

Refinement of the use of non-human primates in scientific research. Part II: housing, husbandry and acquisition

AE Rennie and HM Buchanan-Smith*

Department of Psychology, University of Stirling, Stirling FK9 4LA, Scotland, UK

* Contact for correspondence and requests for reprints: h.m.buchanan-smith@stir.ac.uk

Abstract

In order to safeguard the welfare of laboratory-housed non-human primates, refinement techniques should be applied to every aspect of the life of animals used in the laboratory, from birth to death, with the aim of both minimising harm and maximising well-being. In this second part of a three-part review we summarise published information on housing and husbandry practices, and describe ways to minimise contingent inhumanity associated with the use of primates in laboratories and their breeding and supply (where inhumanity is defined as the infliction of distress). We also discuss methods by which the welfare of these animals can be maximised on a day-to-day basis. The principles of enrichment, aspects of the housing environment, social and physical enrichment and acquisition are discussed. Refinement of the influence of humans and experimental procedures are discussed in Parts I and III of this review, respectively.

Keywords: animal welfare, environmental and social enrichment, housing, husbandry, refinement, transportation

Introduction

With the aim of harmonisation, the essence of Russell and Burch's (1992) original concept of refinement and the most progressive recent concepts of refinement since have been incorporated into the following definition of refinement, proposed by Buchanan-Smith *et al* (2005).

"Any approach which avoids or minimises the actual or potential pain, distress and other adverse effects experienced at any time during the life of the animals involved and which enhances their well-being"
(Buchanan-Smith *et al* 2005).

Refinement techniques that can be used to minimise harm and maximise the well-being of animals during procedures are discussed in part III of this review. However, in order to satisfy the ethical and scientific need to reduce contingent harm, arising indirectly as a result of the use of animals in science, and to maximise well-being on a day-to-day basis, refinement must also be applied to routine housing, husbandry and care practices, and during the process of acquisition and transportation. Such practices are considered likely to have a particular impact on the welfare of non-human primates (henceforth primates) destined for, or currently in use in, laboratories because of their capacity for suffering in inadequate environments, the manner in which they may legally be acquired and the relatively large distances over which they are often transported.

Although many of the refinements discussed in this review have been discussed previously in the literature, information regarding the use of refinement in primates can be

difficult to find as data on primate species are published in a diverse selection of journals. This second part of a three-part review summarises published literature on housing and husbandry, and provides a sample of the types of refinements that could be incorporated into normal practice in laboratories. With a focus on Europe, it also includes a description of current practices still in common use globally (eg single housing) and summarises the scientific evidence as to why these should not be continued. With careful use, based upon knowledge of species-specific needs, these refinements have the potential to greatly improve the welfare of laboratory-housed primates, whilst reducing contingent harm, in accordance with the definition of refinement proposed by Buchanan-Smith *et al* (2005).

Primate housing and husbandry and the use of enrichment

The environment in which primates are kept has a significant effect on their well-being. The concept of environmental enrichment has been applied to the laboratory environment in an effort to promote well-being. In the USA, the legal requirement to consider the psychological well-being of laboratory-housed primates has resulted in a significant change in attitude to housing and husbandry of primates in the laboratory and provided momentum for the use and development of enrichment strategies. Environmental enrichment was defined by Shepherdson (1998) as: "an animal husbandry principle that seeks to enhance the quality of captive animal care by identifying and providing the environmental stimuli necessary for

optimal psychological and physiological well-being” (Shepherdson 1998, p 1).

Thus, environmental enrichment is a refinement which maximises the well-being of laboratory-housed primates. The scale of enrichment techniques varies widely, from the complete redesign of housing to the introduction of small toys but, according to Shepherdson’s definition, all are considered enrichments if they can be shown to positively affect the well-being of laboratory-housed primates (Shepherdson 1998). Evidence shows that the proper use of enrichment can improve the psychological well-being of laboratory-housed primates (Snowdon 1991), indicated by increases in the animals’ ability to cope with challenges, reduction in aberrant behaviours, increased frequency of species-typical behaviour (Pyle *et al* 1996; Wright 1995) and improvements in health and reproductive success (Erwin 1986; Wallis 2002). Despite the potential positive effects of enrichment, misguided attempts at enrichment have the potential to cause harm, for example by causing injury (see review by Bayne 2005; Nelson & Mandrell 2005), causing aggression (Honest & Marin 2006) or when enrichment opportunities are provided but then removed (Bryant *et al* 1988). Other enrichment strategies may be impractical for use in the laboratory environment, for example those which take up too much staff time or which have the potential to affect the outcome of experiments (Newberry 1995; Bayne 2005). Thus, all enrichment strategies must be tested to ensure that their introduction affects welfare positively and that they are practicable in the laboratory. An understanding of species-typical behaviour and physiology is essential for proper assessment of enrichment success and imagination, innovation, motivation and some resources are a requirement during design (Markowitz & Line 1990). The literature on environmental enrichment is vast and cannot be comprehensively covered within the scope of this paper (see Lutz & Novak 2005 for a recent review). However, the range of enrichment strategies and evidence of their effects will be considered and sources of conflict and difficulties that may be encountered during the development of proposed enrichments will be discussed.

Psychological well-being

The ability to express species-typical behaviour and to fulfil behavioural needs has been considered important to the psychological well-being of laboratory-housed primates (Snowdon & Savage 1989; Eaton *et al* 1994; Newberry 1995). The capacity for control and the degree of complexity and predictability of the enrichment are also thought to be important (O’Neill 1989; Sambrook & Buchanan-Smith 1997; Vick *et al* 2000; Bassett & Buchanan-Smith in press). The view of the relative importance of these concepts has changed since the earliest use of environmental enrichment and it is well accepted that the success of enrichment strategies is very much dependent upon the individual and species concerned (Markowitz & Line 1989).

Behavioural needs

As the aim of enrichment is to increase an animal’s behavioural opportunities and to prevent or reduce the expression of abnormal behaviours (including stereotypies), discussions of the concept of behavioural or ethological needs are inevitably and correctly included in the analysis of enrichment strategies. Indeed, the ‘needs’ concept has been incorporated into the European Directive (86/609/EEC), which states that “any restriction on the extent to which an experimental animal can satisfy its physiological and ethological needs shall be limited to an absolute minimum” (European Union [EU] 1986, Article 5, paragraph b).

Thus, European law supports the use of enrichment for laboratory animals. The concept of behavioural or ethological needs was first introduced by Brambell (1965) in a report on the welfare of farm animals in intensive husbandry systems. In this report, it was considered that prevention of the expression of behaviours which the animal is highly motivated to perform could result in frustration and that the degree of frustration experienced would dictate welfare. The performance of such behaviours could therefore be considered an ethological need. Later, Dawkins (1983) attempted to pinpoint exactly what was meant by the concept of behavioural or ethological needs, defining ethological needs as the effect of high levels of causal factors to perform a particular behaviour pattern. Dawkins (1983) argued that true needs (as opposed to ‘luxuries’) could be identified using the principles of consumer demand theory applied to operant and preference tests. Using this principle, only those behaviours that the animal would work hard, or overcome aversive stimuli, to perform could be considered needs. The frustration of behavioural needs is considered to be one of the main causes of stereotypical behaviours in captive animals, where animals are motivated to perform a pattern of behaviour that they cannot perform normally or completely (Mason 1991b). Abnormal and stereotypical behaviours are also likely to occur when the animal is subject to experiences over which it has no control and cannot therefore respond appropriately (Mason 1991b). Thus, the presence of abnormal and stereotypical behaviours has been used as an indicator of poor welfare and inadequate housing and care (Mason 1991a). Abnormal behaviours including stereotypic circling and pacing, eye prodding, self-sucking, depilation, self-mutilation, coprophagy and regurgitation have been observed in laboratory-housed chimpanzees, Old World monkeys and callitrichids (Baskerville 1999; Fritz *et al* 1999; Poole *et al* 1999). The occurrence of abnormal and stereotypical behaviours can be reduced (Watson *et al* 1993; Eaton *et al* 1994; Crockett 1998; Lutz *et al* 2003; Novak 2003; Bourgeois & Brent 2005) or prevented (Lutz & Novak 2005) by the use of carefully considered enrichment strategies, supporting the hypothesis that these behaviours occur as the result of the thwarting of behaviours that the animal is highly motivated to perform (Marriner & Drickamer 1994).

Performance of natural behaviours

The term behavioural need is commonly misused, often in conjunction with the assumption that captive animals must show a full repertoire of species-specific behaviours for optimal welfare (Chamove & Anderson 1989; Veasey *et al* 1996). This proposal falls short if we consider the welfare of animals foraging without success during periods of food shortage or animals showing species-typical predator avoidance behaviour. Veasey *et al* (1996) discussed this misrepresentation of the term behavioural need in the context of wild versus captive behaviour and concluded that the expression of wild-type behaviours may be correlated with good welfare rather than being the cause of good welfare, as is often assumed. Thus, the performance of the full range of species-typical behaviour is not necessary in itself, but the ability to respond in a species-typical manner to stimuli encountered in the captive environment is critical. This idea is developed in analyses of enrichment strategies in terms of control, complexity and predictability.

Control, complexity and predictability

The concepts of control, complexity and predictability are also considered to be important facets of enrichment strategies. However, despite general acceptance that these factors have some bearing on the efficacy of enrichment attempts, few studies have studied their importance in detail. The purported importance of control was stressed by Snowdon and Savage (1989) who stated that “animals cannot passively receive environmental events; they must be able to act on the environment and consequences must result from their actions” (Snowdon & Savage 1989, p 81).

The idea that control was necessary for well-being was established in studies using aversive stimuli in which animals learned that performance of a selected behaviour caused the aversive stimulus to cease (see Overmier *et al* 1980 for a review). In primates, Hanson *et al* (1976) used high intensity noise to test the effects of control of a stressful stimulus in rhesus macaques (*Macaca mulatta*). They found that those animals which could influence the duration of exposure to the noise, by pushing a switch to turn it off, had a plasma cortisol concentration similar to that of animals which were not exposed to the noise. In contrast, those animals which were exposed to the unpredictable noise but could not influence the duration of exposure showed significantly higher plasma cortisol concentrations. A lack of control over aversive events can result in ‘learned helplessness’ or depressive behaviour in which the animal ceases to attempt to respond to its environment and shows reduced learning capacity (Bloomsmith *et al* 2001).

Despite the availability of evidence indicating that the control of stressful events is critical for well-being, there are few such studies in which the need for control of positive events has been examined. However, those studies which do consider control over positive events indicate that this control can have far-reaching positive effects on well-being and development. For example, Mineka *et al* (1986) studied

the long-term effects of a rearing environment in which infant rhesus macaques had control of the schedule of feeding, water availability and provision of treats, in comparison with yoked individuals which had no control of the schedule. In subsequent behavioural tests, individuals which had had control of their feeding schedule showed less fear in the presence of novel objects and in novel environments and showed more exploratory behaviour than yoked subjects. Also, individuals which had had control were more active in their attempts to regain social contact in a separation test than yoked conspecifics. The responses of yoked controls were similar to those observed in infants reared in standard laboratory cages with variation in access to reinforcers, indicating that the ability to control had positively affected the behaviour of the young macaques. However, in the laboratory environment, where the provision of enrichment is dependent upon the availability and motivation of staff, it is also important to consider further the results of the study by Hanson *et al* (1976). Despite evidence of positive effects of control of the noisy stimulus, Hanson *et al* (1976) also found that if control was taken away from the individuals which had previously had control over the noise, the concentration of cortisol in plasma increased to levels similar to the individuals that had never had control. This increase in cortisol was associated with the expression of aggressive behaviours that were not observed in yoked animals, suggesting that loss of control is more stressful than never having had control in the first place.

Sambrook and Buchanan-Smith (1997) agreed that animals need to have a degree of control over events that affect them, but argued that having complete control over all events is also sub-optimal. They proposed that the concepts of novelty and control are linked and that the novelty of an object could be defined in terms of the degree to which the animal has control over it. Thus it is the process of learning to control and overcome the novelty of the stimulus that is rewarding. Once an animal has gained control, its expectations of control rise to meet its ability to control and thus loss of control is stressful, whilst the ability to control everything in its environment results in predictability and regression into boredom. Sambrook and Buchanan-Smith (1997) suggested that a balance between total control and lack of control is optimal and that, by providing objects and environments that suggest controllability but that resist control, responsiveness can therefore be maintained. In 1996, Sambrook and Buchanan-Smith investigated the relative importance of control and complexity to four species of guenons in a novel object study. The results of this study supported the idea that control is important and that an object whose responsiveness is contingent upon the animal’s behaviour towards it becomes the target of more attention than an object that is identical in appearance but does not respond. However, this study also suggested that the complexity of an object *per se* is not important. However, it could be argued that, if the complexity of the object or environment increases its resistance to control, then complexity contributes to enrichment. Sambrook and Buchanan-Smith (1997) also argued that there is an

optimum degree of predictability of events; total predictability may result in behavioural frustration and boredom whereas complete unpredictability results in stress. This view is supported by the work of Markowitz and Line (1989) who found that an apparatus that rhesus macaques can control, but that is also responsive to manipulation, was used by more individuals and for longer than one that is unresponsive. Older animals which have been housed singly for a long period of time do not respond greatly to passive forms of enrichment, but when given even a limited amount of control they show sustained use of responsive equipment and recover more quickly from stressful encounters (Markowitz & Aday 1998). Chamove (1989) also found that objects that responded to manipulation by captive chimpanzees were favoured over inanimate objects and that objects that responded unpredictably were also favoured. This is consistent with the theory that a variable schedule of reward is more reinforcing than a fixed schedule of reward and is likely to reflect the animals' ability to adapt to dynamic natural environments in which animals must learn to respond in effective ways in order to survive (Markowitz & Aday 1998).

