 'social buffering'.

An exception to this rule is the mainly non-gregarious orang-utan, which has a more solitary lifestyle due to a lack of predators and dispersed food sources (Delgado & van Schaik, 2000). There is little information available on the preference of these animals

for social contact vs. individual housing and thus the animal welfare implications for them of social housing are open to debate (Young, 2003). Despite this, most zoos continue to house them socially.

Captive social groupings are theoretically more flexible (Price & Stoinski, 2007) than their wild counterparts, due to a lack of predators and increased food availability. However, this flexibility has limits - in particular the captive environment places constraints on the variable inter-individual distance, fission-fusion social culture and inter-group migration which are common amongst many primate species. Therefore it is important that consideration is given to the normal social structure when planning primate captive environment.

The diversity of social grouping in primates provides potential difficulties for their housing in appropriate groupings in captivity. If the structure is not correct then negative effects such as stress (Plowman et al., 2005), poor reproductive success (Bardi et al., 2001) and abnormally elevated aggression (Erwin & Erwin, 1976) could result. There are, however, ways in which the negative effects of imperfect social groupings, or of normal social groupings kept in a less than ideal environment, can be ameliorated. Many species including the long-tailed macaque use natural visual barriers such as vegetation to hide from conspecifics during agonistic encounters (Waite et al., 2008) or when attempting to avoid predation (van Schaik et al., 1983). This information has been used by several authors to guide the design of visual barriers in captive macaque enclosures, which have been successful in reducing aggressive encounters and increasing affiliative behaviour (e.g. Maninger et al., 1998; Reinhardt & Reinhardt, 1991).

Animals are known to have a preferred ‘individual distance’ – the distance between individuals within a social group (Hediger, 1964). This distance is dependent on species by individual temperament. In wild squirrel monkeys individual distance is estimated at $\geq 3\text{m}$ for 75% of the time budget (Marriot & Meyers, 2005). However in captivity the distance is also affected by the size of the available in space. In several species including squirrel monkeys it has been demonstrated that individual distance increases are positively correlated with increases in available enclosure space (Marriot & Meyers, 2005). Where known, consideration should be given to the preferred individual distance of a species when planning a captive environment. Failure to provide sufficient room to allow this natural spacing may result in increases in aggression (Sannen et al., 2004) or the implementation of coping strategies such as increased allogrooming (Judge & de Waal, 1997). These behavioural changes may be associated with stress. However more research is required in this area as research outcomes have been mixed.

In addition to providing the company of conspecifics, there is also the potential to form mixed-species exhibits of primates in captivity. There is evidence that many primate species voluntarily interact with each other in the wild (e.g. Eckardt & Zuberbuhler, 2004; Mitani, 1991) and this may be a useful source of social enrichment in captivity. Ideally, species should only be kept together when there is observational evidence for their association in the wild. Provided appropriate species are chosen, mixed-species primate exhibits may be associated with an increase in species-typical behaviours, good welfare and an increase in the educational value of exhibits (Leonard et al., 2010).

Temperament and Lifestage

Clearly, the requirements of an enrichment programme for one species may be very

different to the requirements of a species from another order or family. More subtly the requirements for different individuals may vary according to sex, age or health factors and this should be taken into consideration. The importance of temperament (both species characteristics and individual personality traits) and lifestage should not be underestimated in the planning of a captive environment.

Species Differences

Primates generally show signs of stressful excitement in response to unfamiliar humans (e.g. zoo visitors) in the vicinity of their enclosure. These signs may include an increase in locomotion, increase in agonistic behaviour and a decrease in affiliative behaviour (Hosey, 2008). However, some species fail to exhibit this stress-related response. The black lion tamarin (*Leontopithecus chrysopygus*), for example, has been described as 'relaxed' due to a lack of behavioural changes in the presence of zoo visitors (Wormell et al., 1996). This may suggest that this species is more resilient and thus suitable for placement in an enclosure with higher visitor density, or in an enclosure with more exposure. If it can be demonstrated that a physiological stress response is also reduced or absent, this has the potential to influence the best way in which new individuals may be introduced to an established social group. It may also influence the most appropriate design for a captive enclosure.

Species differences in the response to a novel object have also been described within the same family. Titi monkeys (*Callicebus spp.*) have been shown to be more reactive, both behaviourally and physiologically, than the related squirrel monkey (Hennessy et al., 1995). Thus it could be argued that extra attention should be paid to minimising the stress associated with husbandry events such as enclosure moves or the introduction of

new partners in known stress-reactive species such as the titi monkey.

Species differences in temperament can be marked even within a genus. Clarke and Mason (1988) demonstrated marked differences between the emotional responses of three macaque species (rhesus, long-tailed and bonnet macaques) to social stimuli. The rhesus macaque was shown to be more aggressive and the long-tailed macaque more fearful in response to novel social stimuli.

Individual Differences

Individual differences may affect the response to an unfamiliar enclosure or enrichment device. Neophobia may be influenced by rearing situation (e.g. natural or human-reared), however, there is evidence to suggest neophobia is an innate personality trait (Timmermans et al., 1994). Neophobia may result in increased stress or the failure to utilize objects or areas which might otherwise have a positive impact on welfare. Social rank may also have a profound impact on behaviour and enrichment usage. Thus careful observation of captive individuals is important in order to predict the best method by which enclosure moves, social introductions and the introduction of enrichment manipulanda may be undertaken.

Gender Differences

There may also be gender differences in response to manipulations of the environment. A greater response was seen in female vs. male mangabeys (*Cercocebus torquatus torquatus*) following introduction of foraging enrichment (Blois-Heulin & Jubin, 2004). Similarly, female rhesus macaques were observed to be more interested in

videostimulation enrichment (Platt & Novak, 1997).

Age differences

Animals' lifestages should be taken into account in enclosure design. The age of primates will influence in particular the efficacy of enrichment, the quality of social relationships and the ease with which they will move around the environment. Failure to take into account the differing needs of juvenile, adult and geriatric primates may have a substantial impact on health and welfare.

Evidence from Japanese macaques suggests that male interest in external stimuli such as video enrichment may decrease with age (Tsuchida & Izumi, 2009), although this effect may be confounded by age-related changes in rank. Aged chimpanzees have been shown to interact less both with objects within, and the structure of, their enclosure (Baker, 2000). A range of simple toys had no effect on the behaviour of aged rhesus monkeys in a captive situation (Line et al., 1991) although this was disputed by the findings of Novak et al. (1993) who found that aged individuals continued to show an interest in familiar objects when they were socially housed. These results show that age may have an effect on the efficacy of enrichment devices, which may be of less interest to geriatric individuals. The provision of a more actively responsive environment and carefully considered social enrichment could be more beneficial in improving the welfare of older animals.

Aged primates may also become less socially flexible than younger counterparts (Veenema et al., 2001). This may account for apparently socially withdrawn older individuals. Evidence from captive chimpanzees suggests that older individuals exhibit lower levels of aggression than younger counterparts (Baker, 2000). Aged females may

also show more submissive behaviour (Baker, 2000). This information has important implications for the housing of older individuals, who may be less able to form new social relationships if introduced to new groups. Both young and old primates may appreciate the introduction of visual barriers to the enclosure to allow them an escape from social interactions (Waite et al., 2010) both in newly-formed and in established groups. When put together this information suggests that the continued provision of a stable social group should be of great importance when considering the future of aging adult primates.

The mobility of older primates may be restricted by joint problems (e.g. arthritis) or by reduction in visual acuity (Waite et al., 2010). Structural modifications such as ramps can be used to improve the accessibility of raised areas of an environment for arboreal species (Zucker et al., 1991). The importance of flexible, mobile furniture in maintaining normal physical function in healthy adult animals has been discussed above. In aged animals with reduced mobility a more rigid, immobile structure is likely to be preferred.

It is also important to remember that overall activity levels may be lower in aged primates (e.g. Baker, 2000). This may predispose older animals to obesity, leading to additional health and welfare problems. Control of this problem may require a change in the nutritional composition of the diet. Conversely, juveniles may require more space per animal to allow for play and proper psycho-motor development.

Conclusion

It has been demonstrated that the design of an appropriate captive environment for primates may be more complex than previously thought. A full evaluation of the known anatomical and behavioural adaptations to the natural environment should be undertaken, with this information being used to guide every stage of the design, from initial aspects such as size and substrates, right through to daily environmental enrichment strategies. In doing so the caregiver has the chance to make the best use of available finances and space: improving educational value of zoos; optimizing physical and mental health; and promoting good animal welfare.

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The effect of three environmental enrichment techniques on species-typical behaviours in long-tailed macaques (*Macaca fascicularis*) and pig-tailed macaques (*Macaca nemestrina*)

ABSTRACT

Environmental enrichment is potentially a useful tool in the rehabilitation of captive animals prior to release into the wild. Whilst the efficacy of environmental enrichment is well-documented in improving the welfare of zoo, and particularly laboratory, animals, its use and efficacy in rehabilitation is not. This study investigated the activity time budgets and enclosure utilisation of two captive species of macaques, *Macaca fascicularis* and *Macaca nemestrina*, in a rescue-rehabilitation context. Both species showed some behavioural divergence from wild populations, spending more time inactive and less time in locomotion. The effect of three environmental enrichment treatments (foraging, structural and combined) on behaviour and enclosure usage was investigated. There were significant changes in levels of feeding-foraging ($p=0.001$); inactivity ($p=0.025$) and stress-responsive behaviour ($p=0.013$) across the phases in *M. fascicularis*. *M. nemestrina* showed significant changes in levels of affiliative behaviour ($p=0.005$); feeding-foraging (0.006); locomotion ($p=0.012$) and inactivity ($p=0.009$). The Spread of Participation Index (SPI) was used to investigate the use of the enclosure by both species across the phases. *M. fascicularis* spent substantially more time (80.0% of observed time) in the upper level of the enclosure, as expected given their natural degree of arboreality. *M. nemestrina* showed greater usage of the available space (65.9% of observed time in upper level), reflecting its more terrestrial nature. The study shows that simple, cost-effective enrichment techniques may be useful in the

rehabilitation of captive wild primates. In addition, the study demonstrates that the preferences of primates in the wild and in captivity can be used to guide the design of captive enclosures in a rescue-rehabilitation centre.

KEYWORDS

Long-tailed macaque, pig-tailed macaque, rehabilitation, enrichment, enclosure usage

INTRODUCTION

The long-tailed (*Macaca fascicularis*; Figure 1) and pig-tailed (*M. nemestrina*; Figure 2) macaques are two representatives of over twenty species in the *Macaca* genus. Long-tailed macaques are widespread throughout south-east Asia; pig-tailed macaques are restricted to Brunei, Indonesia, Malaysia and Thailand (Ong & Richardson, 2008).



Figure 1: Sub-adult female and adult male *M. fascicularis*



Figure 2: Adult female *M. nemestrina*

Long-tailed macaques are classified by the IUCN Red List of Threatened Species as 'Least concern' and pig-tails as 'Vulnerable'; populations of both are declining (Ong & Richardson, 2008; Richardson et al., 2008). They face pressure due to removal from the wild for laboratory research, illegal pet trade, hunting and habitat loss (Ong & Richardson, 2008; Richardson et al., 2008; Eudey, 2008).

A number of organisations now undertake rescue, rehabilitation and release of macaques. Scant literature is available regarding appropriate techniques for rehabilitation, particularly with reference to environmental enrichment. However, useful information can be gained from enrichment work undertaken in other settings such as zoos or laboratories (e.g. Mallapur et al., 2007; Boccia & Hijazi, 1998).

Environmental enrichment has been defined as 'improvement in the biological

functioning of captive animals resulting from modifications to their environment' (Newberry, 1995). Thus a successful enrichment programme uses changes to the environment to improve the welfare of captive animals - typically by encouraging species-typical behaviours (Mallapur et al., 2007); reducing the occurrence of abnormal or species-atypical behaviours (Boccia & Hijazi, 1998) or changing activity budgets to more closely resemble wild counterparts (Kerridge, 2005).

There are two main reasons to encourage proper implementation of environmental enrichment in a rescue-rehabilitation context. Firstly, if animals are to be truly rehabilitated and prepared for release into the wild they must be physically and psychologically capable of survival or welfare and conservation will be severely compromised. Environmental enrichment can be a key tool in the rehabilitation process: improving physical fitness, problem-solving skills (Meehan & Mench, 2007) and manual dexterity.

Secondly, inevitably some rescued animals will never be fit for release due to physical problems such as dental disease, previous malnutrition, injury or permanent psychological problems. Environmental enrichment can be just as important for individuals who will live out their lives in captivity. Enrichment can be used to improve physical fitness; reduce the risk of obesity (Wolfensohn & Honess, 2005); prevent boredom (e.g. Honess & Marin, 2006); improve social interactions (Chamove & Moodie, 1990; Honess & Marin, 2006) and reduce the development of stereotypies (Boccia & Hijazi, 1998). These changes may reflect improved quality of life.

The many potential benefits of environmental enrichment are clear. However, if real

improvements to animal welfare are to be made it is crucial that any new enrichment technique is properly validated: by defining the aims of the enrichment and then demonstrating the safety and efficacy of the technique, (Young, 2003).

The aim of this study was to record the activity budgets and enclosure usage of groups of long-tailed (Study A) and pig-tailed (Study B) macaques and to assess the effect of three enrichment treatments on these parameters. The enrichment methods chosen were simple, low-cost treatments which could, if successful, be easily replicated in the future.

Three hypotheses were investigated.

H₁ = alterations in activity budgets are seen in the presence of foraging enrichment vs. structural enrichment vs. combined foraging-structural enrichment scenarios

H₂ = the introduction of enrichment techniques induces a change in behaviour towards wild-type activity budgets

H₃ = the introduction of enrichment techniques in the upper levels of an enclosure induces increased usage of the upper levels of the enclosure

MATERIALS AND METHODS

Study location

The International Animal Rescue (IAR) Primate Rehabilitation Centre in Ciapus, Java, Indonesia is involved in the rescue, rehabilitation and release of macaques (primarily *M. fascicularis* and *M. nemestrina*) and slow lorises (*Nycticebus* spp.) confiscated or surrendered from the illegal pet trade or rescued due to habitat destruction. In the case of animals unfit for release due to physical or psychological problems permanent sanctuary is provided. Depending on rehabilitation and socialisation schedules animals may spend 6-24 months at the centre before release. Data collection was undertaken between March and June 2011.

Study Subjects

Study A was conducted on a stable social group of seven long-tailed macaques undergoing rehabilitation. The group consisted of two adult males; one adult female; two sub-adult females; one juvenile female and one juvenile male.

Study B was conducted on six pig-tailed macaques which were maintained in a permanent sanctuary situation. They were housed in three stable, heterosexual pairs.

With the exception of one of the juvenile male long-tailed macaques, all of the animals had been sterilised prior to commencement of the study. The full history of the individuals prior to arrival at the centre was unknown; most had come via other rescue rehabilitation centres.

Housing and husbandry

Feeding

The macaques were fed a variety of foods daily from a selection of locally available fruit, vegetables and fresh forage plus rice, peanuts, boiled eggs, tofu, tempeh, crickets and mealworms.

Food was provided over seven feedings which took place between 0700 and 1600. The food was thrown onto the cage roof to provide additional opportunities for foraging either from the roof itself or from the floor if foodstuffs fell through the roofing mesh.

Study A

The housing complex consisted of six interconnected cages each measuring approximately 3 (l) x 3 (w) x 3(h) metres. The cages were well-ventilated with a bamboo roof providing shelter and shade. The furniture showed slight variation between cages but the standard layout included large branches pointing upwards from the centre of the cage with smaller branches laid horizontally to the walls of the cage; rope and tyre swings and a wooden rest box (Figure 3).



Figure 3: Example cage furniture in Study A

The layout of the housing complex enabled social enrichment not only from cage-mates but also via visual, auditory, olfactory and tactile communication with individuals in

adjacent cages.

Each day between the morning and mid-day observation sessions the animals were moved between adjacent cages in order to allow thorough cage cleaning. This allowed a daily environmental enrichment by varying the visual, aural and olfactory stimuli available from the surrounding environment.

Study B

The sanctuary complex in which two of the pairs (Groups Ba and Bb) were housed was separate to the rehabilitation cages. The cages measured approximately 3.5 (l) x 3.5 (w) x 3 (h) metres, slightly longer and wider than the cages in Study A but otherwise similarly-sized. A tinted plastic roof provided shelter and shade over approximately half the cage. The furniture again showed slight variation between the cages but was similar in design to that in Study A: branches, rope and tyre swings and a wooden rest box (Figure 4).



Figure 4: Example cage structure and furniture in Study B

Visual, auditory and olfactory communication was possible between the cages but physical contact such as grooming was not.

Each day between morning and mid-day observations the animals were contained in one side of the cage by a mesh partition in order to allow cage cleaning of the other half.

Following cleaning the animals were allowed to access to the full cage once more.

Group Bc was housed in the same style of accommodation as in Study A.

Experimental Design

A pilot study was undertaken for ten days prior to the start of data collection for the main study. This period allowed accurate recognition by the observer of the individual animals, familiarisation with the data collection software (JWatcher V1.0), refinement of the ethogram and habituation of the animals to the observer's presence.

It is important to produce a structured plan and schedule for enrichment (Bloomsmith et al., 1991; Wolfensohn & Honess, 2005; Young, 2003). Whilst an enrichment programme exists at IAR, it had some room for refinement: an evidence-base for its efficacy and an improved enrichment schedule. It was decided to devise and test one foraging and one structural enrichment device. A within-subjects A-B-C-D-A experimental design was used to allow the group to act as its own control. An un-enriched condition at the beginning and end of the study provided control for potentially confounding temporal/developmental changes in behaviour. (Young, 2003).

The first enrichment options was bamboo branches on the mesh cage roof (Figure 5).



Figure 5: Foraging enrichment (bamboo on cage roof)

Both long-tailed and pig-tailed macaques are primarily arboreal feeders (Rodman, 1979). The macaques at IAR already receive rooftop feeding. Chopped fruits and vegetables were thrown onto the mesh cage roof, which encourages hand-eye coordination and natural arboreal feeding postures (Britt, 1993). However during the pilot study it was observed that almost all of the food fell through the mesh to the floor. Whilst this allows normal ground foraging behaviour, any advantage of rooftop feeding is lost. It was suggested that smaller diameter mesh could be used to prevent this. However concern arose about extra work and wastage of retained food. Dickie (1998) used straw on the roof of old-world monkey enclosures in a zoo setting to slow the passage of foodstuffs; the straw then had to be manipulated by the monkeys before they could access all the food. Straw was not easily available for this study; a cheap and safe alternative was bamboo. Despite being ubiquitous in south-east Asia, bamboo is not eaten by wild macaques (Yeager, 1996). Bamboo was used in other enrichment devices at IAR with no reported problems (IAR keepers, pers. comm.), and therefore used on cage roofs as an easily removable, cheap alternative to straw in the first enrichment phase. The primary aim of this phase was to provide increased complexity of foraging opportunities by providing an additional substrate; this also had the potential to reduce monopolisation of high-value food items by dominant individuals. This treatment also caused more food to remain on the roof, allowing the animals to make more use of the upper levels of the cage. In addition the effect of the bamboo on the roof also mimicked the effect of the forest canopy, providing a more naturalistic environment.

The second enrichment was a multi-purpose piece of cage furniture: a large tunnel measuring approx 1(l) x 0.5(d) metres, consisting of a bamboo frame with hessian sacking panels (Figure 6). This was suspended from the ceiling of the cage by rubber

bungee cords, holding the structure in place but providing some flexibility and movement of the tunnel.



Figure 6: Structural enrichment (hessian tunnel)

The tunnel was designed to serve several functions. One potential use was in the stimulation of play. Play in juvenile mammals promotes behavioural and emotional versatility, locomotor coordination and manual dexterity (Spinka et al., 2001).

Secondly, the tunnel could provide locomotor exercise by providing a mobile substrate across or through which the macaques could move. The adjustments in locomotion and posture required due to the movement may mimic those required to negotiate the natural movement of tree branches (Young, 2003), improving balance and coordination. Lastly, the opaque nature of the tunnel structure meant that it would act as a visual barrier.

Visual barriers help to reduce anxiety and aggression by giving individuals a place to retreat in response to a threat (perceived or real) (see Honess & Marin, 2006 for a review) and by providing privacy may help to improve the quality of social relationships in primates (Reinhardt & Reinhardt, 1991).

The study was divided into five phases:

Phase 1 (P1) consisted of a pre-enrichment baseline phase.

Phase 2 (P2), the foraging enrichment phase (Figure 5).

During Phase 3 (P3) the bamboo layer was maintained to continue to provide foraging enrichment and the structural enrichment was added.

Phase 4 (P4) required the removal of the bamboo layer of foraging enrichment with the structural enrichment (tunnel) left in place.

Finally the tunnel was removed to allow Phase 1 to be repeated as a post-enrichment control phase (P5).

Each phase of the study lasted five days. A two-day rest period was allowed between each phase; this allowed the changes to the environment to be made 48 hours before data collection for the next phase began, allowing for habituation to the changes to occur before data collection commenced.

The observer viewed the animals from a consistent position outside the cages which allowed visual access to all areas of the enclosure whilst not inducing an overt defensive or aggressive response from the animals. The most suitable observer position was established during the pilot study.

Each animal was observed for 20 minutes three times daily (morning session: 0710-0945; mid-day session: 1030-1345; afternoon session: 1415-1705) using a focal continuous sampling technique (Altmann, 1974). Each individual was sampled in a different observation slot on each of the five days in each phase. The order of sampling the individuals was randomized.

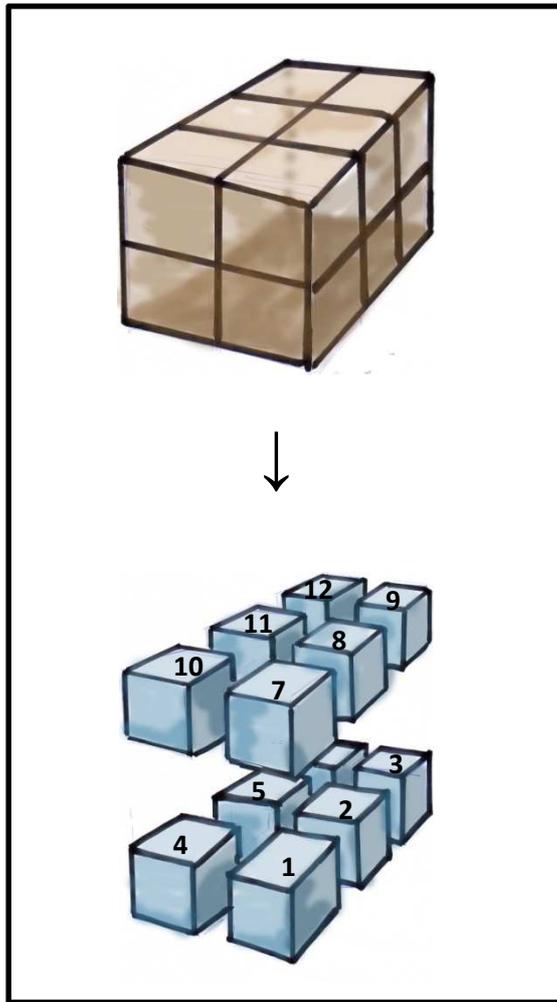


Figure 7: Exploded diagram of cage structure indicating relative position of zones 1-12

Behaviour was recorded contemporaneously using a pre-defined ethogram (see Appendix 1) and JWatcher V1.0 data capture software (www.jwatcher.ucla.edu). The software allowed the recording of the frequency and duration of behaviours; in addition the enclosure was hypothetically divided into 12 equally-sized 'zones' (Figure 7); the zone where each behaviour occurred was recorded as a modifier.

Data Analysis

Following initial graphical analysis of the data the behaviours were grouped for analysis (Appendix 1) into appropriate functional categories – aggressive behaviours (AF), affiliative behaviours (AF), feeding-foraging behaviours (FF), locomotor behaviours (LO), inactivity (IA) and stress-related/self-directed behaviours (SR).

IBM SPSS Statistics 19 was used to undertake a series of Friedman's 2-way ANOVA tests for three or more matched groups with post-hoc pairwise tests between groups including corrections for multiple comparisons. The test was repeated for each of the six groups of behaviours. Threshold significance for rejecting the null hypothesis was set at $p \leq 0.05$.