Housing conditions and enrichment

In accordance with the European Directive (86/609/EEC), "all experimental animals must be provided with housing, an environment, at least some freedom of movement, food, water and care which are appropriate to their health and well-being" (EU 1986, Article 5, paragraph a).

Details of how these provisions should be met are given in Appendix A to the European Convention (ETS 123), which lists acceptable ranges and minimum standards of provision for most aspects of the housing environment including cage size, ventilation, temperature, humidity, lighting, noise, alarm systems, health monitoring, feeding, watering, the provision of bedding, cleaning and the provision of exercise (European Commission [EC] 1986). These recommendations are currently being revised, but their present status dictates the minimum standard of housing conditions for laboratory-housed primates in Europe. In practice, the selection of housing and husbandry practices is dependent upon many factors, including the use of the animal at the time and the related need for human contact, age, research needs, personnel safety, animal safety, staff experience, economic considerations, climate and the degree of urbanisation. For example, breeding and stock animals are usually held in different accommodation from that in which animals on experiment are held (Baskerville 1999). The cages used for experiments are commonly the most restrictive an animal will experience (Baskerville 1999). Implicit within the European guidelines are the practicalities associated with laboratory use of primates. Whilst providing a bare minimum of protection for primates housed in laboratories, they promote the needs of the institute, scientist and care worker. It must be accepted that the needs of staff involved in the use of primates in laboratories are important, especially in terms of safety, but it is also critical in the revision of the guidelines to find a better balance between the needs

of staff and those of the animals. Laboratory housing must take into account costs, practicality and experimental requirements as well as the needs of the laboratory-housed animals.

Environmental parameters

Temperature and humidity

Appendix A to the European Convention (ETS 123) includes recommendations on the rate of ventilation of animal rooms and acceptable temperature and humidity ranges. A ventilation rate of 15–20 air changes per day is considered adequate for all species in this guide. It is also stated that relative humidity should be maintained at $55 \pm 10\%$ and that humidities below 40% and above 70% should be avoided. These very general recommendations do not take into account the very different ecology of the range of primate species kept in laboratories. For example, New World species typically inhabit warm but very humid habitats in the rainforest, whereas baboons may live in comparatively arid climates. However, control of the range of humidity within the suggested bounds is likely to be more easily maintained than more extreme states of humidity. Similarly, the current Appendix A recommends that the temperature of primate housing should be maintained at 20–28°C for New World species, whereas Old World primates should be housed in rooms kept at 20–24°C (EC 1986). Although maintenance of the environment at this temperature is unlikely to adversely affect welfare, this recommendation does not take into account the range of temperatures at which primates would live in the wild. The maintenance of temperature and humidity within the currently required ranges is practical in that they ensure that the working environment is not uncomfortable for the staff. It is noted in the current Appendix A that the temperature and humidity range suitable for very young primates is smaller than that for adults, a difference that must be taken into account (EC 1986). The species-specific differences in environmental requirements are recognised in the ongoing revisions of Appendix A. It is noted that fluctuations in humidity are less well tolerated by marmosets (*Callithrix spp*) and tamarins (*Saguinus spp*) and that these species should not be exposed to humidity of less than 30% as respiratory disorders may result. Poole *et al* (1999) noted that the relative humidity should be in the range 40–60%. In the revised Appendix A, species-specific variations in temperature requirements are also recognised. A temperature range of 23–28°C is recommended for housing marmosets and tamarins and similar temperatures are considered appropriate for squirrel monkeys (24–26°C). A wider range of temperatures is considered appropriate for the majority of macaque species used in laboratories and for baboons (16–25°C). However, it is noted that a temperature range of 21–28°C is more appropriate for the long-tailed macaque.

Lighting

Although recommendations regarding the appropriate temperature and humidity for housing primates in laboratories are given in the current Appendix A to the European

Convention (ETS 123), little consideration is given to light intensity in primate housing (Reinhardt 1997a). Instead, Appendix A states that there is a need to satisfy the biological needs of the animals and to provide a safe working environment. Evidence shows that lighting levels can affect both the breeding success of laboratory-housed primates and their behaviour. For example, in common marmosets, bright conditions have been shown to increase breeding success and activity, whereas dim conditions inhibit breeding and result in reduced activity (Heger *et al* 1986). In contrast, however, Schapiro *et al* (2000) found no statistically significant differences in behaviour in long-tailed macaques (*Macaca fascicularis*) housed in cages that varied in illumination. In natural conditions light intensity varies from 100 000–150 000 lux in bright sunlight to 5–10 lux in dim moonlight (Clough 1999). Recommendations for the light intensity of animal rooms range from 150 to 400 lux in the centre of the room (Clough 1999). However, lighting levels in animal rooms are not constant and those housed in lower tier cages may experience light of a much lower intensity than those in the top tier (Reinhardt & Reinhardt 2000a). Consideration should also be given to the wavelength of light as different types of bulb emit light of different wavelengths (fluorescent lights emit more green–yellow light [500–650 nm], whereas incandescent lamps emit light at the red end of the spectrum [600–700 nm]) (Clough 1999). The range of colours that primates can see should thus be taken into account when selecting the lighting system (Strasser 1970 cited in Clough 1999). It has been shown that exposure to natural light can reduce the occurrence of abnormal behaviours in young rhesus monkeys (O'Neill 1989) and it has been suggested that choices of the intensity and potentially the wavelength of light should be provided, matching the choices made by primates in the wild between sunlight and shade (Buchanan-Smith 1997). If it is not possible to provide natural light in the laboratory (for physical or scientific reasons), it has been recommended that artificial light that provides a wide range of wavelengths in a natural way (without introducing harsh contrasts) should be used (Clough 1999). However, care should be taken when selecting an appropriate lighting regime for primates. Lights that simulate sunlight are available commercially but it has been found that the use of these lights has both positive and negative effects on the behaviour of primates with comparison to artificial fluorescent lighting. Novak and Drewsen (1989) compared the behaviour of laboratory-housed rhesus macaques before and after exposure to a lamp designed to simulate natural light. They found that monkeys exposed to both the light and radiation from the lamp showed an increase in affiliative behaviour which persisted when the animals were returned to normal artificial light. In contrast, monkeys which were exposed to the light from the lamp but were protected from the ultra-violet (UV) radiation showed an increase in affiliative behaviour which declined again when the animals were returned to fluorescent lighting. Monkeys exposed to UV radiation also showed more aggressive and sexual behaviour and showed greater urinary cortisol responses to

stress than those exposed only to the light from the lamp. Thus, it appears that, in rhesus monkeys, exposure to a light source which simulates natural light can result in changes in behaviour that are likely to be indicative of increased psychological well-being but exposure to UV radiation from these light sources may not be so beneficial. In contrast, marmosets and tamarins benefit from exposure to UVB radiation, which reduces the incidence of metabolic bone disease and improves immunity (Hampton *et al* 1966; Lopez *et al* 2001). However, no empirical data on the effect of UVB radiation on the behaviour and psychological well-being of marmosets and tamarins have been found.

It has been recommended that light should be faded in and out at the start and end of each day to simulate dusk and dawn, so that the animals are not plunged into darkness or light (Buchanan-Smith 1997). As most primate species naturally inhabit regions close to the equator, a 12-hour light/dark cycle is considered to be most appropriate, but low intensity light should be provided at night to allow animals to readjust their position without danger. Adjustment of day length can also be made to simulate natural seasonal changes, which may also aid breeding (Buchanan-Smith 1997). The need to control lighting within the laboratory has been acknowledged in the revision of Appendix A to the European Convention (ETS 123).

Noise

Ventilation, heating systems, automated washing machines, alarms, and general human and animal activity all create noise. The use of easily cleaned stainless steel caging and hard surfacing on walls and floors makes the job of the care worker easier, but it also increases the noise levels in the environment. It should be noted that the ability of humans to perceive sound is very much less developed than that of most other animals and the level of sound that we perceive in the laboratory is likely to be very much less than that which primates perceive (Clough 1999). This is particularly true of New World species, which communicate using high-pitched frequencies and are known to be able to hear ultrasonic frequencies (Sales *et al* 1999). Sudden loud noises can cause fear and continuous exposure to loud uncontrollable noise has been found to be stressful to primates (Hanson *et al* 1976). The current European recommendations do not include specification of acceptable noise levels (EC 1986), but UK guidelines recommend that background noise in the laboratory should not exceed 50 dB (Home Office 1989) and in the draft revision of Appendix A of the European Convention (ETS 123) it is recommended that background noise in the laboratory should not exceed 65 dB for more than short periods of time. The limits on noise recommended in the UK guidelines are supported by Clough (1999), who considered that if background noise is maintained below 50 dB, adverse effects on biology should be prevented. The use of bedding, floor substrate and wooden furniture can dampen noise to some extent but sources of ultrasound, for example from dripping taps and computer monitors, should be identified and shielded or removed where possible (Clough 1999). The provision of low-level

background noise, like soft music or the radio, has been investigated as a means of masking sudden, loud and/or unfamiliar noises and as a form of enrichment. For example in a recent study, Howell *et al* (2003) found that exposure to music, loud enough that the lyrics and melody could be heard, resulted in a decrease in aggressive or agitated behaviours and in active and exploratory behaviours and in an increase in affiliative inactive behaviours like grooming in chimpanzees (*Pan troglodytes*). Howell *et al* (2003) noted that the reduction in aggressive or agitated behaviour was most pronounced in the morning, when routine husbandry procedures were carried out, and that the increase in affiliative behaviour was most pronounced in groups composed entirely of females. An increase in affiliative behaviour was also recorded in rhesus monkeys during exposure to jazz music and occurred irrespective of whether the monkeys could or could not control their duration of exposure to the music within a 2-hour period (Novak & Drewsen 1989). O'Neill (1989) noted that abnormal behaviours associated with confinement in winter housing, including stereotypical behaviours and self-mouthing, were reduced when young rhesus macaques were exposed to classical music.

Although music and masking sounds have apparently positive effects in some studies, not all attempts to enrich the lives of captive primates with music and other sounds have produced clear results. For example, after exposure to rainforest sounds adult lowland gorillas (*Gorilla gorilla*) showed more frequent locomotion, thought to be indicative of agitation, whereas infants spent less time clinging, suggesting that the sound successfully masked the noises produced by caretakers, ventilation systems and other animals. It was concluded that the rainforest sounds were enriching for the infant gorillas but increased agitation in the adults (Ogden *et al* 1994). It is possible that the masking of routine husbandry noises induces stress because the animals are no longer able to monitor the position and activity of staff. It should also be noted that such masking noises must be selected to suit the species concerned. Much of the sound produced by a radio is of a frequency that is thought to be imperceptible to rats (Clough 1999) and may also be imperceptible to New World primates (McDermott & Hauser 2004). It has also been suggested that the sounds intended to mask aversive noises in the laboratory may inadvertently mask communications between conspecifics (Newberry 1995), the effects of which are likely to be dependent on the nature of the communications that are masked.

Cage size

According to Appendix A of the European Convention (ETS 123), the vertical height of cages provided for primates should be the greatest dimension and is considered to be just as important as the floor area, although this is emphasised only for simian primates and apes. The guidelines also state that it is important that the animal can stand fully erect and that those species that brachiate can extend their bodies fully without their feet touching the floor. Recommended

sizes range from that for primates weighing less than 1 kg (callitrichid species), for whom the minimum required cage size is 0.25 m² with a height of 0.60 m, to that for primates weighing 15–25 kg, for whom a floor area of at least 1.5 m² and a cage height of 1.25 m are recommended. According to the guidelines, these cages can hold either one or two animals.

The minimum standards are considered by many to be inadequate because they are based upon the weight of the animal and do not consider the animals' linear dimensions. This is problematic for certain species, for example the minimum required cage height for the relatively light long-tailed macaque is actually less than the head-to-tail length of the animal. This means that long-tailed macaques housed in a cage of minimum size cannot perch in the cage without their tails touching the ground (Buchanan-Smith *et al* 2004). The current minimum cage size also does not allow for adequate exercise, species-specific differences in behaviour or the incorporation of adequate environmental enrichment (Poole *et al* 1994; Baskerville 1999).

The assumption in Appendix A of the European Convention (ETS 123) that lighter animals require less space than heavy animals is also refuted when we consider that the weight of an animal is closely associated with its age, and that younger lighter animals are generally more active than older adults (Poole *et al* 1994). In response to these criticisms of the 1986 guidelines, experts at the 1993 Berlin Workshop on the Accommodation of Laboratory Animals in Accordance with Animal Welfare Requirements developed new recommendations for cage size, allowing for proper extension of body parts in all species and the incorporation of cage furniture that would allow for the expression of more species-typical behaviour (Poole *et al* 1994). For marmosets a minimum of 1.0 m² of floor space was recommended for one to two adults and 0.25 m² extra space was required for each additional animal. A recommended cage height of 1.5 m was proposed. In larger species, 3 m² of floor space was recommended for adult cercopithecoids of more than 5 kg with a cage height of 1.5 m (Poole *et al* 1994). Thus, the importance of vertical height in the cage was emphasised for the small and naturally arboreal species but not prioritised to such an extent for Old World primates, many of which live semi-arboreal lives in the wild. In practice, it is important that a distinction is made between different species of Old World monkeys as the extent to which the vertical dimension of the cage is used varies between even the most commonly used species of macaque. Rhesus macaques are naturally the most terrestrial of the macaques, whereas long-tailed macaques are a mainly arboreal species (Baskerville 1999). The importance of cage height to common marmosets was demonstrated by Ely *et al* (1998), who found that they used the upper part of the cage in preference to the lower half. Although the provision of vertical space appears to be important, the positive effects of increased cage height can be negated if a tiered caging system is used. Cage height is thought to be important to accommodate primates' need for a vertical escape response.