The Spread of Participation Index (SPI) (Dickens, 1955; Plowman, 2003) was calculated for enclosure usage, for each species in each phase of the study (1-5). It provides a simple description of how evenly a captive animal (or group of animals) are using available space in an enclosure. It is calculated using the following formula:

$$\text{SPI} = \frac{M(\text{nb} - \text{na}) + (\text{Fa} - \text{Fb})}{2(\text{N} - \text{M})}$$

(N= total number of observations in all zones; M= mean frequency of observations/zone; na= number of zones with observations >M; nb= number of zones with observations <M; Fa= total observations in all zones with observations <M; Fb= total observations in all zones with observations >M).

The resulting score varies from 0 to 1; score of 0 indicates maximum enclosure use, i.e. all zones within the enclosure being used equally. A score of 1 indicates that only one zone within the enclosure is being used.

Personal Contribution to the Study

Following initial discussions with the supervisor and a literature review I planned the experimental design. Some minor adjustments were made later after input from the supervisor, particularly with reference to the enclosure usage component of the study. I was responsible for all data collection. Some suggestions were made by the supervisor as to the most appropriate statistical tests for use in the data analysis. I then researched these and carried out the statistical analysis. Advice was taken from the supervisor as to some aspects of the interpretation of these tests.

RESULTS

This section presents the data collected during this study on the effect of the presence of three enrichment treatments (bamboo leaves on the roof of the cage (P2); both bamboo leaves and hessian tunnel in place (P3); hessian tunnel in place (P4)) on the behaviour and enclosure usage of long-tailed (Study A) and pig-tailed (Study B) macaques.

Study A: *M. fascicularis*

Activity budgets

Figures 8(a-e) show the average activity budgets for the long-tailed macaques. In the pre-enrichment phase (P1) the most time was spent inactive (27.4%), followed by locomotion (17.6%), foraging (17.4%), feeding (12.4%), social grooming (11.9%), self-grooming (4.1%) and vigilance (3.9%) (Figure 8a).

During the foraging enrichment phase (P2) the proportion of time spent foraging increased (Figure 9a), replacing locomotion as the second largest component of the activity budget (Figure 8b). Otherwise the ranking of the most commonly-observed behaviours was similar when the bamboo leaves were in place to that observed in the pre-enrichment phase (P1).

During the combined enrichment phase (P3), foraging overtook inactivity and locomotion as the largest component of the activity budget. Feeding also increased to a proportion of time greater than locomotion during this phase (Figure 8c). A large drop in time spent engaged in self-directed grooming was also seen (Figure 9b).

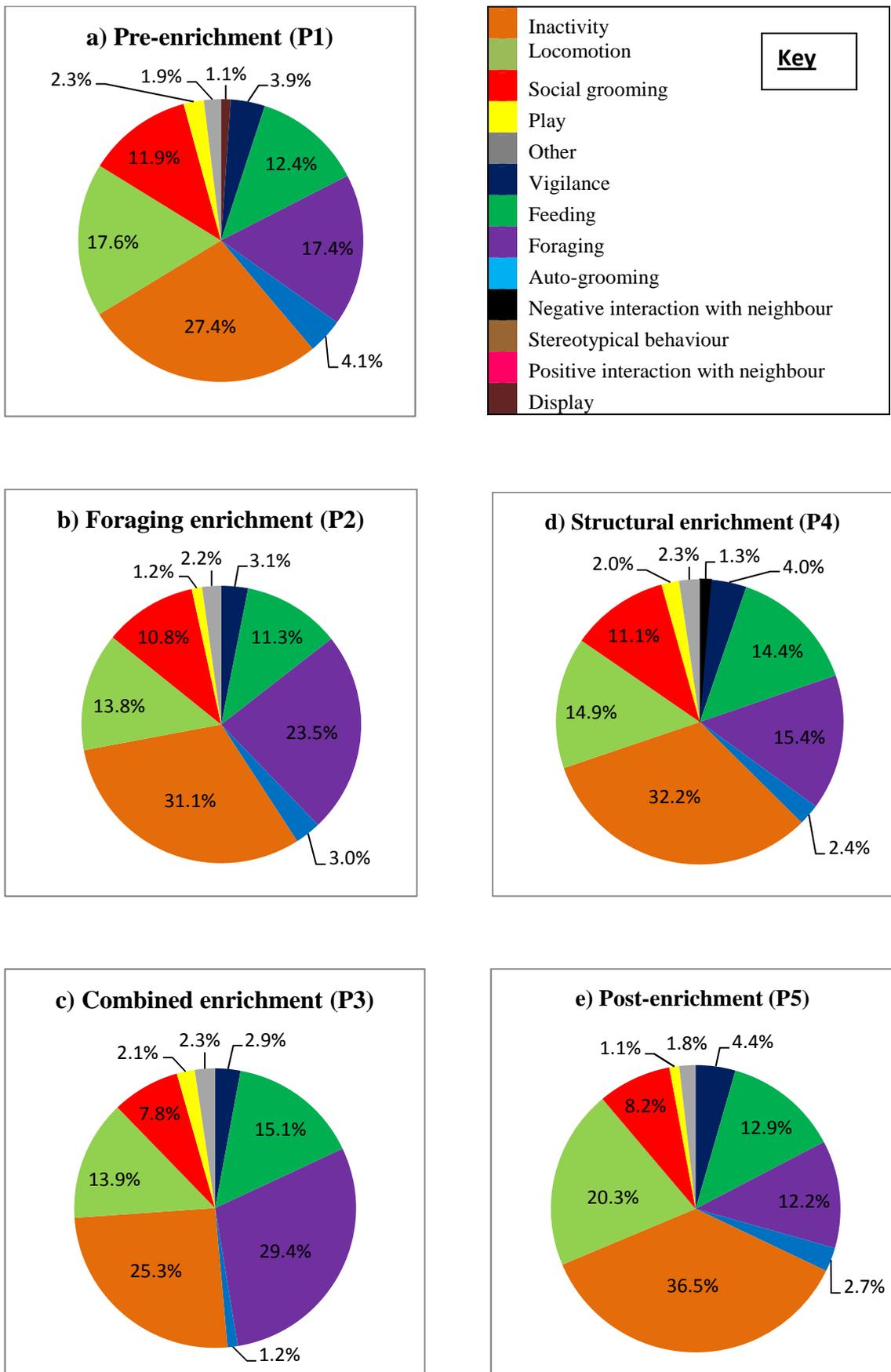


Figure 8 (a-e): Average activity budget (*M. fascicularis*) during study phases a) P1; b) P2; c) P3; d) P4; e) P5

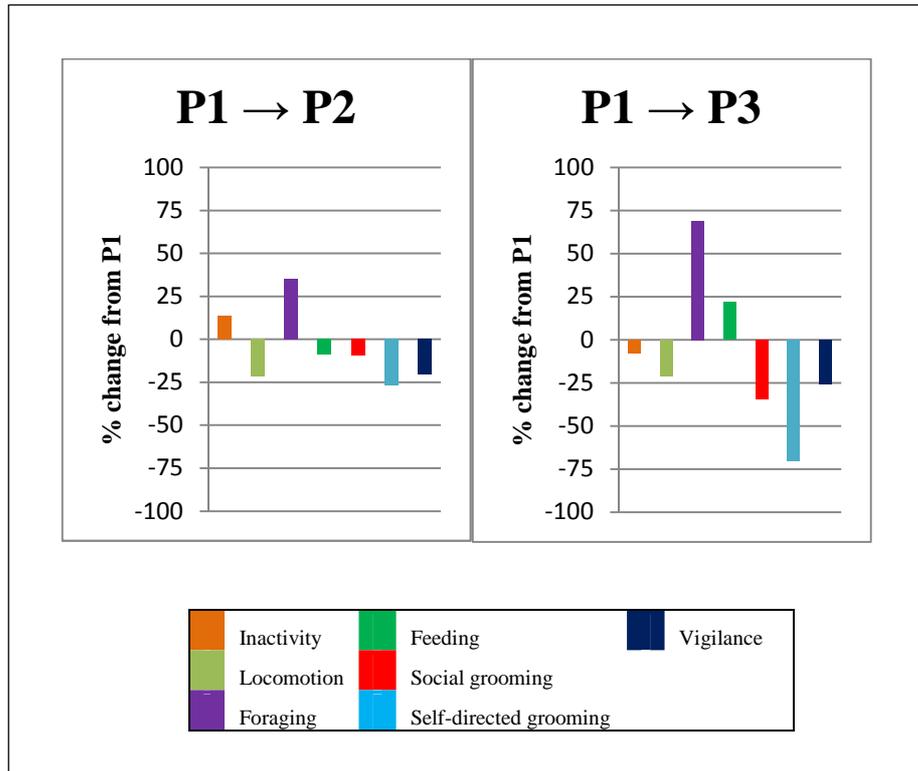


Figure 8 (a,b): Percentage change in proportion of time spent engaged in behaviours from
a) P1 to P2; b) P1 to P3

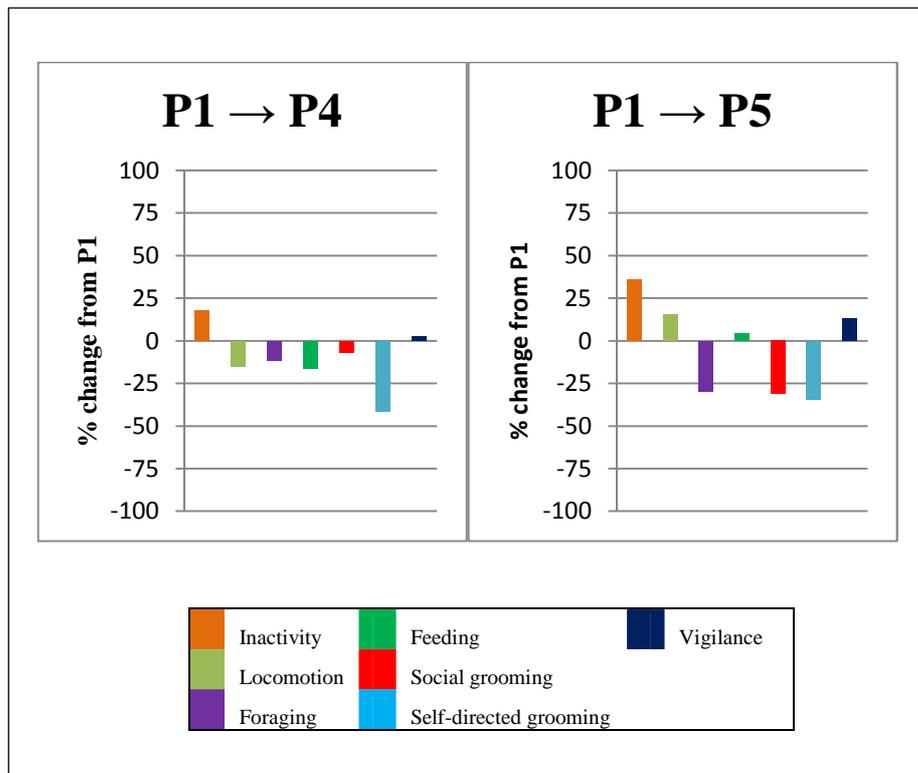


Figure 8 (c,d): Percentage change in proportion of time spent engaged in behaviours from
a) P1 to P4; b) P1 to P5

During the structural enrichment phase (P4), when the tunnel was in place, (Figure 8d) the pattern of activity was similar to that observed in the pre-enrichment phase (P1) although there was a drop in levels of self-directed grooming in this phase similar to that seen in P2 (Figure 9c).

In the final, post-enrichment phase (P5) a slight change in the pattern of activity was observed. Locomotion increased, now forming the second largest component of the activity budget. Compared to the pre-enrichment phase (P1), feeding increased slightly and foraging reduced slightly to form the third and fourth largest components of the activity budget respectively (Figure 8e).

Behavioural responses to enrichments

The behaviours recorded were combined to form functional behaviour categories for analysis, as described previously. Figure 10 shows the mean percentage time spent in each group of behaviours across the phases by the long-tailed macaques.

There were no statistically significant differences in behaviour between the two un-enriched phases (P1 and P5) and thus data from these two phases was combined and the means were pooled throughout the rest of the behavioural analysis.

Mean levels of aggressive behaviours (AG) in long-tailed macaques remained low throughout the study (0.62 – 2.10% of time spent; Figure 8) and there were no statistically significant differences in their levels between the phases (Table 1).

Levels of affiliative behaviour (AF) were lowest during P3, the combined enrichment phase (11.0%) (Figure 8) but there were no statistically significant differences in time spent engaged in affiliative behaviour across the phases (Table 1).

There was a statistically significant difference in levels of feeding-foraging behaviour

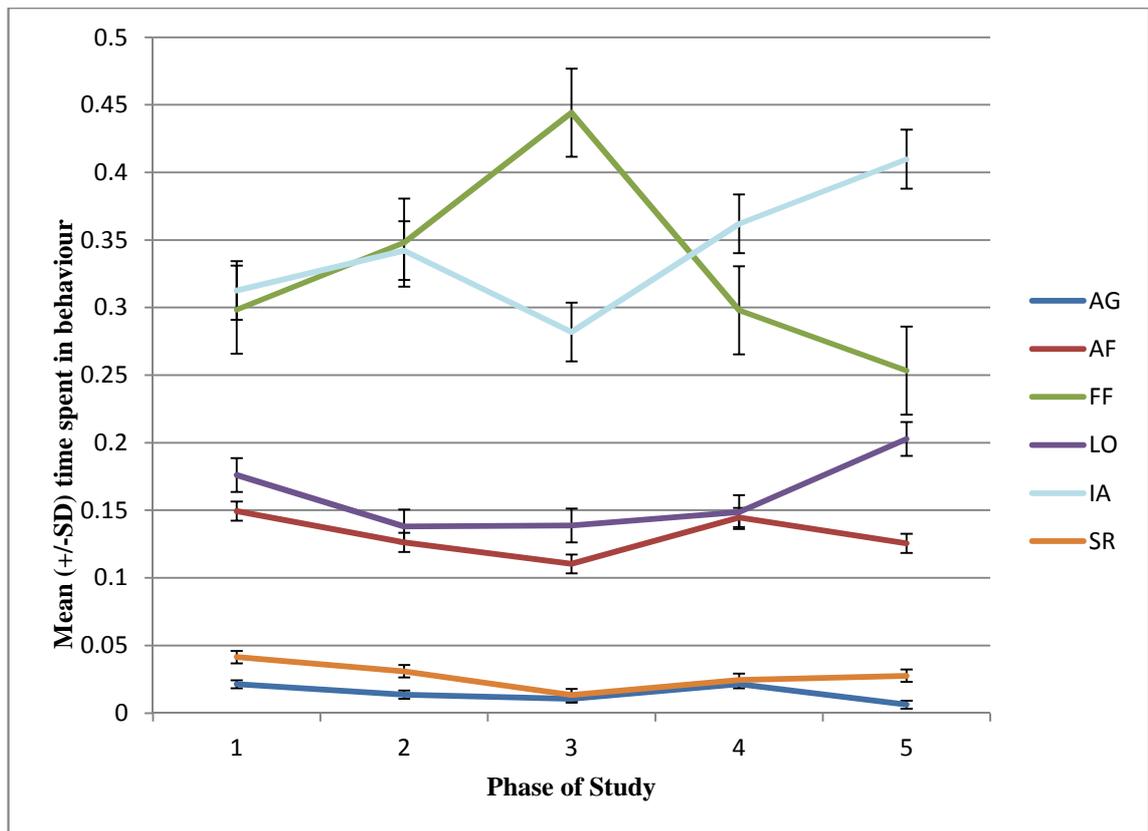


Figure 10: Percentage time spent engaged in each behaviour for *M. fascicularis* across the phases (AG – aggressive; AF – affiliative; FF – feeding-foraging; LO – locomotion; IA – inactivity; SR – stress-related)

Table 1: Results of Friedman’s tests for *M. fascicularis* behaviour changes across the phases **Bold** indicates significant result; *, **, *** indicates degree of significance; NS=not significant

Behaviour	Friedmans Test Statistic	Degrees of Freedom	Total N	Significance (p)
Aggressive (AG)	5.571	3	7	0.134 NS
Affiliative (AF)	6.257	3	7	0.100 NS
Feeding-foraging (FF)	16.029	3	7	0.001 ***
Locomotion (LO)	3.514	3	7	0.319 NS
Inactivity (IA)	9.343	3	7	0.025 **
Stress-related (SR)	10.714	3	7	0.013 **

(FF) in the long-tailed macaques across the phases (Table 1). The post-hoc pairwise comparisons reported a significant increase in feeding-foraging behaviour between the un-enriched phases and P3, the combined enrichment phase (27.6% to 44.4%; post-hoc pairwise comparison $p = 0.006$) and a decrease when the bamboo leaves were removed to leave only the tunnel (44.4% to 29.8%; post-hoc pairwise comparison $p = 0.006$) (Figure 10).

Levels of locomotion (LO) in long-tails were higher during the un-enriched phases, P1 and P5 (Figure 10) than the enrichment phases, however these differences were not significant (Table 1).

Levels of inactivity (IA) were lowest during P3 (28.2%), (Figure 10) when both enrichments were present. There was a significant difference in inactivity levels (Table 1) across the phases. Inactivity increased from 28.2% to 36.2% when the bamboo leaves were removed between P3 and P4 to leave only the tunnel (post-hoc pairwise comparison $p=0.023$).

There was a significant difference in levels of stress-related (SR) behaviours across the phases (Table 1). In the long-tailed macaques they were lowest during P3 (1.3%) (Figure 10). Post-hoc pairwise comparisons showed a significant increase between P3 (1.3%) and P4 (2.5%) ($p = 0.023$), when the bamboo leaves were removed leaving only the tunnel; and between P3, the combined enrichment phase (1.3%) and the un-enriched phases ($p=0.043$).

Enclosure usage

The long-tailed macaques spent more time at higher levels of the cage, zones 7-12, (80.0% in un-enriched phases) than at lower levels, zones 1-6 (Figure 11; Appendix 2).

There was no statistically significant difference across the phases (Friedman's $X^2 = 1.800$, d.f. = 3, n=7, p=0.615).

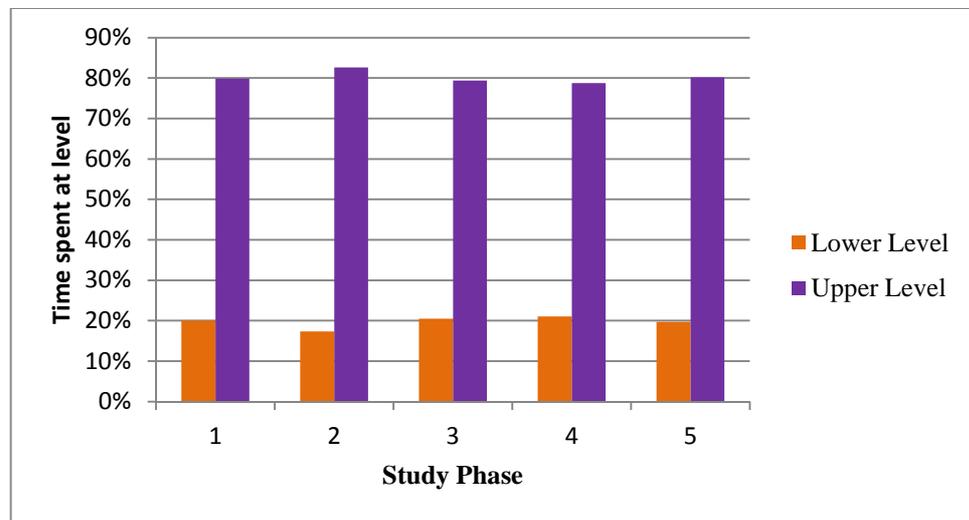


Figure 11: Percentage time spent at upper (>1.5m height) and lower levels (<1.5m height) of enclosure; *M. fascicularis*

The scores on the Spread of Participation Index were generally low (0.18 – 0.29) but increased to 0.51 in P5, suggesting poorer utilisation of the available space in the post-enrichment phase (Figure 12).

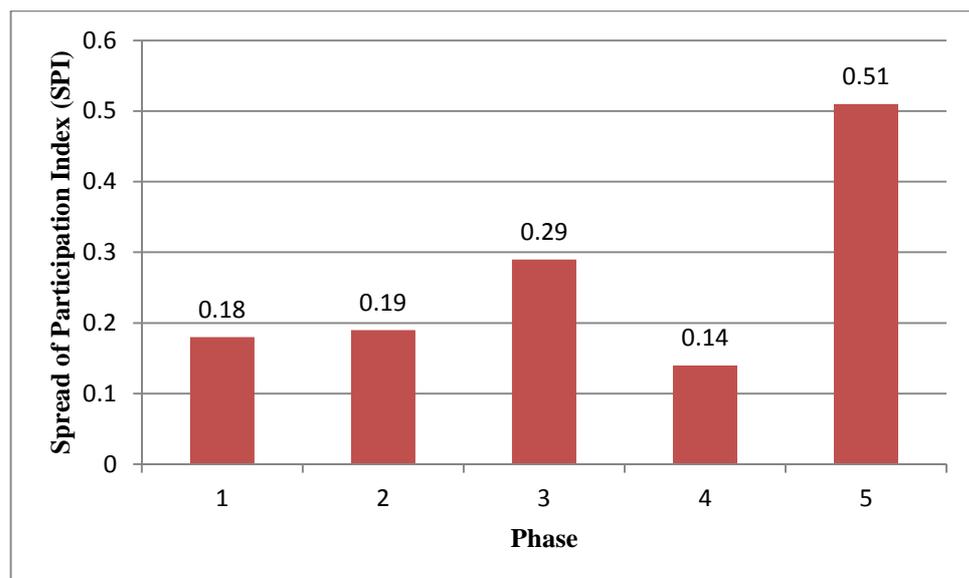


Figure 12: *M. fascicularis* SPI across the phases

Study B: *M. nemestrina*

Activity budgets

Figure 13 (a-e) shows the average activity budgets for the pig-tailed macaques. In the pre-enrichment phase the most time was spent inactive (51.7%), followed by locomotion (12.2%), self-directed grooming (9.1%), foraging (8.4%), feeding (7.8%), social grooming (5.6%) and vigilance (4.2%).

With the addition of the bamboo leaves on the roof of the cage, foraging levels increased (Figure 14a), overtaking locomotion as the second largest component of the activity budget in P2, the foraging enrichment phase. Feeding levels increased slightly (Figure 14a), forming the fourth largest component of the activity budget. Self-directed grooming increased as a percentage of the time budget, but dropped in rank from third to fifth largest component of the activity budget (Figure 13b). Inactivity remained the largest component of the time budget (Figure 13b).

In the combined enrichment phase, P3, the pig-tailed macaques' general pattern of activity was very similar to that seen in the foraging enrichment phase, P2 (Figure 13c). There was a decrease in inactivity and an increase in foraging compared with P1, the pre-enrichment phase (Figure 14b). Levels of vigilance increased noticeably (Figure 14b).

During P4, with the tunnel in place, the pattern of activity changed substantially. As in the pre-enrichment phase, inactivity was the largest component of the activity budget; this was followed by locomotion and self-directed grooming, which reached its highest levels in this phase (Figure 14d). There was an increase in feeding when the tunnel was in place when compared to the pre-enrichment phase (Figure 13c). Time spent on