It is also likely that animals in the lower tier are inspected less thoroughly because they are not as easy to see, both because of limited lighting and because the carer must bend to see clearly (Reinhardt & Reinhardt 2000a). Poole *et al* (1999) and Baskerville (1999) stated that marmosets, tamarins and Old World monkeys show a preference to look down on handlers. From this vantage point they can properly assess the magnitude of danger. The restriction of the vertical flight response in lower tier caging may be a source of stress as the individual is unable to respond in a species-appropriate manner to perceived dangers, for example the sudden appearance of a handler (Baskerville 1999; Poole *et al* 1999). Ely *et al* (1998) examined this preference in habituated common marmosets and found that the preference for height in the cage was associated with the height of the handler's face, suggesting a desire to interact with the handler rather than to retreat beyond their reach. These results demonstrate that if a positive working relationship is developed (Rennie & Buchanan-Smith 2006) vertical flight should not occur in response to caretakers entering a room but that in fact the presence of handlers in the room can be enriching (Ely *et al* 1998).

In an investigation to determine the effects of cage size on behaviour, appetite and urinary cortisol in pig-tail macaques (*Macaca nemestrina*), Crockett *et al* (2000) found that appetite and urinary cortisol were unaffected by housing in cages ranging from 22% to 148% of the recommended size (USA recommendations). The study also found that behaviour was unaffected in all but the smallest of the cages, which was so small that it effectively prevented any locomotion at all. However, it was noted in this study that no cage furniture (for example perches) was included. Bayne and McCully (1989) found that housing rhesus macaques in the next available cage size (USA standards), a change in cage size that might practically be offered, in fact increased the occurrence of self-directed, abnormal behaviours. This demonstrates that increased cage size alone does not constitute an enrichment if no further enrichment is provided to enable the animal to respond appropriately to challenges associated with life in the laboratory. In contrast, Draper and Bernstein (1963) found that, in rhesus macaques, large increases in cage size had a significant effect on behaviour and greatly reduced the occurrence of stereotypical behaviours. The cages used in this study were much larger ($0.91 \times 0.91 \times 0.91$ m, $1.2 \times 0.91 \times 2.44$ m and $7.32 \times 14.63 \times 2.44$ m [length \times width \times height] for small, medium and large cages respectively) than those studied by Crockett *et al* (2000) and Bayne and McCully (1989) but, perhaps more importantly, were constructed from wire on which the monkeys could climb and hang. Thus, when housed in the larger cages the monkeys were able to make use of the whole space in a species-typical manner. Buchanan-Smith *et al* (2004) argued that a suite of characteristics (including morphometric, physiological, ecological, locomotor, social, reproductive and behavioural characteristics) should be used to determine minimum cage size.

Cage furniture

In order to ensure that primates use their allotted space to the fullest extent, the furnishing of the cage must be considered carefully. It is also essential that the furniture does not unduly interfere with cleaning, feeding, capture and, importantly in the laboratory, easy inspection of the occupants. In the smallest cages, the opportunities for enrichment are obviously fewer, but small changes can have a disproportionately positive effect on welfare. The principles of enrichment of cage design and structure are the same regardless of the size of the cage.

The provision of perches adds a vertical dimension to a barren cage and gives the occupant a vantage point and in rhesus macaques (Reinhardt 1994b) and New World monkeys (Buchanan-Smith 1997) offers space to groom. Where space will allow, the provision of multiple perches of different diameters has been recommended (Roder & Timmermans 2002) and introduces variety that can stimulate very different behaviours. For example, Caine and O'Boyle (1992) found that red-bellied tamarins (*Saguinus labiatus*) tended to show more wrestling play on flat horizontal perches and more chasing play on thinner branch-like structures. In New World monkeys the provision of swings, slings, ladders and ropes, which move in response to movement by the cage occupant, adds an element of controllable unpredictability to a very simple enrichment (Buchanan-Smith 1997). Such structures can be made of a variety of materials including PVC (Reinhardt 1997b), rubber, wood (Buchanan-Smith 1997) or metal (Kelley & Hall 1995). In the case of marmosets, the provision of wooden branches allows the performance of species-typical gnawing and scent-marking and in macaques, the provision of wooden perches or blocks has been recommended because it increases species-typical manipulation and gnawing, a possible element of dental care (Reinhardt 1997c). The use of wooden furniture is important for all callitrichid species as they have claw-like rather than flat nails on all digits except for the thumb and therefore have difficulty gripping smooth metallic and plastic surfaces. Although wooden structures will need to be replaced more frequently than the highly resistant PVC and metal alternatives, they are cheap (Baskerville 1999) and can still be cleaned in standard cage-cleaning machines or by hand (HM Buchanan-Smith personal observation 2006). They also provide a higher degree of responsivity and texture as well as dampening noise (Baskerville 1999; Poole *et al* 1999; Eckert *et al* 2000). It is commonly supposed that the animals prefer wood to metal and plastic substrates (Baskerville 1999; Eckert *et al* 2000), but no published empirical data on such a preference could be found.

Although studies have shown that Old World primates can benefit from the provision of structural enrichment, their response varies depending on the enrichment offered. For example, Dexter and Bayne (1994) reported no change in the occurrence of abnormal behaviour in adult rhesus macaques which were provided with different types of swing. The authors concluded that swings do not constitute

an enrichment for singly-housed adult rhesus macaques. In contrast, Kopecky and Reinhardt (1991) compared the use of swings with that of perches as means of enriching cages of paired, adult, female, rhesus macaques. They found that perches were used eight times more often than swings and that swings distracted the animals for a negligible time period. The authors proposed that this preference arose because perches allowed the macaques to sit in a species-typical, relaxed posture near the front of the cage from where they could view the environment outside the cage more easily. This demonstrates the need to consider species-typical behaviour when selecting appropriate enrichments for primates of different species.

Wild marmosets and tamarins seek security by climbing high into trees and hiding in dense vegetation. Caged callitrichids benefit from the provision of similar refuges by the inclusion of wooden nest boxes high in the cage (Poole *et al* 1999). Thus, callitrichids typically retreat into nest boxes to rest for the night, a habit which is beneficial for human carers as the animals remain active during the day and thus the nest box does not normally prevent easy inspection of the cage occupants. Similarly, families of owl monkeys (*Aotus spp.*) naturally seek the shelter of a hollow in a tree trunk or in dense foliage in which to sleep during daylight hours and benefit from the provision of a nest box in which the whole family can rest (Erkert 1999). However, because owl monkeys are only active at night it is beneficial to maintain their 12-hour light/dark cycle so that at least some of the animals' waking hours occur during working hours (Erkert 1999). Low lighting must be provided to allow inspection of the animals. Wood is preferable for construction of nest boxes because, unless well ventilated, breath condensate can collect on the inside of metal and plastic boxes and on the fur, making the animals wet, and it has been suggested that wet fur falls out more easily (Poole *et al* 1999). Screens can also provide refuge, particularly from aggressive encounters (Chamove 1984), and resulted in increased affiliative behaviour in groups of marmosets and tamarins (McKenzie *et al* 1986). The beneficial effects of screens were found to be less in stable social groups (McKenzie *et al* 1986). Care must be taken that screens do not interfere with inspection of the animals. Indeed, retreat to a refuge for long periods of time and avoidance of companions can often be a sign of a health and/or welfare problem (Wolfensohn & Honess 2005).

A further means of enrichment, which has been used mainly with the common marmoset (*Callithrix jacchus*), is the addition of a small veranda to the front of the cage. This provides additional space in the cage but also provides a vantage point from which individuals can see the activities of conspecifics in other cages and of staff more clearly. Studies have shown that verandas are the most highly preferred area in the cage (Ely *et al* 1998). However, their placement must be carefully considered as they bring individuals into closer proximity. This has the potential to lead to arousal and redirected aggression towards cagemates (HM Buchanan-Smith personal observation 2006).

The selection of a good floor substrate can encourage the animals to use the floor space, even in arboreal species like the common marmoset that are naturally less inclined to do so (McKenzie *et al* 1986). This effectively increases the amount of usable space in the cage (Chamove and Anderson 1989). Many authors recommend a solid floor and suggest that it should be covered with wood shavings, straw or a similar substrate (McKenzie *et al* 1986; Buchanan-Smith 1997; Poole *et al* 1999; Roder & Timmermans 2002). Food can be scattered amongst such substrates to provide foraging enrichment (McKenzie *et al* 1986; Newberry 1995).

Enrichment can be provided for animals housed in small cages by allowing them access to a separate large play room or cage on a rotational basis. In studies in rhesus macaques, Japanese macaques (*Macaca fuscata*) and capuchins (*Cebus apella*) (Bryant *et al* 1988; Tustin *et al* 1996; Wolff & Ruppert 1991) such cages were used to provide enrichment for singly housed animals. Although this system of rotational enrichment resulted in an increase in active behaviours in both the play cage and the home cage (Tustin *et al* 1996) and could be managed safely for the majority of singly caged animals (Wolff & Ruppert 1991), the positive effects appear to be less for older animals which had been singly caged for a long period of time before visits to the play cage were introduced. These individuals sat in one place for the entire exercise period.

It should be noted that although the use of such cages has the potential to be beneficial, the removal of a primate from his or her home cage can be stressful (Reinhardt *et al* 1990), especially if the animal is unused to the procedure. Care should be taken to ensure that the animals get used to moving to the play room or cage on a regular basis and that transfer is achieved using the least stressful possible means. It is proposed that, although the rotational use of a play cage may appear beneficial whilst in use, it is possible that the loss of enrichment on return to the home cage is more stressful than the lack of such enrichment in the first place, in accordance with evidence showing that loss of control is stressful (Hanson *et al* 1976). This theory is supported by Bryant *et al* (1988) who concluded after examination of several enrichment strategies that rotational group use of a play area was less beneficial not only than continuous access to a pair-mate within the home cage but also than the introduction of enrichment to the home cage. However, this should not be taken to imply that animals destined for single housing should not be socially housed whenever possible. Primates will be better socially adjusted and better able to cope with the challenges that they face in laboratory experimentation if they have a secure social environment. The work of Novak (2003) and Lutz and Novak (2005) shows that the age at which rhesus macaques are put into single housing impacts on whether they will develop abnormal (stereotypical and self-injurious) behaviours. Therefore, maintaining primates in species-appropriate social conditions for as long as possible is advisable.

Cage space can be increased in standard caging systems by linking more than one cage together with tubing. This has been achieved with both New and Old World monkeys (Baskerville 1999; Poole *et al* 1999). Such tubing moves when the monkeys move through it, creating a responsive substrate and a degree of unpredictability. It has been found that monkeys spend a large proportion of their time in cage links which can be used as a vantage point from which more of the colony room and other animals in the colony can be seen (Scott 1991).

Novel objects and feeding enrichment

Toys and other enrichment devices have also been introduced to cage environments to increase species-typical behaviour. Their provision is dependent upon cost and the motivation and time of staff and therefore must be cheap (or free) and easy to deliver. It is imperative that such toys are relatively safe, even on destruction, so that attempted enrichment does not result in harm. Examples of enrichment toys and devices include interactive computer games activated by a joystick (Bloomsmith *et al* 2001), moving and standing water (Parks & Novak 1993), pools for diving (Anderson *et al* 1992), mirrors, both hand-held and attached to the wall (Brinkman 1996), Nylaballs® and other items suitable for chewing (Tustin *et al* 1996), phonebooks (Brinkman 1996), cardboard or plastic tubes and containers (Buchanan-Smith 1997). In a study of a wide range of toys provided for single-housed, male, long-tailed macaques, Brinkman (1996) found that those toys that were manipulable and could be carried around were used most frequently. Species-specific differences in the use of such objects should be considered if maximum enrichment is to be gained from their use. For example, interactive toys given to the common marmoset must be small and light enough for the animal to move or carry around (Buchanan-Smith 1997). Rotation of toys can help to maintain novelty (Brinkman 1996; Buchanan-Smith 1997).