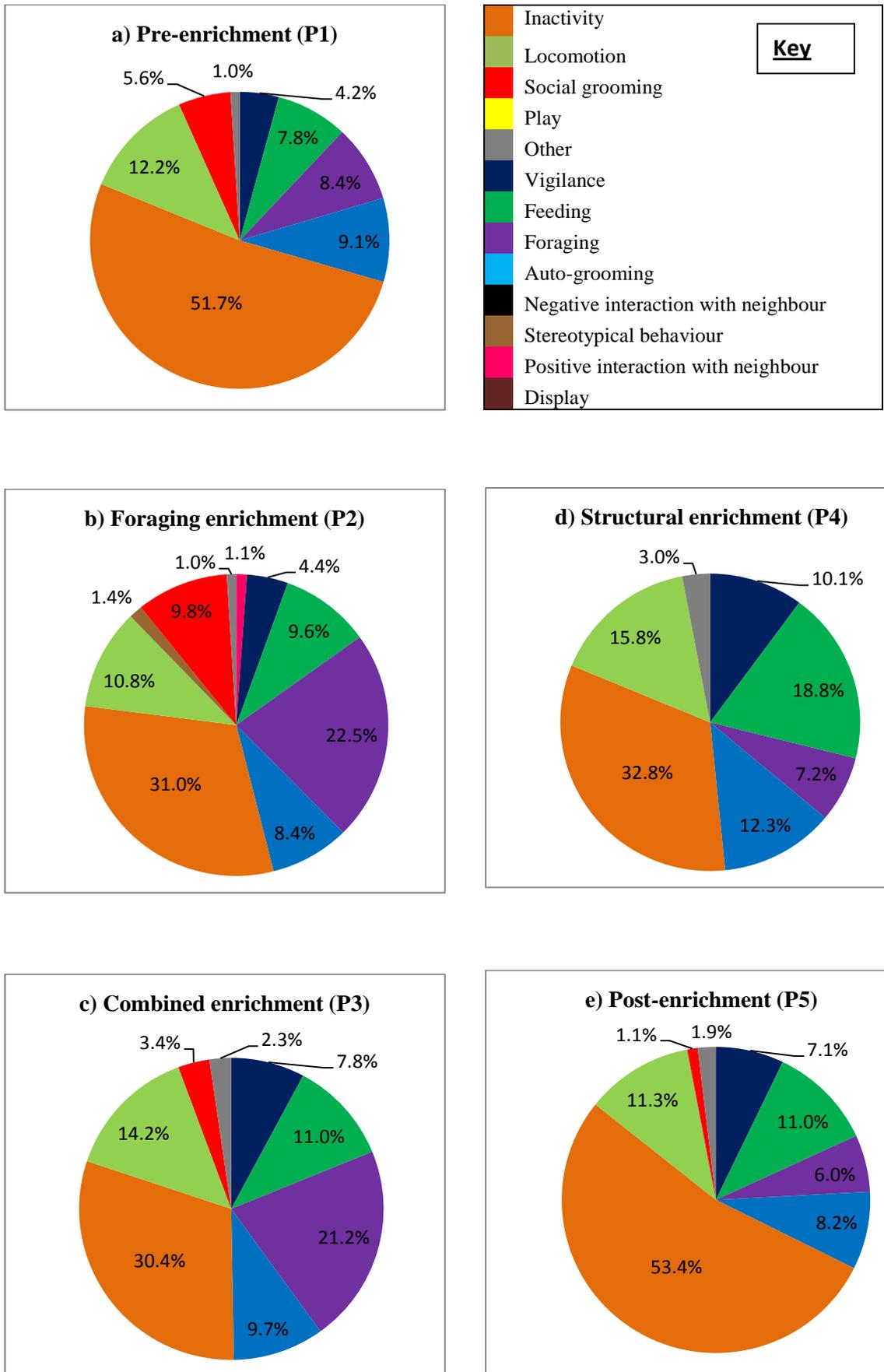


Figure 13 (a-e): Average activity budget (*M. nemestrina*) during study phases a) P1; b) P2; c) P3; d) P4; e) P5

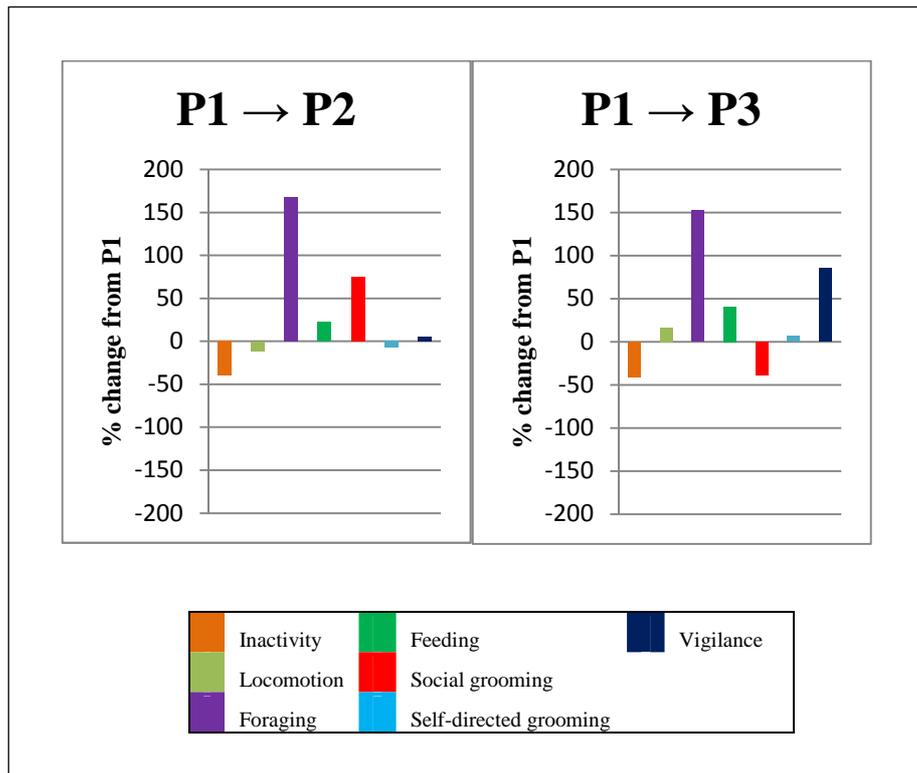


Figure 14 (a,b): Percentage change in proportion of time spent engaged in behaviours from
a) P1 to P2; b) P1 to P3

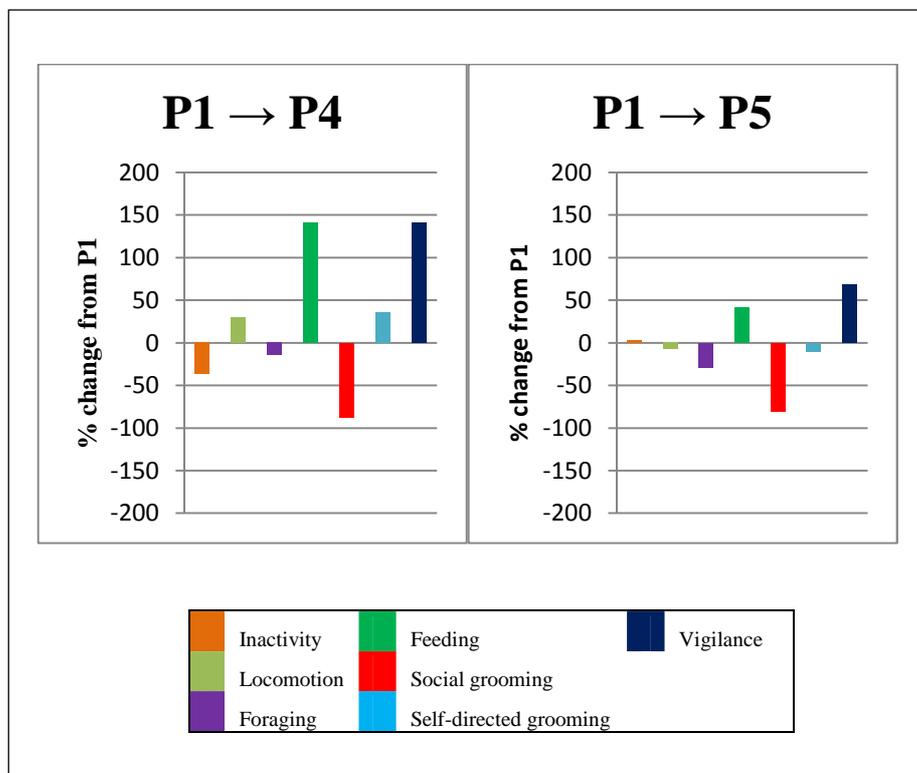


Figure 14 (c,d): Percentage change in proportion of time spent engaged in behaviours from
a) P1 to P4; b) P1 to P5

vigilance increased in this phase (Figure 13c) and time spent on social grooming decreased dramatically to <1% (Figure 13c).

In the final, post-enrichment phase (P5) the general pattern of activity in the pig-tailed macaques was very similar to that seen in the initial pre-enrichment phase (P1) (Figure 13d). Social grooming however was much lower in P5 than in P1 (Figures 13d and 14e).

Behavioural responses to enrichments

Figure 15 shows the mean percentage time spent by the pig-tailed macaques in each of the groups of behaviours across the phases.

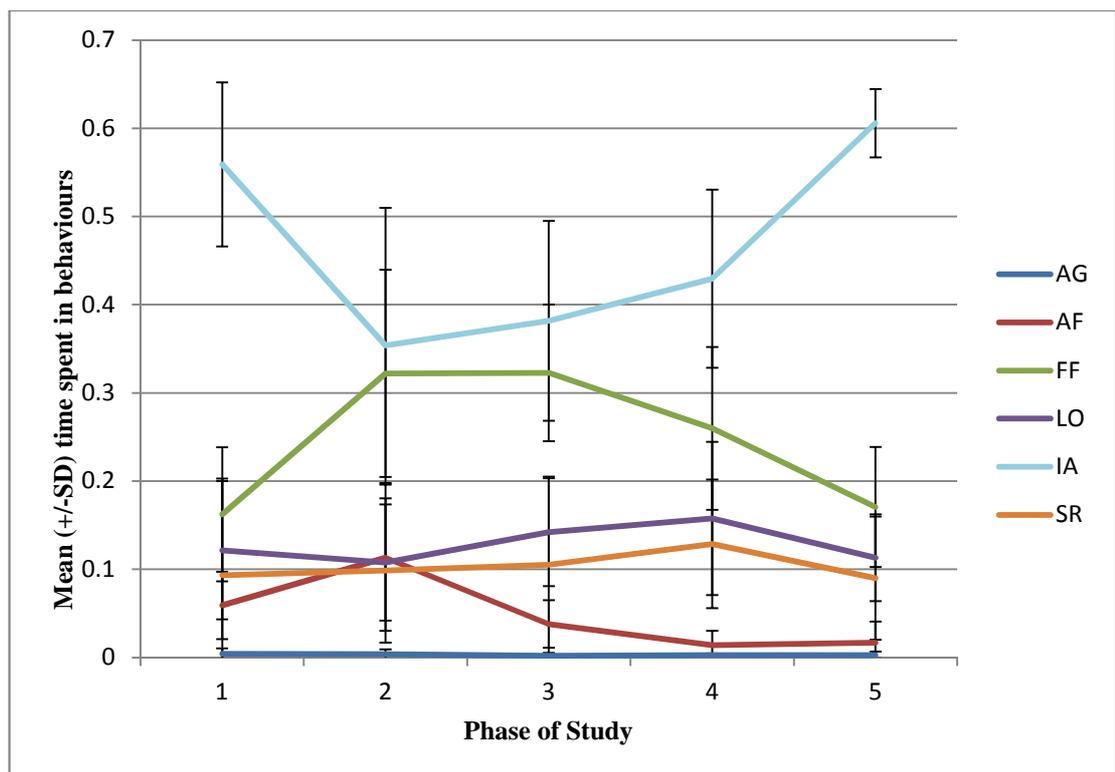


Figure 15: Percentage time spent engaged in each behaviour for *M. nemestrina* across the phases (AG – aggressive; AF – affiliative; FF – feeding-foraging; LO – locomotion; IA – inactivity; SR – stress-related)

As in Study A, there were no statistically significant differences in behaviour between the two un-enriched phases (P1 and P5) of Study B, and thus the data from these two phases was pooled and the means used throughout the rest of the behavioural analysis.

Table 2: Results of Friedman's tests for *M. nemestrina* behaviour changes across the phases **Bold** indicates significant result; *, **, *** indicates degree of significance; NS=not significant

Behaviour	Friedman's Test Statistic	Degrees of Freedom	Total N	Significance (p)
Aggressive (AG)	1.000	3	6	0.801 NS
Affiliative (AF)	12.800	3	6	0.005 ***
Feeding-foraging (FF)	12.600	3	6	0.006 ***
Locomotion (LO)	11.000	3	6	0.012 **
Inactivity (IA)	11.600	3	6	0.009 ***
Stress-related (SR)	6.600	3	6	0.086 NS

Mean levels of aggression (AG) remained very low throughout the study (0.19 – 0.41% of time spent; Figure 15). There was no statistically significant difference in levels of aggressive behaviour between the phases (Table 2).

There was a significant difference in levels of affiliative behaviour (AF) across the phases (Figure 15; Table 2). Pairwise comparisons showed that there was a significant decrease in levels of affiliative behaviour between P2, the bamboo leaves and P4, the tunnel (Post-hoc pairwise comparison $p = 0.002$).

Another significant difference was found in levels of feeding-foraging behaviour (FF) across the phases (Table 2). Pairwise comparisons showed that this resulted from an increase in pig-tailed macaque feeding-foraging behaviour between the pooled un-enriched phases and the phases where the bamboo leaves were present - P2, the foraging enrichment phase ($p = 0.044$) and P3, the combined enrichment phase ($p = 0.005$) (Figure 15).