Primates are adapted to spend most of their waking hours foraging and feeding (Anderson & Chamove 1984). For example, long-tailed macaques spend more than 50% of their time either foraging or feeding (Wheatley 1980 as cited by Baskerville 1999). In the laboratory, food is often provided in an easily accessible form and much of the time that should naturally be spent feeding remains unused. Furthermore, when primates are housed in social groups, it is common for the more dominant individuals to monopolise easily accessible food sources (Tardif & Richter 1981; Michels 1998). Thus, extending the time spent feeding has been one of the main targets of enrichment strategies for all captive and laboratory-housed primates (eg Snowdon & Savage 1989). All or a proportion of the daily allowance of food can be presented in enriched feeding systems. Care must be taken that all animals are still able to obtain sufficient food. This can be achieved by feeding specifically designed complete foods in the morning with enriched feeding provided later in the day as it is important to ensure that the animals continue to obtain balanced nutrition (Wolfensohn & Honess 2005). The provision of a foraging

substrate in which small items of feed (eg grain or sunflower seeds) can be scattered and then foraged for has been found to increase species-typical foraging and to reduce aggression (Chamove *et al* 1982; Anderson & Chamove 1984). Similar foraging opportunities can be provided by means of foraging trays, which may be easier to remove and keep clean (Spector *et al* 1994). Food can also be buried in straw, or placed in puzzle feeders from which the primate can obtain a desired food item simply by persistent manipulation or by learning the 'trick' to solve the puzzle (eg Murchison & Nolte 1992; Box & Smith 1995; Murchison 1995; Pyle *et al* 1996; Buchanan-Smith 1997; Glick-Bauer 1997). More simply, food can be given in a form that requires manipulation and processing before eating, for example by feeding nuts in their shells and fruit that has not been peeled (Buchanan-Smith 1997), or by freezing juice (Schapiro *et al* 1996) or small items of food within ice cubes. Spreading feeds over a wider area and ensuring that items take longer to eat also makes it more difficult for dominant animals to monopolise the feed. Frozen items may also aid cooling if primates are exposed to warm climatic conditions. These feeding enrichments not only increase the time taken to feed but also increase the animals' choice about when to feed and what to feed on. Species-specific feeding enrichments have been designed and used with great success. For example, McGrew *et al* (1986) developed a wooden gum-feeding device for common marmosets, in which the marmosets could gouge through the wood in a naturalistic manner to obtain gum arabic. Anecdotal evidence in the white handed-gibbon (*Hylobates lar*), and quantitative evidence from preference studies in stump-tailed and rhesus macaques and in chimpanzees indicate that primates may prefer to work to obtain their food rather than obtain it more quickly for free (contrafreeloading) (Markowitz 1982; Anderson & Chamove 1984; Menzel 1991; Reinhardt 1994a). Studies have shown that the predictability of feeding has a significant effect on the psychological well-being of laboratory-housed primates. It has been shown that highly predictable schedules of feeding can be associated with food anticipatory activity, characterised by increases in arousal and activity and the occurrence of stereotypical behaviours (Mistlberger 1994; Bloomsmith & Lambeth 1995). Bassett (2003) found that common marmosets showed more signs of arousal and anxiety prior to feeding when they were fed on an unreliable temporal schedule and with unreliable signals than control animals. This feeding schedule is analogous with schedules commonly seen in laboratory husbandry systems, where noises associated with food preparation and delivery may be associated with the delivery of food, with the food being delivered to other animals or being delayed. In contrast, those marmosets that were fed on an unreliable temporal schedule but were given a reliable signal informing that feeding would occur showed no change in behaviour with respect to controls. Bassett (2003) suggested that the provision of a reliable signal given just prior to feeding could therefore be used to reduce stress associated with food anticipation and frustration of

feeding motivation. Bassett and Buchanan-Smith (in press) provided a thorough review of the behavioural and physiological effects of the predictability of aversive and appetitive stimuli, and the application of experimental findings to animal husbandry in practice.

Section summary and conclusions

The introduction of enrichments has been found to reduce stress and frustration, increase primates' ability to cope with stressful experiences and improve their health and reproduction. To be most effective, enrichments must be appropriate for the species concerned but also should not hinder laboratory practice unduly. The complexity and predictability of enrichments are important as these characteristics affect the rate at which the animal can learn to exert control over the enrichment.

The temperature and humidity must be appropriate to the species and age of primates. Natural wavelengths of light are most appropriate, although the effects of exposure to UVB radiation vary with species. The provision of choice between light and shade and an artificial dawn and dusk are thought to be beneficial. Background noise should be kept to a minimum and ultrasonic noise should be eliminated where possible. Music can be beneficial to mask sudden noises but may reduce ease of communication and prediction of significant events.

The animal's size, age and natural propensity for activity and arboreality should be taken into account in determining cage dimensions. Cage height is considered to be important to highly arboreal New World primates, although relationships between staff and animals should be such that caretakers do not cause a vertical flight response. Cage furniture should maximise useable space and facilitate expression of a range of species-typical postures and behaviours. Object enrichments must be appropriate to the species but, with thought and motivation, can easily be delivered on a routine basis with little cost. Feeding enrichment should be used to increase foraging time and food manipulation and reduce the possibility of food monopolisation.

Social enrichment and husbandry of primates

No method of enrichment for laboratory-housed primates has been found to be as effective as the presence of conspecifics (Hennessy 1984; Reinhardt 1990; Schapiro *et al* 1996), especially those favoured by the individual (Smith *et al* 1998), and an inherent need for social companionship has been recognised in most primate species (eg Harlow & Harlow 1962). However, it has been noted that, although all infant primates require social contact, species-specific differences exist in the optimal social grouping (Novak & Suomi 1991). For these reasons, guidance on the ideal grouping and social dynamics for laboratory-housed primates should be taken from natural populations (Buchanan-Smith 1997), matching their social environment as closely as possible with that to which they are adapted through evolution.

Single housing

Single caging of primates has traditionally been the housing method favoured by researchers, in an attempt to minimise experimental variation (Hartner *et al* 2001). Single caging also allows relatively easy and safe access to the animals, facilitates monitoring and reduces the risk of injury and disease transmission associated with social housing (Kessler *et al* 1985; Line 1987; Hartner *et al* 2001), thus further reducing experimental variation (Baskerville 1999; Hartner *et al* 2001). It is now widely recognised that single housing of primates is detrimental to psychological well-being in the majority of primate species, preventing social interaction and, because single cages are typically small and barren, reducing scope for enrichment and the expression of species-typical behaviours (Hartner *et al* 2001). The evidence of psychological distress as a result of social isolation is extensive and dates back to the early 1960s when the effects of social isolation on primates were the subject of considerable interest in relation to human development (eg Harlow & Harlow 1962). Harlow and Harlow (1971) described several abnormal behaviour patterns in socially deprived rhesus macaques of all ages, including self-sucking and biting, rocking, abnormally passive behaviour and stereotypical behaviours. Similarly, studies by Gluck and Sackett (1974) showed that the occurrence of self-aggression was more common in socially isolated individuals of both sexes. Single caging can result in loss of condition, nervous behaviour and an increased incidence of injury, disease and mortality in both New and Old World primate species (Reinhardt 1990; Poole *et al* 1999). Such effects are likely to increase experimental variation rather than reduce it (Garner 2005). For example, Gwinn (1996) found that singly housed squirrel monkeys lost more weight after the application of a test substance than those that were housed in pairs. Detrimental effects of poor psychological well-being on the immune system have also been indicated (Laudenslager *et al* 1982, 1990; Coe 1993; Clarke *et al* 1996; Gust *et al* 1996; Johnson *et al* 1996a). For example, individuals experiencing social stress have been found to be more susceptible to disease whereas those receiving affiliative behaviour showed more rapid immune system recovery (Gust *et al* 1996). Contrary to the belief that single housing reduces injury and disease transmission, Reinhardt (1990) found that, during one year, only 10% of socially housed rhesus monkeys required non-experimental veterinary treatment. In contrast, more than 25% of singly housed rhesus macaques required such veterinary treatment (Reinhardt 1990). Serious wounding occurred in only 0.8% of socially housed animals in 36 months. Further, Schapiro *et al* (2000) found that socially housed rhesus macaques showed enhanced immune responsiveness in comparison with singly housed individuals following challenge with gastrointestinal pathogens and *Staphylococcus aureus*. They therefore argued that immunological studies carried out on singly housed animals may be more difficult to interpret and that, in order to study the effects of ecologically relevant immune challenge, primates must be housed in an ecologically relevant environment, for example a stable

species-typical social structure and management system that minimises stress.

Old World monkeys continue to be housed in single cages more frequently than the smaller callitrichid species, mainly because of their size and the comparatively higher risk associated with handling them. However, the traditional view that primates, particularly macaques, are dangerous and aggressive is changing (Reinhardt 2002) and more of those involved in primate care accept that aggression directed towards handlers is most likely to occur when the animal feels threatened or insecure (Hartner *et al* 2001).

Breeding in single cages

Although single caging is most commonly used for animals on experiments, some establishments continue to house primates in single cages full-time. Baskerville (1999) described how timed breeding of Old World monkeys can be carried out in a single caging system by introducing the female to the male's cage for mating and removing her again when mating has taken place. This system allows the production of infants to suit demand and ensures that the pregnant female can be easily monitored. For competent mothers, the birth of an infant probably improves well-being as the infant provides social contact and a natural focus for her maternal behaviour. However, for these mothers, the return to single housing when the infant is taken away at weaning has considerable adverse effects (Seay *et al* 1962; Coe *et al* 1983). In contrast, for new and/or incompetent mothers, continuous exposure to the infant may represent a source of stress (Capitaniao *et al* 1985). Therefore, this system not only has significant detrimental effects on the adults involved but also results in abnormal physical, behavioural and psychological development in infants, as normal social interaction with numerous conspecifics of varying ages is prevented (Harlow & Harlow 1962). Satisfactory (or normal) socialisation, including experience of normal maternal care and play (Fagen 1993), has been shown to be critical for the maintenance of health and growth (Green 1990) and to prevent the development of abnormal and stereotypical behaviours (Harlow & Harlow 1971). Abnormal or inappropriate social behaviour, incompetent or absent sexual behaviour as an adult and reduced maternal aptitude occur in individuals which are not raised maternally (Harlow & Harlow 1962; Mitchell *et al* 1966; Suomi 1978; Capitaniao 1986; Ljungberg & Westlund 2000). Ruppenthal (1992) showed that the offspring of singly caged mothers are more likely to be subordinate when socially housed.

Timed breeding has not proven to be a successful production strategy in squirrel monkeys (Mendoza 1999) or in marmosets and tamarins (Poole *et al* 1999). Meanwhile in nocturnal lemurs, males and females naturally meet only to breed and thus timed matings may be the most appropriate means of breeding these animals in the laboratory (Bearder & Pitts 1999).

Social enrichment in single cages

It is noted that some experimental protocols may still require single housing and that it is not always possible to

house primates in alternative systems if a suitable partner(s) cannot be found (Line *et al* 1991; Watson 2002). In these circumstances, refinements to reduce the detrimental effects of isolation must be used. Numerous potential methods of inanimate enrichment are described above but in addition it is vital to provide some social enrichment in single housing systems and complete social isolation should never occur. The ability to observe other singly housed conspecifics can be beneficial and physical contacts (eg holding hands or grooming) between individuals in adjacent cages are commonly observed (Wolff & Ruppert 1991; Brinkman 1996; Crockett *et al* 1997). Anderson and Chamove (1986) found that the provision of a mirror to isolated infant stump-tailed macaques partially compensated for the lack of social interaction with conspecifics, although these individuals were still less responsive than individuals raised with a peer (Anderson & Chamove 1984). Interaction with humans can be seen as a form of social enrichment and animals which develop a bond with their regular carers may actively seek such interactions (Waitt & Buchanan-Smith 2002). This may explain why animals take part in positive reinforcement training sessions voluntarily, as it provides an opportunity for social interaction as well as an opportunity to learn and to gain rewards.

Isosexual pairing

As an alternative to single housing, primates in laboratories can be housed in isosexual pairs. Such pairing is considered to be a useful means of keeping stock animals (Baskerville 1999; Poole *et al* 1999). Although this grouping is unnatural for the species most commonly used in laboratories, evidence shows that such pairing can improve well-being. Isosexually pair-housed rhesus macaques spend more than 20% of their time grooming one another (Reinhardt & Cowley 1990; Reinhardt 1991), a behaviour used to maintain social cohesion and known to reduce heart rate and tension within groups of primates (Nieuwenhuisen & de Waal 1982; Schino *et al* 1988; Boccia *et al* 1989). Grooming has also been shown to result in the release of β -endorphin, indicating a physiological basis for reward in both groomer and groomee (Keverne *et al* 1989). The transition from single housing to pair-housing has also been reported to stop the occurrence of self-biting behaviour in rhesus macaques that had been observed self-biting over a period of 4 years (Reinhardt 1999) and to reduce other abnormal behaviours including abnormal postures, stereotypic actions, stereotypic locomotion and self-abuse (Line *et al* 1990). Further, Schapiro and Bushong (1994) showed that isosexually pair-housed rhesus macaques had diarrhoea less frequently than singly housed individuals. Hennessy (1984) found that isosexually pair-housed squirrel monkeys showed reduced responsiveness to stressful stimuli in the presence of a newly introduced pair-mate than they did when exposed to the stressor in isolation, even if they had experienced little social contact prior to pairing. Thus, during any stressful experience associated with laboratory use, including routine husbandry and procedures, the presence of a companion may increase the ability of individual primates to cope.

Factors influencing isosexual pair formation

Studies by Erwin (1986) indicated that bonds between female macaques and baboons can endure despite separation for up to 2.5 years. This work also demonstrated that relations between familiar males tended to be more amicable than those between unfamiliar males. Several factors influence the ease with which pairs may be formed, including the species concerned and the age, sex and previous experience of the individual.

In rhesus macaques, the social experience of individuals can significantly affect their compatibility during pairing or grouping, as socially inexperienced individuals show less appropriate social behaviour than those reared naturally (Mitchell *et al* 1966). Species differences in the ease with which primates will accept unfamiliar individuals must be considered. For example, in callitrichid species it has been suggested that marmosets are likely to be more difficult to mix than tamarins because young tamarins tend to migrate to new groups whilst marmosets remain in their natal group (Poole *et al* 1999). Aggression tends to occur more frequently and to be more serious between sexually mature primates (Goosen *et al* 1984; Lynch 1998; Majolo *et al* 2003b). In macaque species aggression tends to be more severe between sexually mature males (Crockett *et al* 1994; Watson 2002), although females are also aggressive to unfamiliar females. In marmosets and tamarins, females have a tendency to be more aggressive to female conspecifics than to males and males are less aggressively reactive overall than females (French & Inglett 1989; Rothe & Darms 1993). Owl monkeys of the same sex should not be housed together as aggression is common, resulting in severe injury (Erkert 1999). These differences are the result of species differences in social dynamics and behavioural ecology.

As an alternative to pairing adult primates, several studies have shown that mature animals can be successfully paired with sexually immature, but socially experienced, animals of the same sex (Reinhardt *et al* 1987; Majolo *et al* 2003b). As play behaviour is most often observed between infants or between an adult and an infant (Volland 1977; Fagen 1981), this cross age pairing may result in the added benefit of increasing play and socially directed activity in the older individual (Majolo *et al* 2003b). Alternatively, immature animals can be paired with conspecifics of the same age and sex. In marmosets, the simplest and least disturbing means of pairing is to take the oldest same sex pair of twins from a family group and to house them together (Poole *et al* 1999; Majolo *et al* 2003b). Sub-adult long-tailed, pig-tail and rhesus macaques of the same sex have also been introduced and paired without serious aggression (Reinhardt 1995; Cardinal & Kent 1998; Watson 2002). It has therefore been recommended that where isosexual pairing of primates is the only alternative for social enrichment, the pairing of socially experienced but sexually immature individuals with either a peer or with an adult should be preferred (Baskerville 1999; Poole *et al* 1999). However, although adults do show more aggression (Majolo *et al* 2003b), the supposition that all previously isolated adult primates of

limited social experience are impossible to pair is unfounded (Harlow & Harlow 1962), although compatibility varies with species, age and sex (Crockett *et al* 2001).

Studies have shown that, in a period of non-contact familiarisation in socially neutral surroundings (ie not within the home cage/room of either individual), respective dominance statuses can be established through behavioural displays whilst contact aggression is prevented. Gwinn (1996) also found that previously singly housed squirrel monkeys could be paired after gradual introduction, using a pole and collar to control aggressive interactions initially, and with careful observation to identify compatible pairs. Rhesus, stump-tailed, long-tailed and pig-tail macaques and female common marmosets have all been successfully paired in the laboratory environment (Line *et al* 1990; Reinhardt 1994c; Reinhardt *et al* 1995; Byrum & St Claire 1998; Cardinal & Kent 1998; Lynch 1998; Watson 2002; Majolo *et al* 2003b). Using these techniques, it has been concluded that compatible social partners, showing clear and stable dominant/subordinate relationships can be found for most individuals (Reinhardt 1994b; Marks *et al* 2000; Hartner *et al* 2001).

Despite the evidence that compatible pairs can be formed between primates of the same sex, care must be taken that the pairing is beneficial for both partners. Lack of aggression, depression or injury and the occurrence of food sharing can be used to monitor the continued compatibility of the paired rhesus macaques (Hartner *et al* 2001) and aggression arising between pairs can be reduced by the provision of enrichment (Majolo *et al* 2003a), although care must be taken that sufficient enrichments are provided so that they are not monopolised by the dominant individual. Although overt aggression may not be apparent, questions about compatibility must constantly be asked and the pair monitored on a regular basis. This is particularly true in same-sex marmoset pairs and male–male macaque pairings which deviate significantly from the natural tendency of these species (Crockett *et al* 1994; Majolo *et al* 2003b). Ideally compatible group mates should affiliate (eg groom, huddle) with each other.

Heterosexual pairing

Heterosexual pairing is most frequently used for common marmosets and other callitrichid species (Poole *et al* 1999), owl monkeys (Erkert 1999), and galagos, lorises and tarsiers (Bearder & Pitts 1999). It is not generally used for Old World species in the laboratory (Baskerville 1999). In common marmosets, heterosexual pairing represents a much more natural grouping than isosexual pairing and this is reflected in the comparative ease with which such pairs can be formed and maintained. Even without a pre-pairing familiarisation period, sexually mature male–female pairs of marmosets have been formed simply by the introduction of two animals to a home cage (Johnson *et al* 1996b). During the first weeks of pairing sexual and affiliative behaviours predominate in common marmosets, although the frequency of sexual behaviour declines over time (Woodcock 1982; Johnson *et al* 1996b). However, it should

be noted that previously heterosexually paired marmosets may take longer to pair up with new partners if a partner is lost through naturally occurring or experimentally induced illness or death, as a stable, monogamous pair-bond develops between long-term partners (Smith *et al* 1998; Gerber *et al* 2002). Introduction to potential new partners can be associated with aggression as well as sexual behaviour (Gerber *et al* 2002). It is likely that the formation of heterosexual pairs of marmosets would also benefit from some pre-pairing familiarisation, if not to ease pair-formation directly, then at least to ensure that individuals that show particularly high aggression towards one another are not placed together. Owl monkeys are also monogamous and heterosexual pairs can also be housed together successfully (Erkert 1999). Tamarins, including the saddle-back tamarin (*Saguinus fuscicollis*) and the cotton-top tamarin (*Saguinus oedipus*), breed best in monogamous pairs (Price & McGrew 1990) but can also be successfully housed in stable sexually active, compatible triads comprising one female and two males (Caine 1993). Galagos (*Galago spp*), lorises (*Loridae*) and tarsiers (*Tarsius spp*) are not naturally monogamous species. In the wild males and females live in their own (sometimes overlapping) territories. However, because these species show some social behaviour and may play and sleep together, it has been recommended that these primates also be kept in heterosexual pairs (Bearder & Pitts 1999). Further empirical studies examining the most appropriate and practical method of housing prosimian species in the laboratory would be of benefit.

Families and harem groups

Heterosexual pairs of callitrichids and their offspring can be kept together in a family group of 8–10 individuals, with juveniles from previous litters remaining in the group to help rear the most recent infants (Poole *et al* 1999). This system is close, although not identical, to the social dynamics of callitrichids in the wild (Stevenson & Rylands 1988) and is the most appropriate system for housing callitrichids used in laboratories (Price & McGrew 1990; Rothe & Darms 1993). Similar small, family groups have been recommended for housing owl monkeys (Erkert 1999) and for galagos, lorises and tarsiers (Bearder & Pitts 1999). Harem grouping, of one male with several females, is the most natural housing system for macaques in laboratories (Baskerville 1999). This system provides the most appropriate housing system for breeding and rearing infants, allowing a full range of appropriate social interactions to aid proper development of social, sexual and parental behaviour (Harlow & Harlow 1962; Mitchell *et al* 1966; Suomi 1978; Capitano 1986). If there are many females in the harem group, juvenile males can be introduced, ensuring that, when older males are removed from the group, disruption is minimised (Baskerville 1999). Harems can be contained within large pens with indoor and outdoor areas, large cages and within rooms. Very large corral enclosures containing harems tend to be used by source-country breeders (Baskerville 1999). In the laboratory, animals can be housed in such group-housing systems during some

experiments, particularly if a single caging or handling facility is attached. In this way individuals can be isolated for short procedures, before being returned to the group (Baskerville 1999).

Population control in harems and family groups

In breeding colonies, conception normally occurs sooner after the birth of offspring than in wild populations because of the ready availability of nutrients. In this situation, contraception may be used to increase the inter-birth interval, ensuring that females regain condition between births and that infants are born in accordance with demand. The condition prior to pregnancy is particularly important in callitrichid species where twins or triplets are the norm and lactation is therefore particularly energetically costly. The relative welfare benefits and risks associated with vasectomy, contraceptive implants, prostaglandin injections, intrauterine devices and immuno-contraception as methods of population control in primate species were reviewed by Sainsbury (1997) and Glatston (1998). The suitability of different methods of contraception will vary on a case-by-case basis, depending primarily upon the use of the animal at the time and upon the health and reproductive status of each individual. It is unclear which of the contraceptives mentioned might be considered to have the least impact on well-being as all appear to have significant disadvantages. Extension of inter-birth intervals is a refinement from the perspective of the individual but if more animals are then needed in breeding establishments in order to cope with demand, a conflict between refinement and reduction becomes apparent.

Weaning

In contrast, in commercial breeding groups, it is often considered necessary to reduce inter-birth intervals in order to maximise production (Goo & Fulgate 1984). One of the methods by which this is achieved is by the early weaning of infants. In the wild, weaning refers to the point when the infant stops suckling but usually refers to the time that the infant is removed from the mother in captive situations (Wolfensohn & Honess 2005). In the wild, weaning usually occurs at around 14 months in cynomolgus macaques but youngsters remain with their mothers until the next baby is born, which can be for up to 2 years (inter-birth intervals being between 12 and 24 months for both rhesus and cynomolgus macaques) (Smith & Boyd 2002). In Old World monkeys artificial weaning may be as low as 90 days (Welshman 1999) and guidelines vary considerably (Wolfensohn & Honess 2005). Social contact is particularly important for development, when the motor, sensory and emotional systems of youngsters begin to mature and become fully integrated and they become extremely involved in exploratory behaviours and social learning (Wallis & Valentine 2001). Such early weaning is stressful, resulting in overt behavioural and physiological manifestation of distress in rhesus and long-tailed macaques, including 6.6% weight loss, a transient rise in cortisol, depression-related behaviour lasting at least 7 days, increased locomotion (a behaviour associated with arousal

and agitation) and close contact with peers (Seay *et al* 1962; Koyama & Terao 1986). These changes were alleviated to some extent by the presence of a nurse female, although some effects were still apparent in these nursed juveniles (Koyama & Terao 1986). Therefore, the welfare costs of early weaning outweigh the potential benefit of increased production as a commercial practice and natural weaning should be promoted. Further, whereas in macaques early weaning has been reported to result in the earlier onset of fertility in females (Goo & Fulgate 1984), studies in baboons have shown that the earlier the infant was separated from the mother the longer the interval before postpartum oestrus and the later the next infant was born (Wallis & Valentine 2001). The shortest inter-birth interval was found when the infant remained in the natal group until maturity and weaning occurred naturally (Wallis & Valentine 2001). It is possible that this difference was associated with distress in the mother as a result of separation from her infant and shows that early weaning may not always improve production. Careful investigation is needed to ensure that early weaning is necessary to reduce inter-birth intervals in other primate species and is not the product of misapplication of theory from species to species.

Hand-rearing

Some mother–infant separation may be used routinely in the laboratory for welfare reasons. In common marmosets, the female may often produce more infants than she is able to feed and assistance or hand-rearing may become necessary. This may be done either by rearing one individual entirely artificially or by providing the mother with assistance by giving infants supplementary feeding on a rotational basis. Studies have shown that separation, even for the short time required to feed the infant, can result in significant stress and significant behavioural abnormalities and in long-term differences in the ability of the individuals to cope with later psychosocial stress (Dettling *et al* 2002a, b). This increases the variability in animals used and hence in the experimental results. Further investigation is needed to evaluate the relative welfare costs and benefits of this practice but currently the practice of selective euthanasia of the weakest individuals in triplet and quadruplet marmoset litters may prove to be a more humane, and more scientifically sound, option than rotational hand-rearing. This is already practised in some laboratories in the UK. It has been shown that in some circumstances adult marmosets will accept infants that are not their own (Watson & Petto 1988). Such fostering might provide an alternative to rotational hand-rearing and euthanasia of some infants from large litters or for orphaned individuals. Further data on the feasibility of fostering on a larger scale and of the comparative behavioural, physiological and psychosocial effects of fostering and rotational hand-rearing would be of use to fully evaluate the costs and benefits of each. It may also be possible to use positive reinforcement to train marmosets to station while their infants are given supplementary feeding while still on the carrier's back.

Gang housing

Weaning may also be required when family groupings of laboratory-housed primates become too big. Weaned juvenile primates could be housed in pairs but it is also common practice to house sexually immature primates in large, same-sex 'gangs' of unrelated individuals. In the case of common marmosets, these social groupings may also be made up of the oldest offspring removed from social groups that have become too large (Poole *et al* 1999). This grouping is also unnatural and aggression escalating to serious fighting is common, resulting in severe stress in the majority of individuals. Johnson *et al* (1996b) studied the effects of such social grouping on the adrenocorticotrophic hormone, cortisol and behaviour of common marmosets and found that cortisol was elevated with respect to that seen in stable paired marmosets. Social relationships are most critical during development, and deprived or defective social contact during development can have serious consequences for psychological well-being and the ability to cope with stress in later life (Johnson *et al* 1991, 1996a). In contrast, in squirrel monkeys large groups of same and mixed sex individuals that are all of a similar age occur naturally (Mendoza 1999). In these groups aggression occurs only rarely and is more common (although less severe) between females. Conception and infant viability have been reported to increase in this system of housing (Schiml *et al* 1996). However, it should be noted that naturally occurring groups have essentially unrestricted space in which aggression can be avoided. In the restricted space of the laboratory setting, agonistic encounters may occur more frequently and must still be monitored. It has been reported that agonistic encounters usually occur at times of excitement and Mendoza (1999) recommended that the individual that initiates arousal should be removed from the group when aggression occurs frequently, rather than removing the most aggressive individual, as group stability can usually be regained.

Westergaard *et al* (2000) reported that reproductive performance was better in multi-male multi-female groups than in harem-housed groups of rhesus macaques. However, there were many factors, other than group composition, that could have influenced infant survival in this study. These included the number of animals in each group, which was higher in the harem system, and the degree of enrichment, which was less in the harem grouping. The success of peer group housing is therefore dependent upon the needs of the species but enrichment and group size also have an influence on the potential success of this housing system.