Locomotion (LO) was highest in P3 and P4, the combined and structural enrichment phases. A significant difference was found in levels of locomotion (Table 2). Post-hoc pairwise comparisons demonstrated that there was a statistically significant increase in levels of locomotion between the pooled un-enriched phases and P4, when the tunnel was in place ($p = 0.022$).

Levels of inactivity were significantly different across the phases of the study (Table 2). Inactivity decreased during the enrichment phases (Figure 15). There was a significant difference in inactivity levels between the pooled un-enriched phases and the two phases with bamboo leaves in place - P2 (foraging enrichment) ($p = 0.01$) and P3 (combined enrichment) ($p = 0.044$).

Levels of stress-responsive behaviours were lower - but not significantly so (Table 2) - in the un-enriched phases (P1 and P5) than in the enrichment phases (P2-4).

Enclosure usage

The pig-tails spent more time in the upper ($>1.5\text{m}$) part of the cage, zones 7-12 (65.9% in pooled un-enriched phases) (Figure 16; Appendix 2) than at lower (<1.5) part, zones 1-6. There was no statistically significant difference in this figure across the phases (Friedman's $X^2 = 6.600$, d.f. = 3, $n=6$, $p=0.086$).

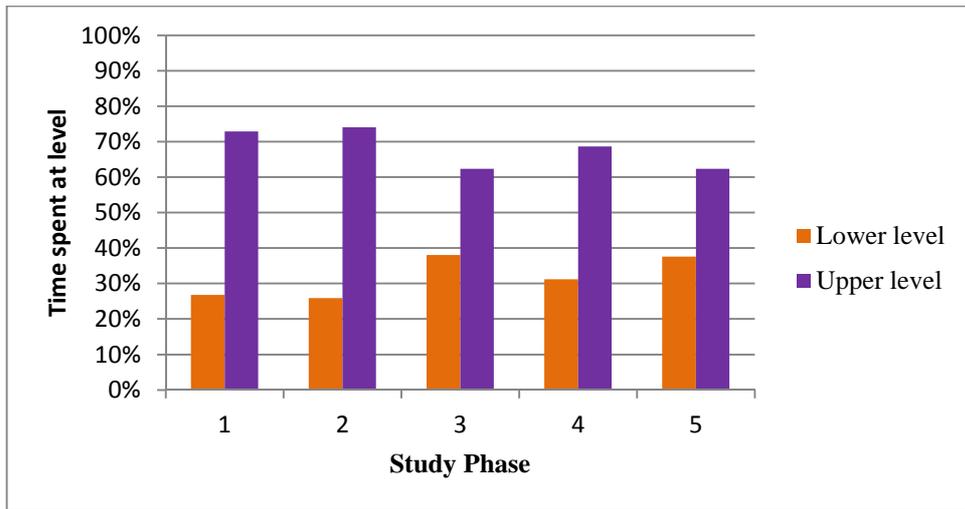


Figure 16: Percentage time spent at upper (>1.5m height) and lower levels (<1.5m height) of enclosure; *M. nemestrina*

The scores on the Spread of Participation Index were low (<0.01 – 0.16), suggesting relatively even use of the available space in the enclosure (Figure 17).

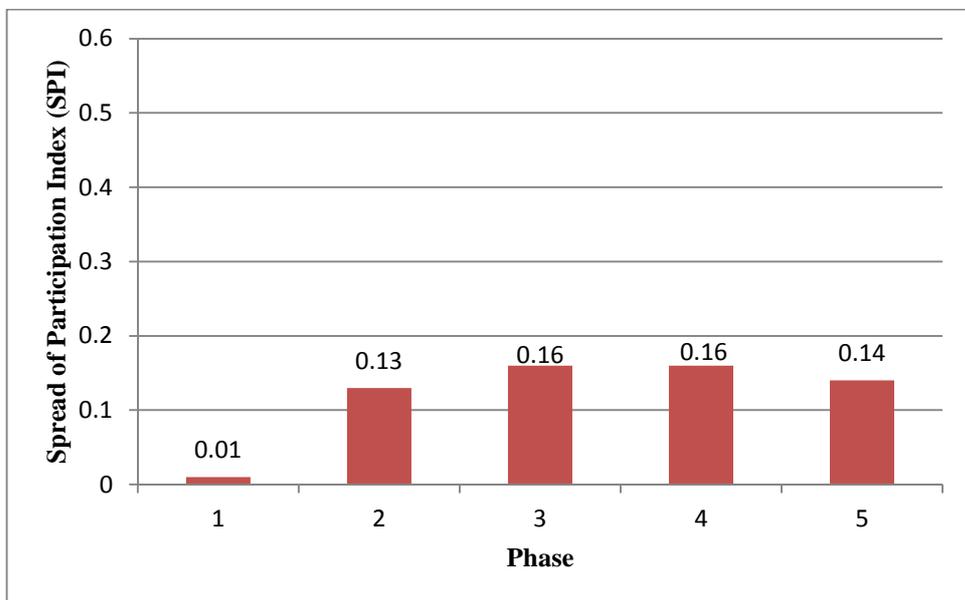


Figure 17: *M. nemestrina* SPI across the phases

DISCUSSION

Time Budgets – Comparisons Between Captive and Wild Populations

Time is a limited resource for animals. Activity budgets provide information about time allocation. Some aspects will be controlled by necessity (e.g. food acquisition); other activities (e.g. affiliative behaviours) may be more flexible. Comparing captive animals' activity budgets with wild conspecifics can highlight differences which may reflect compromised animal welfare and/or impact on future survival.

Long-tailed Macaques

Several studies on wild activity budgets of long-tailed macaques have been undertaken, including in Mauritius (Sussman & Schaffer, 2008), Vietnam (Son, 2004) and Malaysia (Md-Zain et al., 2010) (Table 3).

Comparison with these studies suggests the IAR macaques show some behavioural divergence from wild populations (Table 3). In particular they are much more inactive and locomote less.

The proportion of time spent on feeding activities is similar to Sussman and Schaffer (2008) but higher than Md-Zain et al. (2010) where the consumption of non-natural, high calorie foods such as 'bread, rice, carbonated drinks and ice cream' may account for a reduced feeding time in this primarily frugivorous species (Wheatley, 1980; Yeager, 1996).

The results for the current study show some variation from Paramasivam (2010) (also this site) who reported that male long-tailed macaques spent less time

Table 3: Comparison of activity budgets in a number of studies of *M. fascicularis*

STUDY	HABITAT	Percentage time spent engaged in behaviours:			
		INACTIVITY	LOCOMOTION	FEEDING-FORAGING	AFFILIATIVE BEHAVIOURS
Son, 2004 (Dry season)	Wild (provisioned) mangrove forest	31.66	17.67	19.62	9.20
Son, 2004 (Wet season)	Wild (provisioned) mangrove forest	36.47	18.1	24.99	7.18
Sussman & Schaffer, 2008	Introduced (non- provisioned)	22	23	30	13
Md-Zain et al., 2010 (9 groups of macaques)	Wild (provisioned) university campus	16.13 -20.26	18.00 - 31.36	16.29 - 24.02	2.31 – 13.00
Paramasivam, 2010	Captive (rescue centre)	29.1	8.1	24.1	14.5
Current study, un- enriched (pooled P1, P5)	Captive (rescue centre)	36.1	18.9	27.6	13.7
Current study, enriched (P3)	Captive (rescue centre)	28.2	13.9	44.4	11.0

inactive, in feeding-related behaviours and in locomotion; time spent grooming was similar (Table 3).

Pig-tailed Macaques

When un-enriched (pooled P1/P5), the pig-tailed macaques' activity budget is dominated by inactivity (58.2%), followed by feeding-foraging (16.7%), locomotion (11.7%), self-directed behaviours (9.0%) and affiliation such as allogrooming (3.8%). Literature reporting wild activity budgets for this species is scant. However a review (Pollard & Blumstein, 2008) compiled data from five *Macaca* species. The most inactive (Barbary macaque *M. sylvanus*), spent only 38.5% of time resting. It is likely therefore that the 58.2% of time spent inactive in this study is higher than in wild conspecifics. Locomotion constituted 15.0% (*M. silenus*) to 23.2% (*M. mulatta*) of the activity budget. It is probable that locomotion levels in this study are lower than in wild conspecifics, unless pig-tailed macaques are atypical of the genus.

Behavioural Responses to Enrichments

This section compares the results with published data, and with the hypothesised findings: that introduction of enrichment would change activity budgets towards wild-type behaviour; that the three enrichment options would each result in alterations in the activity budgets.

There were no statistically significant differences in any behaviour category between the pre- and post-enrichment phases (P1 & P5) for either species, discounting time-dependent behavioural changes in the enrichment phases (P2-P4) (Young, 2003).

Aggressive Behaviour

Overall aggression was low. In both species aggression was lower in P3 - combined enrichment - than P1, P2 and P4. However this was not significant. This is consistent with decreased aggression associated with enrichment reported elsewhere (Weld & Erwin, 1990; Bayne & Dexter, 1992). Aggression can increase after enrichment removal (Blois-Heulin & Jubin, 2004), however, aggression was lowest post-enrichment (P5) for the long-tailed macaques. It is difficult to explain this post-enrichment decrease in the absence of an enrichment-associated increase in aggression; however any decrease in aggression improves welfare by reducing injuries and stress (Honeiss & Marin, 2006).

Affiliative Behaviour

There were no significant differences in affiliative behaviour with enrichment in long-tailed macaques. However affiliation was lower with foraging enrichment (P2, P3), as reported in stump-tailed macaques (*M. arctoides*) where exploration of enrichment was associated with reduced social behaviour (Marquez-Arias et al., 2009). Here pig-tailed macaques showed more affiliative behaviour in P2 (foraging enrichment) than any other phase; significantly higher than P4. Allo-grooming can ameliorate stress via release of chemicals (e.g. oxytocin, endorphins) in the central nervous system (Dunbar, 2010). This increase in grooming may indicate an attempt to reduce stressful neophobic responses to a novel stimulus.

Levels of affiliative behaviour were lower in pig-tailed than long-tailed macaques: a possible species-level difference in normal behaviour for which there is scant literature from the wild. Another explanation may be group composition. The

long-tail macaques were housed in a mixed-sex, mixed-age group resembling wild grouping structure. In contrast the pig-tailed macaques were housed in unnatural heterosexual pairs. Whilst preferable to individual housing, this does not allow a full repertoire of normal social behaviour: for example the formation of female-female allo-grooming dyads typical among female-bonded cercopithecines (e.g. macaques, baboons) (Silk et al., 2006a,b). The lack of a choice of grooming partners may account for the lower levels of affiliation seen in these pig-tailed macaques.

Feeding-foraging Behaviours

Both species showed a significant increase in feeding-foraging behaviour between un-enriched (pooled means P1/P5) and combined enrichment (P3). An increase in feeding-foraging was also observed between pooled P1/P5 and P2, the foraging enrichment phase. However this was only significant in the pig-tails. Although un-enriched feeding-foraging levels were not substantially different from wild observations, an increase in feeding-related behaviour with balanced nutrition, particularly where inactivity is reduced, reflects reduced boredom and improved welfare (Honest & Marin, 2006). A willingness to work for ordinary food ('contra-free-loading') has been described in several primate species including rhesus macaques (Reinhardt, 1994) and stump-tailed macaques (Anderson & Chamove, 1984). A review of contra-free-loading (Inglis et al., 1997) raises the possibility that foraging is motivated not only by hunger, but also by a desire to obtain information about the environment. The gathering and holding of knowledge has the potential to increase feelings of control over the environment, which is in turn associated with an improvement in welfare (Sambrook & Buchanan-Smith, 1997).

Locomotion

There was no significant difference in locomotion between the phases for pig-tailed macaques. However decreased locomotion was observed during enrichment phases. Crowding stress can result in increased non-stereotypic pacing (rhesus macaques: Judge & de Waal, 1993). Thus a potential explanation for reduced locomotion during enrichment is that it resulted in reduced stress in the group.

Pig-tailed macaques showed a significant increase in locomotion between un-enriched and structural enrichment (P4) phases. Adding a visual barrier was expected to lower stress and anxiety by allowing individuals to retreat from perceived threats and by improving the quality of social relationships amongst cage mates (Reinhardt & Reinhardt, 1991), potentially reducing anxiety-related pacing (Judge & de Waal, 1993). However, structural enrichment is often used to increase activity levels, providing extra travel routes and encouraging better use of space. The increased locomotion in P4 may have resulted from exploration of the structural enrichment in the absence of foraging enrichment which accounted for much of the available time budget in P2 and P3.