Need for monitoring and management of social housing

The benefits of housing primates socially are clear and animals housed in appropriate social combinations can, if successfully managed, be free from injury, high rates of disease transmission, social distress and under-nourishment (Reinhardt 1990). Maintenance of social colonies is dependent upon careful observation for changes in social

compatibility. It should be noted that negative interactions are part of social relationships and aggression can result in both injury and mortality. Subordinate individuals can show signs of chronic social stress including depressive behaviours (Shively *et al* 1997). Care must be taken that such negative interactions do not get out of hand in the laboratory environment. Any destabilising influences, including birth of an infant, movement of the group and rehousing, removal or introduction of an individual, may result in an increase in aggression in the group (Erwin 1979; Hambright & Gust 2003). Dominant animals can monopolise food and preferred resources (Tardif & Richter 1981; Brennan & Anderson 1988; Deutsch & Lee 1991) and care must be taken to ensure that the introduction of an enrichment device does not therefore adversely affect welfare of subordinate individuals. Extra resources must be provided so that subordinate animals can go to another resource if they are moved on by a dominant animal. Sufficient social space must be provided so that subordinate animals can show appropriate subordinate behaviour towards dominant individuals, moving away to an appropriate distance when challenged (Reinhardt & Reinhardt 2000b). The importance of the ability to control social interactions was shown in studies by Bloomsmith *et al* (2001) who examined the effects of control of enrichment devices in chimpanzees. In this study chimpanzees which had control over the appearance of a video of conspecifics showed more solitary play than yoked conspecifics. At the same time, more scratching (considered a sign of anxiety in primates [Maestriperi *et al* 1992; Cilia & Piper 1997]) was observed in individuals which could not control the appearance of the video of conspecifics. The inclusion of visual barriers within the cage can allow subordinate individuals to retreat in response to movement or threatening gestures from the dominant partner, thus increasing the relative social space (Reinhardt & Reinhardt 2000b). Although the value of such cage enrichments is generally accepted, it cannot be assumed that such visual barriers will prevent outright aggression entirely, as any significantly destabilising event is likely to result in transient increases in aggression (Baskerville 1999). Further, McCormack and Megna (2001) found that the provision of barriers resulted in a reduction in non-contact aggression including threats, vocalisations and chases but no change in the frequency of contact aggression including biting and grabbing. Such barriers may also reduce the visibility of the primates to technicians, making routine welfare checks more arduous. It is imperative that all individuals in the group are frequently observed to ensure that none are subject to stress-inducing levels of aggression, particularly during transitions in social groupings. Caution should be exercised when animals are removed and then reintroduced to groups after procedures, especially if the animal is compromised in any way, as abnormal behaviour may result in aggression from other members of the group and the dominance hierarchy within the group may be disturbed (Hambright & Gust 2003). Reintroduction is possible even after long-term absences but staff must be on hand to observe and separate animals

which are agonistic if necessary (Kessler *et al* 1985). Individuals, particularly adult males, which experience frequent agonistic responses from the group have been shown to experience significant stress, in terms of both hypothalamo-pituitary-adrenal (HPA) activation and immune cell measures (Gust *et al* 1993). It should also be noted that, for scientific reasons, long periods (up to a year) of acclimatisation to new social systems should be allowed where possible, because the effects of changes in social environment can take time to become apparent (Schapiro *et al* 2000). Overcrowding in social groups has the potential to increase agonistic encounters but studies have shown that social dynamics are more important to the nature of social interactions in the group than group size (McIntyre & Petto 1993). Indeed, rhesus macaques have been shown to be able to adapt their behaviour to avoid conflict during short-term crowding (Judge & de Waal 1993). Despite potential problems, evidence shows that, if well managed with consideration of species, sex, age group and experience on an individual basis, appropriate social enrichment can be provided for all species of laboratory-housed primate studied (Reinhardt 1990). With appropriate husbandry and management, social enrichment can improve psychological well-being and reduce the stress associated with experiments, thus increasing their validity.

Outdoor housing

Access to outdoor enclosures is generally considered to be beneficial for laboratory-housed primates (but see Wolfensohn & Honess 2005), mainly because of the increased scope for enrichment in this environment. The space provided for each individual is increased because all of the animals in the enclosure must be able to access an environmentally controlled portion of the enclosure at all times. This area must fulfil the space requirements applicable to entirely indoor facilities. Within this larger enclosure, there is space to provide more structural enrichment allowing the primates to express more species-typical locomotive behaviours. There can also be more opportunity for feeding enrichments like scatter feeding. The environment itself is more enriched, with the primates being exposed to a much wider range of sensations including natural light (including radiation), different background noise, smells, insects, birds and weather. The controllability of all environmental parameters is dramatically reduced when laboratory-housed primates are allowed access to the outdoors, particularly in temperate climates. All primates should have access to shelter from both sun and inclement weather. This, and the ability to return inside to an environmentally controlled, draught-free enclosure, ensures that the animals benefit from a choice of environment. Contact with wild animals (including contact with faecal material) should be prevented to ensure that the health and well-being of laboratory-housed primates is not compromised by diseases transmitted from such contact. Access to outdoor enclosures may not be a feasible option for specific pathogen-free animals (Wolfensohn & Honess 2005).

The benefits of outdoor housing have been demonstrated in a range of species (eg chimpanzees, Clark *et al* 1982; rhesus macaques, O'Neill 1989; common marmosets, Pines *et al* 2002). For example, O'Neill (1989) showed that the occurrence of abnormal behaviour was greatly reduced in young rhesus macaques which had been reared without mothers and with 5 hours of contact with peers each week when housed outdoors. However, O'Neill also found that returning the juveniles to indoor enclosures resulted in an increase in self-mouthing and the expression of stereotypical behaviours, such that the expression of these behaviours occurred more frequently than had been recorded prior to outdoor housing. These results are in agreement with the proposal that loss of control (in this case access to the enriched environment) may be more stressful to laboratory-housed primates than never having had control in the first place (ie never receiving access to the outdoors). This conclusion supports the work of Bryant *et al* (1988) who found that home cage enrichment was more beneficial overall than the provision of rotational access to an enriched playroom. Further evaluation of the use of outdoor facilities in temperate climates, including the security implications, would be valuable.

Section summary and conclusions

Social enrichment is the most effective form of enrichment but must be managed in an appropriate manner for the species concerned, with reference to natural populations. Single housing is used mainly to facilitate research but is recognised to be detrimental to physical and psychological well-being, reducing the range of species-typical behaviour, resulting in inhibition of the immune system and a higher frequency of expression of abnormal behaviour. Single housing systems are used more commonly for Old World primates because of the perceived danger associated with handling them. Timed breeding in single cages is considered inappropriate for most primate species because social space is limited, both for the mother and her infant, the opportunity for social development is greatly reduced and the mother must be returned to isolation when the infant is artificially weaned. If unavoidable, singly housed primates must be socially enriched by housing them in close proximity, allowing visual, auditory, olfactory and physical contact. Isexual housing is also relatively unnatural but is preferable to single housing as the presence of a compatible conspecific has been shown to reduce stress and increase the ability to cope. Compatibility of individuals is dependent on species, age, sex and social experience. Non-contact familiarisation/socialisation can be used to assess compatibility and allow dominant/subordinate relationships to be established without aggression. Heterosexual pairing is more natural for callitrichid species and is recommended for owl monkeys and for some prosimian species. In these cases, if the pairs breed they can be kept with offspring in family groups. Harem housing is the most natural system for housing Old World monkeys. It is particularly appropriate during breeding and for the development of infants.

Contraception is important in group housing systems to ensure that the supply of infants matches demand and to allow females to maintain condition. Early weaning to increase interbreeding intervals should be avoided where possible to allow juveniles to develop socially, especially if they are to be used for breeding themselves. Separation for hand-rearing is stressful and can influence development and the ability of the animal to cope with challenges in later life. As an alternative to rotational rearing of marmoset triplets, supplementary feeding of all infants on the carrier's back, euthanasia of the smallest infant or fostering could be attempted.

Gang-housing is more stressful than pair or family group housing in marmosets but is a naturally occurring grouping in squirrel monkeys. Reproductive success in macaques can also be higher in this system than in harems. Outdoor housing provides greater environmental variability and may provide greater scope for enrichment but must be carefully managed, particularly in temperate climates. All socially housed primates should be observed frequently to ensure that social stability is maintained and that no individual receives excessive social stress.

Acquisition and transportation

The process of the acquisition of primates and their transportation to the research facility is another aspect of the life of a laboratory-housed primate that could be significantly refined (Wolfensohn & Honess 2005). Many factors have the potential to affect the welfare of the primates during acquisition and transportation. First, the individual is captured, in many cases isolated and confined and access to food or water may be restricted. During transportation the primate may be exposed to a range of environmental stressors including fluctuations and extremes in temperature and humidity, excessive noise and novel movements. Husbandry is carried out by unknown handlers, which may be particularly important if stopovers are required (Malaga *et al* 1991). Finally, on arrival at the destination, the individual will be exposed to a novel environment, unknown handlers and, in some cases, to unknown conspecifics. However, the magnitude of the effect of exposure to such stressors on the welfare of primates is not yet fully understood. The stress associated with transportation can result in inhibition of the immune system and, as a result, clinical signs of disease may develop in previously apparently healthy animals (LABA/LASA 1993) and thus pre-transportation health checks must be thorough and stress must be minimised. This is particularly important in wild-caught animals which are likely to be harbouring sub-clinical infections and for whom the novel process of capture, confinement, transportation and subsequent captivity is likely to be more stressful. Studies of transportation in calves have shown that health monitoring must be continued for several weeks as clinical signs of disease may develop some time after the transport event (Knowles 1995).

By law in Europe, wild-caught primates may only be used in science in exceptional circumstances (EU 1986). The transportation of animals for use in research must be carried

out within the provisions of the European Directive (91/628) on the Protection of Animals during Transport which is currently under revision, the European Convention (ETS 123) and according to the Resolution on the Acquisition and Transport of Laboratory Animals adopted by the Multilateral Consultation in May 1997 (Council of Europe 1997). These are general provisions applying to all animals and include the requirement that the travel should be carefully planned and carried out without avoidable delay, that all animals should be fit to travel, handled carefully and that they must be protected from inadequate ventilation, extremes of temperature, lack of feed and water and should be transported in suitable containers. If the animals are to be transported by air, the International Air Transport Association (IATA) Live Animal Regulations must be followed (International Air Transport Association [IATA] 2003). These regulations include husbandry standards for animals being transported and provide specifications for containers that should be used. Enforcement of these regulations in India resulted in a considerable reduction in transport-related deaths in macaques (Cullum 1966).

The common marmoset breeds well in captivity (Poole *et al* 1999) and is more commonly bred 'in-house' than other primate species (Rennie & Buchanan-Smith 2005), although breeding of other primate species is carried out across Europe. Provided that the housing and husbandry used are appropriate for the species concerned, 'in-house breeding' is an important refinement of laboratory practice, as the need for long distance transportation is eliminated (although animals are still likely to be relocated from time to time) and exposure to the majority of the stressors associated with transportation is avoided. Furthermore, by maintaining standardised husbandry routines across the research establishment (as far as possible) and using positive reinforcement to socialise and habituate the young primates to staff, other animals and procedures from an early age, the stress associated with relocation of in-house-bred primates could be greatly reduced (Prescott & Buchanan-Smith 2003).

In contrast, a much greater proportion of the Old World monkeys that are used in research are imported from source countries (Owen *et al* 1997; Rennie & Buchanan-Smith 2005). New World monkeys are also imported, to a greater or lesser extent, depending on the country concerned (Rennie & Buchanan-Smith 2005). All imported primates must be transported by air and road to the user establishment in journeys that can last several days (Malaga *et al* 1991). These animals are more likely to experience stress as a result of transportation than those relocated within establishments, as the degree of change and the duration of exposure to stressors are greater. However, by careful use of species-appropriate refinements, the degree of stress experienced can be reduced. Details of general measures that can be used to reduce the stress experienced by primates during transportation are provided in the LABA/LASA guidelines for the care of laboratory animals in transit (LABA/LASA

1993) and in the IATA Live Animals Regulations. More detailed species-specific recommendations are made in The UFAW Handbook on the Care and Management of Laboratory Animals (Baskerville 1999; Erkert 1999; Poole *et al* 1999) and by Wolfensohn and Honess (2005).

In the revision of European regulations relating to the transportation of animals, it has been recognised that animals are exposed to the most stress during confinement, and loading and unloading. These regulations refer mostly to primates being transported for agricultural and domestic purposes but data from laboratory-based studies indicate that loading and unloading are likely to be the most stressful components of the transportation process applied to primate species. It has been shown that capture, confinement in a transport cage and relocation to another room, even within the same establishment, can result in activation of the HPA axis, diarrhoea and injury (Line *et al* 1987; Luttrell *et al* 1994). Although the severity of these problems can be reduced with the use of positive reinforcement training (Klein & Murray 1995; Reinhardt 1992; Scott *et al* 2003), elevated cortisol has been recorded in trained macaques confined in a transport cage for as little as 5 minutes (Line *et al* 1987). Although it is generally considered that the degree to which individual primates are affected by transportation is dependent upon the distance travelled, duration of the journey, degree of social contact permitted, degree of protection afforded by the transport container (Swallow 1999) and competence of the staff involved, one quantitative study of 450 wild-caught owl monkeys suggested that the duration of the journey may not be as important as the age of the animals (Malaga *et al* 1991). On arrival, younger owl monkeys (juveniles and sub-adults) had lost more weight than adults regardless of the time spent in transit (3–4, 6–7 or 9–14 days). However, when the animals were weighed again after 30 days in their new laboratory environment the younger animals appeared to have adapted better, showing a gain in weight with respect to their pre-transit weight. In contrast, adults did not regain the weight they had lost during transit. Younger animals may be more reactive to novelty because they have less experience of the changes which may have contributed to the greater magnitude of weight loss in these animals during transportation. It was supposed that adult animals did not regain the weight lost during transportation as a result of social stress as they were unable to establish appropriate boundaries by scent-marking because of the close proximity of the other animals. Honess *et al* (2004) compared the behaviour of cynomolgus macaques in an overseas breeding facility and following transportation by air to a new location. The transport and relocation caused significant changes indicative of stress, with no return after 1 month to behavioural patterns observed at the breeding centre. These studies illustrate the need to determine the most appropriate age for transportation and the need to ensure that animals are fully acclimatised to their new environment before they are included in scientific studies.