Inactivity

Inactivity in long-tailed macaques was lowest during the combined enrichment phase (P3). This is consistent with increased feeding-related behaviour. Inactivity increased significantly from P3 to P4. Again this is consistent with decreased foraging when foraging enrichment was removed.

The effect of foraging enrichment on inactivity in pig-tailed macaques was even more apparent, being significantly reduced in P2 and P3 consistent with increased foraging. The pig-tailed macaques' un-enriched inactivity is concerning, being

considerably higher (52.5%) than observed in various wild macaques (maximum = 38.5%, *Macaca sylvanus*: Pollard & Blumstein, 2008). A reduction in inactivity during enrichment represents more species-typical behaviour and improved welfare. An active lifestyle may help prevent obesity, skeletal problems (Rothschild & Woods, 1992) and boredom (Wemelsfelder, 1993).

Stress-related behaviours

This category includes abnormal, 'stereotypic' and self-directed behaviours (e.g. auto-grooming, self-scratching) whose increase may reflect increased levels of stress or anxiety (Maestripieri et al., 1992; Manson & Perry, 2000; McDougal, 2011). Scratching and auto-grooming in primates are considered examples of displacement activities (Maestripieri et al., 1992), i.e. seemingly irrelevant behaviours performed due to internal conflict or frustration (Tinbergen, 1952). The reason for the development of stereotypic abnormal behaviour in captive animals is not fully understood. One hypothesis is that the performance of stereotypic behaviours may reflect animals' attempt to 'cope' with stress by, for example, inducing opioid release (Cronin et al., 1985; Wiepkema et al., 1987), although this has been disputed (Dantzer, 1991).

Levels of stress-related behaviours were substantially lower across the phases in long-tailed than pig-tailed macaques. A meta-analysis (Swaisgood & Shepherdson, 2006) of enrichment therapy found baseline levels of stereotypy in zoo primates of 1-3% of total activity budget. Here the un-enriched level for long-tailed macaques was 3.4% and pig-tails was 9.2%. All the pig-tailed macaques were older and had been in captivity longer than the long-tails. Length of time spent without company of conspecifics is a known risk-factor for developing

stereotypic behaviour in primates (Lutz et al., 2003) and thus this longer period in a restricted social context may explain higher levels of abnormal behaviour in this species. Clearly, the aim should be to allow animals sufficient coping mechanisms and control over their environment to eliminate abnormal behaviour. However, reducing stress-related behaviour levels to less than the zoo average may be a more realistic goal at IAR.

Stress-related behaviours were lower in P3 than P4 and both un-enriched phases in long-tailed macaques. This conflicted with Swaisgood & Shepherdson (2006) who found feeding, non-feeding and combined enrichments to be equally effective, reducing levels of stereotypic behaviour by 56-58%.

There was no significant change in stress-related behaviours across phases in pig-tailed macaques. This may reflect a failure of the enrichment to impact on their abnormal behaviour. Mason et al. (2007) note that it is possible for an overall welfare improvement to remain masked by a 'scar' of stereotypic behaviour which is ingrained and persists despite improved conditions. Further work is necessary to differentiate between success and failure of enrichment therapy for the high levels of abnormal behaviour in these rescued individuals. For example, extending the study duration may result in decreased abnormal behaviour over time.

These results confirm the hypotheses that:

H₁ = alterations in activity budgets are seen in the presence of foraging enrichment vs. structural enrichment vs. combined foraging-structural enrichment scenarios.

H₂= the introduction of enrichment techniques induces a change in behaviour towards wild-type activity budgets.

Enclosure Usage

Both species spent more time in upper levels of the enclosure (>1.5m) than in lower, ground levels (<1.5m) across all the phases of the study. There was no significant effect of enrichment on the total time spent in the upper or lower levels of the enclosure. This results in the rejection of the third hypothesis:

H₃ = the introduction of enrichment techniques in the upper levels of an enclosure induces increased usage of the upper levels of the enclosure.

However, both species already exhibited species-typical patterns of enclosure usage. Long-tailed macaques spent 80.0% of their time in the upper levels during un-enriched phases compared with 65.9% for pig-tails. This is consistent with published literature on other captive long-tails which found that they had a preference for the higher parts of their enclosure (Watson & Shively, 1996).

Wheatley (1980) reported that wild long-tailed macaques spent only 2% of time on the ground, preferring the lower to middle canopy (Ungar, 1996). Pig-tailed macaques feed primarily in the middle canopy. However, in contrast to the flight response of long-tails which escape upwards into the canopy when startled (van Schaik et al., 1983), pig-tails descend and escape through the undergrowth at ground level (Rodman, 1979).

This has implications for housing at IAR where the highest cages are approximately 3m high. Building more naturalistic cages of, for example, 12m in

height is impractical due to cost and location; however a height extension would improve welfare (Waite et al., 2008). Increased cage height is associated with decreased stereotypic (Watson & Shively, 1996), self-directed (scratching) and aggressive behaviour and increased social grooming (Honest et al., in review). The evidence from published literature (e.g. Rodman, 1979; van Schaik et al., 1983; Waite et al., 2008; Watson & Shively, 1996) and the current study would suggest the lower cages are more appropriate for pig-tailed than long-tailed macaques, provided consideration was also given to spatial and social density.

The pig-tailed macaques made some use of all 12 zones during the study and the SPI remained low across all 5 phases ($<0.01 - 0.16$).

The long-tailed macaques also used all 12 zones with an SPI closer to 0 than 1 in P1-P4 suggesting good usage of space. The macaques were observed in each of the twelve zones. However post-enrichment (P5) the SPI was 0.51, apparently due to an increased preference for zone 7 (Appendix 2). Zone 7 was characterised by the presence of a resting place in each enclosure, either a flattened log or a nesting box.

There was no obvious explanation for this change and with the small sample size and short duration of the study it was not possible to use a more revealing blocking design for the analysis. Factors such as variation between enclosures in external view (e.g. towards other groups) may have confounded the results.

Further data collection may help to clarify preference for different areas of the cages. Another improvement would be to utilise a modified SPI (Plowman, 2003).

This requires zonation of enclosures based on structure and content (e.g. enrichment, perches), rather than equality of size (this study; Dickens, 1995). A

potential issue with this modification is the requirement for a pre-hoc judgement as to the value to animals of areas of the cage.

Improvements to the study

One limitation of this study was the small sample size. Ideally the work would be repeated with every group coming through IAR. This may help reduce the standard deviation in the results (Figure 8, Figure 13; Appendix 3), increasing the power of the study.

A measure of success of environmental enrichment is the longevity of its effect (Tarou & Bashaw, 2007). Foraging devices which release food too quickly are soon ignored when food is no longer available as a positive reinforcer (Vick et al., 2000), and frequent refilling could result in a nutritional imbalance (Wolfensohn & Honess, 2005). However the bamboo was not an enrichment device *per se* but rather a feeding event to be solved up to seven times per day providing a sustained welfare improvement (Meehan & Mench, 2007). A more prolonged study would enable analysis of the long-term impact of the enrichment options on behaviour.

Another improvement would be to analyse which behaviours were being performed in each zone. These data were collected, but due to the small sample size and extended nature of the required analysis they were not utilised. This information may help to guide the design and placement of future enrichment options.

Conclusion

This study shows that behavioural observations can guide the design of housing for macaques in rescue-rehabilitation centres. It also provides evidence that

simple, low-cost enrichment can reduce inactivity and increase feeding-foraging in long-tailed and pig-tailed macaques. This moves their behaviour closer to that of wild conspecifics and together with an associated decrease in boredom represents a welfare improvement. These enrichment options may be useful both in the rehabilitation process of animals destined for re-release and in the housing of those animals permanently resident at IAR.

General Discussion

The main difficulties associated with undertaking this study were those typically associated with field research - in particular climate and communication.

Due to the nature of the data collection method (via laptop computer), data collection became difficult during heavy rainfall. Some shelter was available and so effects on data collection were minimised. However, a waterproof data-collection device would have made this much easier.

Due to time constraints data collection was fairly intensive. This was most evident during the first stage as seven individuals were being continuously observed for three 20 minute periods per day. If the study was to be repeated a less intensive observation schedule may have reduced the risk of observer fatigue.

Communication with the project supervisor was at times difficult due to time zone differences and telecommunication issues. However given the nature of the field study it is difficult to see how this could be improved.

A practical difficulty of the study was the lack of consideration given to the impact of placing a large, opaque structure (the 1 x 0.5m hessian tunnel) in the centre of the cage. Although it did not result in any major problems with data collection, the size, appearance and location of the structure did make continuous observation of individuals more difficult than in the phases of the study where the structure was not present.

A second practical factor which was not fully considered at the outset of the project was differences in the nature of the two species of macaque studied. The long-tailed macaques, whilst inquisitive, were significantly less destructive than the pig-tails. One of the latter males in particular spent a great deal of time making sure every piece of bamboo was carefully manipulated to a point where it could be tipped off the roof of the enclosure. The initial hessian tunnel met a similar fate, with each fixing being carefully removed, all knots untied and the structure ripped apart within a few hours. This was in marked contrast to the long-tailed macaques who used the device generally as intended, and whose exploration was much more 'gentle', allowing the device to last the planned duration without repair or replacement. This highlighted that dexterous primates can undo lots of hard work and potentially destroy enrichment devices. The most important factor to consider is whether any components of the enrichment could pose a hazard to the primates when dismantled. The components of the device in this instance were considered generally safe and used throughout the enclosures at IAR. However, at the first opportunity dismantled components were removed from the enclosure to remove any potential danger. The design of the device was subsequently slightly adjusted to make it more robust.

A number of improvements to the experimental design could be implemented in the future if more time was available. Each phase of the enrichment study lasted five days. A future study could be improved by extending the duration of each phase as this may have revealed longer-term effects on behaviour. A further improvement would be to extend the study from an A-B-C-D-A to a more complex A-B-A-C-A-D-A design, thus allowing the experiment to demonstrate

more clearly that the enrichment phases are not being affected by carry-over effects of the preceding phase or temporal differences in behaviour.

On a similar note, given an extension to the time available the study could be repeated on the same individuals, with the enrichments presented in reverse order. This would help to differentiate any 'order of treatment' effects which would not be apparent from the initial, five phase study.

As with many enrichment studies in captive wild animals, small sample sizes were an issue in this study. Repeating the study with multiple groups would help to increase the power of the data in any future work.

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APPENDIX 1: ETHOGRAM

Behaviour	Description
Displaying	Individual uses body and/or cage to produce noise in a territorial display
Interaction with neighbour (negative)	Aggressive social interaction with a conspecific in an adjacent cage
Cage War	Overtly aggressive behaviour between 3 or more individuals
Aggression	One or more aggressive signals or behaviours performed towards another individual
Chasing	Individual moves away from another individual following an aggressive signal or threat
Fighting	Physical manifestation of aggressive behaviour
Tooth baring/chattering	Fear grimace or oral appeasement gesture
Avoids aggression	Takes action to physically avoid aggressive behaviour from a conspecific
Approaching	Observed individual approaches another individual; non-threatening
Interaction with neighbour (positive)	Affiliative social interaction with a conspecific in an adjacent cage
Being groomed	Individual is groomed by a conspecific
Grooming	Using digits or mouth to remove debris from the coat of conspecific
Sexual behaviour performed	Engaging in copulation or masturbation
Sexual behaviour performed on	Mounted by another individual in sexual manner
Play	Play behaviours such as chasing, wrestling, jumping
Hugs	Ventral to ventral or dorsal contact with brachial limbs encircling body of conspecific
Social interaction	Social behaviour such as sniffing, stroking (excl. grooming, hugging, aggression, interaction with neighbour)
Plays with tunnel	Play behaviour such as chasing, wrestling, jumping in, on or around tunnel
Investigates tunnel	Uses hands or mouth to investigate physical characteristics of tunnel
Drinking	Individual consumes water from pool or drinker
Feeding	Individual consumes food without manipulating; includes chewing and swallowing food from pouch
Foraging	Individual manipulates food before putting in mouth; includes manipulation of foraging substrate
Locomoting	Walking, running, climbing or brachiation
Vigilance	Visual fixation on a conspecific or object in the surrounding environment
Inactivity	Immobility and the absence of other listed behaviours
Hides in tunnel	Uses tunnel to reduce visual contact with conspecifics
Grooming (self-directed)	Using digits or mouth to remove debris from own coat
Stereotypical Behaviour	Performance of abnormal repetitive behaviours eg. Pacing, weaving, overgrooming
Out of sight	Individual cannot be observed
Key:	
	<p>Aggressive/agonistic behaviours (AG)</p> <p>Affiliative/social behaviours (AF)</p> <p>Feeding-foraging behaviours (FF)</p> <p>Locomotory behaviour (LO)</p> <p>Inactivity (IA)</p> <p>Stress-responsive behaviours (SR)</p>