It has been shown that the presence of a favoured conspecific can reduce stress associated with confinement, novelty

and procedures in both New and Old World primates (Crockett *et al* 1993; Smith *et al* 1998). Wolfensohn and Honess (2005) suggested that transporting affiliating pairs together allows for mutual support. They argued that keeping affiliating primates together should extend beyond the transport phase to the destination housing. This is a clear refinement of previous recommendations. Baskerville (1999) and the LABA/LASA guidelines for the care of laboratory animals in transit recommended that Old World primates should be transported in individual containers to minimise the risk of injury as a result of fear-related aggression. Both sets of guidelines recommended that unweaned infants should be carried with their mothers but that they should be checked on a regular basis to ensure that the infant is not being harmed (LABA/LASA 1993; Baskerville 1999). Under IATA regulation, pregnant females and those with suckling young are not accepted for transport. Conversely, it has been recommended that marmosets and owl monkeys be transported in compatible pairs or family groups (Erkert 1999; Poole *et al* 1999), thus eliminating stress associated with separation from favoured conspecifics and exposure to unknown conspecifics on arrival at their destination.

The value of positive interactions with care staff for the well-being of laboratory-housed primates has been discussed at length above. The benefit of positive human-animal interaction and the presence of a known handler during transportation of primates was stressed anecdotally in a report of the translocation of a group of 10 gorillas from the Netherlands to Australia, in which known handlers accompanied the gorillas throughout the journey (Kartzoff 1997). Although it is noted that such careful involvement of known handlers during each phase of transportation is rarely feasible in the commercial transportation of primates, the importance of the competence of any handler encountered during the transportation process is illustrated by Kartzoff's report. Handler training is also critical for the safety of the handlers themselves. In fear-inducing circumstances primates can become particularly dangerous (Reinhardt 2002) and there are many diseases carried by primates which are transmissible to humans (Weber *et al* 1997). Where possible, habituation or desensitisation to transport cages prior to the day of transit is also likely to be beneficial (Laule 1999) and transportation should be avoided where possible.

Section summary and conclusions

Transportation results in the exposure of primates to a wide range of stressors, from capture, isolation, environmental extremes and novelty. The effects of transportation are likely to be more severe in wild-caught animals. The effects of relocation of primates bred 'in-house' can be reduced by standardising husbandry and management and by socialising young animals to both humans and conspecifics. Social contact can reduce stress during transportation. The presence of known handlers and habituation to the transport container may also be of benefit.

Conclusions and animal welfare implications

Refinement techniques must be applied to all aspects of the life of non-human primates in the laboratory, from birth to death, to fulfil our ethical and scientific responsibility to minimise harm and maximise well-being. Thus, refinement of housing, husbandry and care is of great importance. Basic guidance on appropriate housing and husbandry practices is outlined in Appendix A to the European Convention (EC 1986), which is currently being revised. However, these guidelines do not take into account differences in species-specific needs. Many refinements could feasibly be introduced to improve on basic husbandry practices but all must be introduced with the specific needs of the species and, where possible, the individuals in mind. This simple principle applies to the housing environment and caging facilities, object, feeding and social enrichments as well as to breeding practices and the transportation process.

Although many of the refinements discussed in this review are not novel, the best available practices with respect to primates are less well known. In this review we have provided an overview of current thinking on refinement of practice applicable to the housing, husbandry and care of laboratory-housed primates. Used appropriately and in combination with refinement of the procedures in which primates are used and of the impact of humans, both during husbandry and in procedures, the refinements discussed in this review have the potential to both minimise harm imposed upon the primates used in laboratories and to maximise their well-being.

Acknowledgements

We thank Mark Prescott and David Morton for their valuable comments on a draft of this paper, Anna Roberts for all her help, and two anonymous referees whose comments substantially improved the manuscript. AER and HMB-S were supported by a grant from the European Commission (number QLRT-2001-00028).

References

- Anderson JR and Chamove AS** 1984 Allowing captive primates to forage. In: *Standards in Laboratory Animal Management* pp 253-256. Universities Federation for Animal Welfare: Wheathampstead, Herts, UK
- Anderson JR and Chamove AS** 1986 Infant stump-tailed macaques reared with mirrors or peers: social responsiveness, attachment and adjustment. *Primates* 27: 63-82
- Anderson JR, Peignot P and Adelbrecht C** 1992 Task-directed and recreational underwater swimming in captive rhesus monkeys (*Macaca mulatta*). *Laboratory Primate Newsletter* 31: 1-5
- Baskerville M** 1999 Old world monkeys. In: Poole T (ed) *The UFAW Handbook on the Care and Management of Laboratory Animals* pp 611-635. Blackwell Science: Oxford, UK
- Bassett L** 2003 *Effects of Predictability of Feeding Routines on the Behaviour and Welfare of Captive Primates*. PhD Thesis, University of Stirling, Stirling, UK
- Bassett L and Buchanan-Smith HM** in press Effects of predictability on the welfare of captive primates. In: Swaisgood RR (ed) *Animal Behaviour, Conservation and Enrichment*. *Applied Animal Behaviour Science*

- Bayne K** 2005 Potential for unintended consequences of environmental enrichment for laboratory animals and research results. *ILAR Journal* 46: 129-139
- Bayne KAL and McCully C** 1989 The effect of cage size on the behavior of individually housed rhesus monkeys. *Laboratory Animal* 18: 25-28
- Bearder SK and Pitts RS** 1999 Prosimians. In: Poole T (ed) *The UFAW Handbook on the Care and Management of Laboratory Animals* pp 542-558. Blackwell Science: Oxford, UK
- Bloomsmith MA and Lambeth SP** 1995 Effects of predictable versus unpredictable feeding schedules on chimpanzee behavior. *Applied Animal Behaviour Science* 44: 65-74
- Bloomsmith MA, Baker KC, Lambeth SP, Ross SK and Schapiro SJ** 2001 Is giving chimpanzees control over environmental enrichment a good idea? In: *The Apes: Challenges for the 21st Century* pp 88-89. Chicago Zoological Society: Chicago, USA
- Boccia ML, Reite M and Laudenslager M** 1989 On the physiology of grooming in a pigtail macaque. *Physiology and Behavior* 45: 667-670
- Bourgeois SR and Brent L** 2005 Modifying the behavior of singly caged baboons: Evaluating the effectiveness of four enrichment techniques. *Animal Welfare* 14: 71-81
- Box HO and Smith P** 1995 Age and gender differences in response to food enrichment in family groups of captive marmosets (*Callithrix-Callitrichidae*). *Animal Technology* 46: 11-18
- Brambell FWR** 1965 *Report of the Technical Committee to Enquire into the Welfare of Animals Kept Under Intensive Livestock Husbandry Systems*. HMSO: London, UK
- Brennan J and Anderson JR** 1988 Varying responses to feeding competition in a group of rhesus-monkeys (*Macaca mulatta*). *Primates* 29: 353-360
- Brinkman C** 1996 Toys for the boys: environmental enrichment for singly housed adult male macaques. *Laboratory Primate Newsletter* 35: 5-9
- Bryant CE, Rupniak NMJ and Iversen SD** 1988 Effects of different environmental enrichment devices on cage stereotypies and autoaggression in captive cynomolgus monkeys. *Journal of Medical Primatology* 17: 257-269
- Buchanan-Smith HM** 1997 Considerations for the housing and handling of New World primates in the laboratory. In: Reinhardt V (ed) *Comfortable Quarters for Laboratory Animals* pp 74-83. Animal Welfare Institute: Washington DC, USA
- Buchanan-Smith HM, Prescott MJ and Cross NJ** 2004 What factors should determine cage sizes for primates in the laboratory? *Animal Welfare* 13: S197-S201
- Buchanan-Smith HM, Rennie AE, Vitale A, Pollo S, Prescott MJ and Morton DB** 2005 Harmonising the definition of Refinement. *Animal Welfare* 14: 379-384
- Byrum R and St Claire M** 1998 Pairing female *Macaca nemestrina*. *Laboratory Primate Newsletter* 37: 1-2
- Caine NG** 1993 Flexibility and co-operation as unifying themes in *Saguinus* social organization and behavior: the role of predation pressures. In: Rylands AB (ed) *Marmosets and Tamarins: Systematics, Behaviour and Ecology* pp 200-219. Oxford University Press: Oxford, UK
- Caine NG and O'Boyle VJ** 1992 Cage design and forms of play in red-bellied tamarins, *Saguinus labiatus*. *Zoo Biology* 11: 215-220
- Capitanio JP** 1986 Behavioral pathology. In: Mitchell G and Erwin J (eds) *Comparative Primate Biology: Behavior, Conservation and Ecology* pp 411-454. Alan R Liss Inc: New York, USA
- Capitanio JP, Weissberg M and Reite M** 1985 Biology of maternal behavior: Recent findings. In: Reite M and Field T (eds) *The Psychobiology of Attachment and Separation* pp 51-85. Academic Press: London, UK
- Cardinal BR and Kent SJ** 1998 Behavioural effects of simple manipulable environmental enrichment on pair housed juvenile macaques (*Macaca nemestrina*). *Laboratory Primate Newsletter* 37: 1-4
- Chamove AS** 1984 Role of vision in social development in monkeys. *Child Development* 55: 1394-1411
- Chamove AS** 1989 Enrichment in chimpanzees: unpredictable ropes and tools. *Journal of the Association of British Wild Animal Keepers* 16: 139-141
- Chamove AS and Anderson JR** 1989 Examining environmental enrichment. In: Segal EF (ed) *Housing, Care and Psychological Well-Being of Captive and Laboratory Primates* pp 183-202. Noyes Publications: New Jersey, USA
- Chamove AS, Anderson JR, Morgan-Jones SC and Jones SP** 1982 Deep woodchip litter: hygiene, feeding, and behavioral enhancement in eight primate species. *International Journal for the Study of Animal Problems* 3: 308-318
- Cilia J and Piper DC** 1997 Marmoset conspecific confrontation: an ethologically-based model of anxiety. *Pharmacology Biochemistry and Behavior* 58: 85-91
- Clarke AS, Juno CJ and Maple TL** 1982 Behavioral effects of a change in the physical environment. A pilot study of captive chimpanzees. *Zoo Biology* 1: 371-380
- Clarke MR, Harrison RM and Didier ES** 1996 Behavioral, immunological, and hormonal responses associated with social change in rhesus monkeys (*Macaca mulatta*). *American Journal of Primatology* 39: 223-233
- Clough G** 1999 The animals house: design, equipment and environmental control. In: Poole T (ed) *The UFAW Handbook on the Care and Management of Laboratory Animals* pp 94-134. Blackwell Science: Oxford, UK
- Coe CL, Wiener SG and Levine S** 1983 Psychoendocrine responses of mother and infant to disturbance and separation. In: Rosenblum LA and Moltz H (eds) *Symbiosis in Parent-Offspring Interactions* pp 189-214. Plenum Press: London, UK
- Coe CL** 1993 Psychosocial factors and immunity in non-human primates: A review. *Psychosomatic Medicine* 55: 298-308
- Council of Europe** 1997 http://www.coe.int/t/e/legal_affairs_cooperation/biological_safety_use_of_animals/laboratory_animals/Res%20acquisition%20transport.asp. (accessed June 2006)
- Crockett CM** 1998 Psychological well-being of captive non-human primates. In: Sheperdson DH, Mellen JD and Hutchins M (eds) *Second Nature: Environmental Enrichment for Captive Animals* pp 129-152. Smithsonian Institution Press: Washington DC, USA
- Crockett CM, Bellanca RU, Bowers CL and Bowden DM** 1997 Grooming-contact bars provide social contact for individually caged laboratory macaques. *Contemporary Topics in Laboratory Animal Science* 36: 53-60
- Crockett CM, Bowers CL, Bowden DM and Sackett GP** 1994 Sex differences in compatibility of pair-housed adult long-tailed macaques. *American Journal of Primatology* 32: 73-94
- Crockett CM, Bowers CL, Sackett GP and Bowden DM** 1993 Urinary cortisol responses of longtailed macaques to five cage sizes, tethering, sedation, and room change. *American Journal of Primatology* 30: 55-74