APPENDIX 2: ENCLOSURE USAGE

Study A: *M. fascicularis*

	Week 1	Week 2	Week 3	Week 4	Week 5
Zone 1	2.29%	1.40%	3.05%	2.95%	4.10%
Zone 2	2.92%	4.42%	5.86%	4.63%	2.25%
Zone 3	5.69%	5.86%	3.63%	5.80%	4.19%
Zone 4	2.83%	1.78%	3.06%	1.86%	2.24%
Zone 5	3.15%	1.37%	2.48%	2.98%	2.88%
Zone 6	3.18%	2.49%	2.39%	2.88%	4.05%
Lower level total	20.07%	17.32%	20.48%	21.10%	19.71%
Zone 7	20.73%	16.65%	11.90%	14.48%	24.69%
Zone 8	3.23%	6.40%	8.47%	7.25%	4.63%
Zone 9	10.05%	14.25%	15.48%	14.73%	9.24%
Zone 10	15.51%	16.85%	16.04%	12.27%	11.96%
Zone 11	8.03%	6.78%	10.20%	7.70%	10.08%
Zone 12	22.28%	21.67%	17.30%	22.36%	19.60%
Upper level total	79.83%	82.60%	79.40%	78.79%	80.19%

Study B: *M. nemestrina*

	Week 1	Week 2	Week 3	Week 4	Week 5
Zone 1	4.08%	2.73%	2.30%	4.36%	5.64%
Zone 2	4.10%	2.95%	4.07%	4.26%	4.11%
Zone 3	6.42%	6.12%	5.82%	3.28%	6.69%
Zone 4	7.30%	5.46%	10.36%	9.75%	11.57%
Zone 5	1.95%	2.98%	7.19%	3.64%	5.18%
Zone 6	2.97%	5.69%	8.28%	5.96%	4.40%
Lower level total	26.82%	25.94%	38.04%	31.24%	37.59%
Zone 7	23.28%	28.69%	21.58%	17.76%	16.98%
Zone 8	8.22%	7.66%	10.91%	13.79%	9.43%
Zone 9	2.93%	3.30%	2.62%	4.23%	3.28%
Zone 10	21.77%	12.32%	12.77%	16.74%	17.04%
Zone 11	9.19%	9.71%	4.24%	8.36%	6.48%
Zone 12	7.46%	12.32%	10.19%	7.77%	9.15%
Upper level total	72.85%	74.00%	62.32%	68.66%	62.35%

APPENDIX 3: SUMMARY DATA TIME BUDGETS

Study A: *M. fascicularis*

AFFILIATIVE BEHAVIOUR						
ID	AF1	AF2	AF3	AF4	AF5	AFBASE
1	1.50%	1.13%	6.61%	8.09%	3.84%	2.67%
2	10.33%	10.82%	11.12%	15.34%	11.20%	10.76%
3	20.74%	16.07%	15.00%	16.76%	21.81%	21.28%
4	3.95%	19.26%	6.62%	9.48%	15.03%	9.49%
5	17.74%	8.76%	8.72%	14.33%	7.36%	12.55%
6	21.85%	9.26%	4.45%	6.60%	6.88%	14.37%
7	28.43%	23.11%	24.71%	30.64%	21.81%	25.12%
Mean	14.94%	12.63%	11.03%	14.46%	12.56%	13.75%
SD	9.95%	7.39%	6.96%	8.11%	7.24%	7.50%

AGGRESSIVE BEHAVIOUR						
ID	AG1	AG2	AG3	AG4	AG5	AGBASE
1	5.93%	4.31%	1.96%	2.97%	2.09%	4.01%
2	0.92%	1.74%	0.93%	2.34%	0.59%	0.76%
3	2.53%	0.91%	0.49%	1.14%	0.43%	1.48%
4	0.61%	0.37%	1.27%	2.99%	0.14%	0.37%
5	0.52%	0.89%	0.29%	1.85%	0.37%	0.45%
6	0.80%	0.16%	1.70%	1.35%	0.38%	0.59%
7	3.60%	1.15%	0.79%	2.35%	0.35%	1.98%
Mean	2.13%	1.36%	1.06%	2.14%	0.62%	1.38%
SD	2.04%	1.40%	0.61%	0.73%	0.66%	1.30%

FEEDING-FORAGING BEHAVIOUR						
ID	FF1	FF2	FF3	FF4	FF5	FFBASE
1	20.91%	29.55%	33.87%	23.55%	21.08%	21.00%
2	18.91%	28.22%	37.01%	21.29%	18.90%	18.91%
3	37.71%	49.38%	46.50%	42.99%	21.08%	29.39%
4	52.90%	41.60%	57.39%	37.27%	34.36%	43.63%
5	28.07%	35.61%	46.53%	31.97%	26.14%	27.11%
6	29.63%	33.34%	53.29%	32.17%	34.72%	32.17%
7	20.73%	25.98%	36.37%	19.31%	21.08%	20.91%
Mean	29.84%	34.81%	44.42%	29.79%	25.34%	27.59%
SD	12.10%	8.27%	9.01%	8.77%	6.66%	8.61%

LOCOMOTION						
ID	LO1	LO2	LO3	LO4	LO5	LOBASE
1	34.27%	18.08%	16.96%	15.06%	31.87%	33.07%
2	15.86%	15.66%	18.28%	13.76%	17.48%	16.67%
3	18.34%	17.98%	16.61%	16.08%	21.41%	19.88%
4	16.36%	10.93%	10.84%	19.29%	16.46%	16.41%
5	11.13%	11.38%	11.26%	14.29%	16.03%	13.58%
6	13.30%	14.70%	16.69%	19.16%	20.07%	16.68%
7	13.92%	7.86%	6.50%	6.49%	18.57%	16.25%
Mean	17.60%	13.80%	13.88%	14.88%	20.27%	18.93%
SD	7.71%	3.86%	4.37%	4.31%	5.46%	6.49%

INACTIVITY						
ID	IA1	IA2	IA3	IA4	IA5	IABASE
1	36.53%	40.15%	38.02%	46.44%	38.93%	37.73%
2	33.03%	31.69%	27.02%	39.74%	38.90%	35.96%
3	19.29%	14.94%	20.65%	21.46%	23.43%	21.36%
4	25.12%	27.63%	23.81%	30.58%	32.38%	28.75%
5	41.01%	43.19%	33.09%	37.26%	49.95%	45.48%
6	33.41%	42.41%	23.67%	39.80%	37.86%	35.63%
7	30.47%	39.48%	31.01%	38.05%	65.38%	47.92%
Mean	31.26%	34.21%	28.18%	36.19%	40.98%	36.12%
SD	7.21%	10.26%	6.14%	8.00%	13.39%	9.15%

STRESS-RELATED BEHAVIOUR						
ID	SR1	SR2	SR3	SR4	SR5	SRBASE
1	0.73%	6.60%	2.51%	3.82%	2.10%	1.42%
2	20.77%	11.80%	5.56%	7.45%	12.84%	16.80%
3	1.29%	0.60%	0.62%	1.48%	0.43%	0.86%
4	0.98%	0.14%	0.00%	0.30%	1.57%	1.28%
5	1.45%	0.09%	0.04%	0.18%	0.08%	0.77%
6	1.05%	0.09%	0.00%	0.84%	0.00%	0.52%
7	2.72%	2.35%	0.55%	3.09%	2.28%	2.50%
Mean	4.14%	3.10%	1.33%	2.45%	2.76%	3.45%
SD	7.36%	4.50%	2.07%	2.60%	4.54%	5.92%

Study B: *M. nemestrina*

AGGRESSIVE BEHAVIOUR						
ID	AG1	AG2	AG3	AG4	AG5	AGBASE
1	0.54%	1.47%	0.49%	0.55%	0.60%	0.57%
2	0.00%	0.27%	0.30%	0.28%	0.00%	0.00%
3	0.11%	0.15%	0.18%	0.10%	0.19%	0.15%
4	0.03%	0.13%	0.04%	0.00%	0.01%	0.02%
5	1.67%	0.13%	0.12%	0.37%	0.00%	0.83%
6	0.11%	0.10%	0.01%	0.36%	0.92%	0.52%
Mean	0.41%	0.38%	0.19%	0.28%	0.29%	0.35%
SD	0.65%	0.54%	0.18%	0.20%	0.39%	0.34%

AFFILIATIVE BEHAVIOUR						
ID	AF1	AF2	AF3	AF4	AF5	AFBASE
1	2.11%	4.25%	0.56%	0.12%	0.08%	1.10%
2	2.85%	2.20%	0.49%	0.16%	0.29%	1.57%
3	11.74%	18.79%	4.76%	0.65%	0.48%	6.11%
4	8.02%	15.10%	5.49%	4.36%	0.11%	4.06%
5	3.18%	21.83%	4.44%	2.09%	5.81%	4.49%
6	7.54%	5.75%	7.05%	1.07%	3.45%	5.50%
Mean	5.91%	11.32%	3.80%	1.41%	1.70%	3.80%
SD	3.80%	8.30%	2.69%	1.62%	2.39%	2.05%

FEEDING-FORAGING BEHAVIOUR						
ID	FF1	FF2	FF3	FF4	FF5	FFBASE
1	7.40%	14.38%	24.43%	9.84%	9.57%	8.48%
2	9.53%	25.98%	27.55%	23.91%	17.03%	13.28%
3	18.33%	34.99%	36.15%	26.50%	20.23%	19.28%
4	12.69%	28.59%	30.99%	35.04%	8.56%	10.62%
5	26.16%	43.73%	45.89%	25.72%	21.35%	23.76%
6	23.33%	45.60%	28.53%	34.80%	25.68%	24.50%
Mean	16.24%	32.21%	32.26%	25.97%	17.07%	16.65%
SD	7.60%	11.74%	7.75%	9.22%	6.80%	6.83%

LOCOMOTION						
ID	LO1	LO2	LO3	LO4	LO5	LOBASE
1	26.27%	23.47%	23.34%	32.63%	20.00%	23.13%
2	15.05%	8.37%	13.59%	16.85%	11.05%	13.05%
3	4.92%	7.15%	6.77%	9.93%	6.61%	5.77%
4	5.76%	9.88%	11.81%	12.86%	11.08%	8.42%
5	10.76%	4.69%	10.30%	9.47%	6.61%	8.68%
6	10.19%	11.07%	19.46%	12.87%	12.60%	11.40%
Mean	12.16%	10.77%	14.21%	15.77%	11.33%	11.74%
SD	7.83%	6.60%	6.13%	8.68%	4.93%	6.13%

INACTIVITY						
ID	IA1	IA2	IA3	IA4	IA5	IABASE
1	62.69%	52.32%	46.60%	50.78%	66.64%	64.67%
2	70.27%	55.88%	54.04%	50.76%	63.39%	66.83%
3	50.43%	24.25%	29.24%	42.65%	57.63%	54.03%
4	43.96%	22.65%	24.35%	23.56%	60.96%	52.46%
5	53.28%	20.55%	32.56%	46.24%	58.02%	55.65%
6	54.75%	36.66%	42.16%	43.63%	56.73%	55.74%
Mean	55.90%	35.38%	38.16%	42.94%	60.56%	58.23%
SD	9.31%	15.59%	11.32%	10.09%	3.87%	5.99%

STRESS-RELATED BEHAVIOUR						
ID	SR1	SR2	SR3	SR4	SR5	SRBASE
1	0.93%	4.05%	4.53%	6.02%	3.03%	1.98%
2	2.24%	7.26%	3.76%	7.88%	8.19%	5.21%
3	14.41%	14.60%	18.28%	20.10%	14.78%	14.59%
4	29.48%	23.59%	27.26%	23.32%	19.22%	24.35%
5	4.91%	9.00%	6.59%	12.83%	8.15%	6.53%
6	4.00%	0.76%	2.71%	7.15%	0.67%	2.34%
Mean	9.33%	9.87%	10.52%	12.88%	9.01%	9.17%
SD	10.96%	8.19%	9.98%	7.29%	6.99%	8.73%