- Crockett CM, Koberstein D and Heffernan KS** 2001 Compatibility of laboratory monkeys housed in grooming-contact cages varies by species and sex. *American Journal of Primatology* 54 (Suppl 1): 51-52
- Crockett CM, Shimoji M and Bowden DM** 2000 Behavior, appetite and urinary cortisol responses by adult female pigtailed macaques to cage size, cage level, room change and ketamine sedation. *American Journal of Primatology* 52: 63-80
- Cullum LE** 1966 Air transport of monkeys from India. *Journal of the American Veterinary Medical Association* 149: 909-911
- Dawkins MS** 1983 Battery hens name their price: consumer demand theory and the measurement of ethological 'needs'. *Animal Behaviour* 31: 1195-1205
- Dettling AC, Feldon J and Pryce CR** 2002a Early deprivation and behavioral and physiological responses to social separation/novelty in the marmoset. *Pharmacology Biochemistry and Behavior* 73: 259-269
- Dettling AC, Feldon J and Pryce CR** 2002b Repeated parental deprivation in the infant common marmoset (*Callithrix jacchus*) and analysis of its effects on early development. *Biological Psychiatry* 52: 1037-1046
- Deutsch JC and Lee PC** 1991 Dominance and feeding competition in captive rhesus monkeys. *International Journal of Primatology* 12: 615-628
- Dexter S and Bayne K** 1994 Results of providing swings to individually housed rhesus monkeys. *Laboratory Primate Newsletter* 33: 9-12
- Draper WA and Bernstein IS** 1963 Stereotyped behavior and cage size. *Perceptual and Motor Skills* 16: 231-234
- Eaton GG, Kelley ST, Axthelm MK, Iliff-Sizemore SA and Shigi SM** 1994 Psychological well-being in paired adult female rhesus (*Macaca mulatta*). *American Journal of Primatology* 33: 89-99
- Eckert K, Niemeyer C, Rogers RW, Seier J, Ingersoll B, Barklay L, Brinkman C, Oliver S, Buckmaster C, Knowles L, Pyle C and Reinhardt V** 2000 Wooden objects for enrichment: A discussion. *Laboratory Primate Newsletter* 39: 1-5
- Ely A, Freer A, Windle C and Ridley RM** 1998 Assessment of cage use by laboratory-bred common marmosets (*Callithrix jacchus*). *Laboratory Animals* 32: 427-433
- Erkert HG** 1999 Owl monkeys. In: Poole T (ed) *The UFAW Handbook on the Care and Management of Laboratory Animals* pp 574-590. Blackwell Science: Oxford, UK
- Erwin J** 1979 Aggression in Captive Macaques: Interaction of Social and Spatial Factors. In: Erwin J, Maple TL and Mitchell G (eds) *Captivity and Behavior: Primates in Breeding Colonies, Laboratories and Zoos* pp 139-171. Van Nostrand Co: New York, USA
- Erwin J** 1986 Environments for the captive propagation of primates: interaction of social and physical factors. In: Benirschke K (ed) *Primates: The Road to Self-Sustaining Populations* pp 397-305. Springer Verlag: New York, USA
- European Commission (EC)** 1986 European Convention for the protection of vertebrate animals used for experimental and other scientific purposes. ETS 123. Strasbourg, France
- European Union (EU)** 1986 Council Directive 86/609/EEC. Paris, France
- Fagen R** 1981 *Animal Play Behaviour*. Oxford University Press: Oxford, UK
- Fagen R** 1993 Primate juveniles and primate play. In: Pereira ME and Fairbanks LA (eds) *Juvenile Primates: Life History, Development and Behaviour* pp 182-196. Oxford University Press: Oxford, UK
- French JA and Inglett BJ** 1989 Female-female aggression and male indifference in response to unfamiliar intruders in lion tamarins. *Animal Behaviour* 37: 487-497
- Fritz J, Wolffe TL and Howell S** 1999 Chimpanzees. In: Poole T (ed) *The UFAW Handbook on the Care and Management of Laboratory Animals* pp 643-658. Blackwell Science: Oxford, UK
- Garner JP** 2005 Stereotypies and other abnormal repetitive behaviors: Potential impact on validity, reliability, and replicability of scientific outcomes. *ILAR Journal* 46: 106-117
- Gerber P, Schnell CR and Anzenberger G** 2002 Comparison of a beholder's response to confrontations involving its pairmate or two unfamiliar conspecifics in common marmosets (*Callithrix jacchus*). *Evolutionary Anthropology* 11: 117-121
- Glatston AR** 1998 The control of zoo populations with special reference to primates. *Animal Welfare* 7: 269-281
- Glick-Bauer M** 1997 Behavioral enrichment for captive cotton-top tamarins (*Saguinus oedipus*) through novel presentation of diet. *Laboratory Primate Newsletter* 36: 1-3
- Gluck JP and Sackett GP** 1974 Frustration and self-aggression in social isolate rhesus monkeys. *Journal of Abnormal Psychology* 83: 331-334
- Goo GP and Fulgate JK** 1984 Effects of weaning age on maternal reproduction and offspring health in rhesus monkeys (*Macaca mulatta*). *Laboratory Animal Science* 34: 66-69
- Goosen C, Vandergulden W, Rozemond H, Balner H, Bertens A, Boot R, Brinkert J, Dianske Jansen G, Lammers A and Timmermans P** 1984 Recommendations for the housing of macaque monkeys. *Laboratory Animals* 18: 99-102
- Green WH** 1990 A theoretical model for classical psychosocial dwarfism (psychologically determined short stature). In: Holmes CS (ed) *Psychoneuroendocrinology: Brain Behaviour and Hormonal Interactions* pp 92-112. Springer-Verlag Publishers: London, UK
- Gust DA, Gordon TP, Hambright MK and Wilson ME** 1993 Relationship social-factors and pituitary-adrenocortical activity in female rhesus monkeys (*Macaca mulatta*). *Hormones and Behavior* 27: 318-331
- Gust DA, Gordon TP, Wilson ME, Brodie AR, Ahmedansari A and McClure HM** 1996 Group formation of female pigtail macaques (*Macaca nemestrina*). *American Journal of Primatology* 39: 263-273
- Gwinn LA** 1996 A method for using a pole housing apparatus to establish compatible pairs among squirrel monkeys. *Contemporary Topics in Laboratory Animal Science* 35: 61 (Abstract)
- Hambright MK and Gust DA** 2003 A descriptive analysis of a spontaneous dominance overthrow in a breeding colony of rhesus macaques (*Macaca mulatta*). *Laboratory Primate Newsletter* 42: 8-11
- Hampton JK, Hampton SH and Landwehr BT** 1966 Observations on a successful breeding colony of the marmoset (*Oedipomidas oedipus*). *Folia Primatologica* 4: 265-287
- Hanson JD, Larson ME and Snowdon CT** 1976 The effects of control over high intensity noise on plasma cortisol levels in rhesus monkeys. *Behavioural Biology* 16: 333-340
- Harlow HF and Harlow MK** 1962 Social deprivation in monkeys. *Scientific American* 207: 136-146
- Harlow HF and Harlow MK** 1971 Psychopathology in monkeys. In: Kimmel HD (ed) *Experimental Psychopathology: Recent Research and Theory* pp 203-339. Academic Press: London, UK
- Hartner M, Hall J, Penderhest J and Clark L** 2001 Group-housing subadult cynomolgus macaques in a pharmaceutical environment. *Laboratory Animals* 30: 53-57

- Heger W, Merker HJ and Neubert D** 1986 Low light intensity decreases the fertility of *Callithrix jacchus*. *Primate Report* 14: 260 (Abstract)
- Hennessy MB** 1984 Presence of companion moderates arousal of monkeys with restricted social experience. *Physiology and Behaviour* 33: 693-698
- Home Office** 1989 *Code of Practice for the Housing and Care of Animals used in Scientific Procedures*. HMSO: Cambridge, UK
- Honess PE, Johnson PJ and Wolfensohn SE** 2004 A study of behavioural responses of non-human primates to air transport and re-housing. *Laboratory Animals* 38: 119-132
- Honess PE and Marin CM** 2006 Enrichment and aggression in primates. *Neuroscience and Biobehavioral Reviews* 30: 413-436
- Howell S, Schwandt M, Fritz J, Roeder E and Nelson C** 2003 A stereo music system as environmental enrichment for captive chimpanzees. *Laboratory Animal* 32: 31-36
- International Air Transport Association (IATA)** 2003 *Live Animal Regulations* IATA: Montreal, Canada
- Johnson EO, Kamilaris TC, Carter S, Gold PW and Chrousos GP** 1991 Environmental stress and reproductive success in the common marmoset (*Callithrix jacchus jacchus*). *American Journal of Primatology* 25: 191-201
- Johnson EO, Kamilaris TC, Calogero AE, Gold PW and Chrousos GP** 1996a Effects of early parenting on growth and development in a small primate. *Pediatric Research* 39: 999-1005
- Johnson EO, Kamilaris TC, Carter CS, Calogero AE, Gold PW and Chrousos GP** 1996b The biobehavioral consequences of psychogenic stress in a small, social primate (*Callithrix jacchus jacchus*). *Biological Psychiatry* 40: 317-337
- Judge PG and de Waal FBM** 1993 Conflict avoidance among rhesus monkeys — coping with short-term crowding. *Animal Behaviour* 46: 221-232
- Kartzoff L** 1997 The successful transportation of ten Western lowland gorillas (*Gorilla gorilla gorilla*) from Apenheul Primate Park, the Netherlands to Taronga Zoo, Australia. *Gorilla Gazette* 11: 26-35
- Kelley ST and Hall AS** 1995 Housing. In: Bennett BT, Abee CR and Henrickson R (eds) *Non-Human Primates in Biomedical Research* pp 193-209. Academic Press Inc: San Diego, USA
- Kessler MJ, London WT, Rawlins RG, Gonzalez J, Martinez HS and Sanchez J** 1985 Management of a harem breeding colony of rhesus monkeys to reduce trauma-related morbidity and mortality. *Journal of Medical Primatology* 14: 91-98
- Keverne EB, Martensz ND and Tuite B** 1989 Beta-endorphin concentrations in cerebrospinal-fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology* 14: 155-161
- Klein HJ and Murray KA** 1995 Restraint. In: Bennett BT (ed) *Non-Human Primates in Biomedical Research* pp 286-297. Academic Press: San Diego, USA
- Knowles TG** 1995 A review of post transport mortality among younger calves. *The Veterinary Record* 137: 406-407
- Kopecky J and Reinhardt V** 1991 Comparing the effectiveness of PVC swings versus PVC perches as environmental enrichment objects for caged female rhesus macaques (*Macaca mulatta*). *Laboratory Primate Newsletter* 30: 5-6
- Koyama T and Terao K** 1986 Psychological stress of maternal separation in cynomolgus monkeys: the effect of housing with a nurse female. In: Else JG and Lee PC (eds) *Primate Ecology and Conservation* pp 101-113. Cambridge University Press: Cambridge, UK
- LABA/LASA** 1993 Guidelines for the care of laboratory animals in transit. *Laboratory Animals* 27: 93-107
- Laudenslager ML, Held PE, Boccia ML, Reite ML and Cohen JJ** 1990 Behavioral and immunological consequences of brief mother-infant separation: a species comparison. *Developmental Psychobiology* 23: 247-264
- Laudenslager ML, Reite M and Harbeck RJ** 1982 Suppressed immune-response in infant monkeys associated with maternal separation. *Behavioral and Neural Biology* 36: 40-48
- Laule G** 1999 Training laboratory animals. In: Poole T (ed) *The UFAW Handbook on the Care and Management of Laboratory Animals* pp 21-27. Blackwell Science: Oxford, UK
- Line SW** 1987 Environmental enrichment for laboratory primates. *Journal of the American Veterinary Medical Association* 190: 854-859
- Line SW, Clarke AS and Markowitz H** 1987 Plasma cortisol of female rhesus monkeys in response to acute restraint. *Laboratory Primate Newsletter* 26: 1-4
- Line SW, Morgan KN, Markowitz H, Roberts JA and Riddell M** 1990 Behavioral responses of female long-tailed macaques (*Macaca fascicularis*) to pair formation. *Laboratory Primate Newsletter* 24: 1-9
- Line SW, Markowitz H, Morgan KN and Strong S** 1991 Effects of cage size and environmental enrichment on behavioural and physiological responses of rhesus macaques to the stress of daily events. In: Novak MA and Petto AJ (eds) *Through the Looking Glass: Issues of Psychological Well-being in Captive Non-human Primates* pp 160-179. American Psychological Association: Washington DC, USA
- Ljungberg T and Westlund K** 2000 Impaired reconciliation in rhesus macaques with a history of early weaning and disturbed socialization. *Primates* 41: 79-88
- Lopez J, Wormell D and Rodriguez A** 2001 Preliminary evaluation of the efficacy and safety of a UVB lamp used to prevent metabolic bone disease in pied tamarins (*Saguinus bicolor*) at Jersey Zoo. *Dodo* 37: 41-49
- Luttrell L, Acker L, Urben M and Reinhardt V** 1994 Training a large troop of rhesus macaques to cooperate during catching: analysis of the time investment. *Animal Welfare* 3: 135-140
- Lutz C, Well A and Novak M** 2003 Stereotypic and self-injurious behavior in rhesus macaques: A survey and retrospective analysis of environment and early experience. *American Journal of Primatology* 60: 1-15
- Lutz CK and Novak M** 2005 Environmental enrichment for non-human primates: Theory and application. *ILAR Journal* 46: 178-191
- Lynch RL** 1998 Successful pair-housing of male macaques (*Macaca fascicularis*). *Laboratory Primate Newsletter* 37: 4-6
- Maestripieri D, Schino G, Aureli F and Troisi A** 1992 A modest proposal — displacement activities as an indicator of emotions in primates. *Animal Behaviour* 44: 967-979
- Majolo B, Buchanan-Smith HM and Bell J** 2003a Response to novel objects and foraging tasks by common marmoset (*Callithrix jacchus*) female pairs. *Laboratory Animal Europe* 3: 25-33
- Majolo B, Buchanan-Smith HM and Morris K** 2003b Factors affecting the successful pairing of unfamiliar common marmoset (*Callithrix jacchus*) females: Preliminary results. *Animal Welfare* 12: 327-337

- Malaga CA, Weller RE, Montoya E, Moro J and Buschbom RL** 1991 Mortality and body weight changes in *Aotus nancymai* shipped from Iquitos, Peru to Richland, Washington. *Journal of Medical Primatology* 20: 6-11
- Markowitz H** 1982 *Behavioral Enrichment in the Zoo*. Van Nostrand Reinhold Company Inc: New York, USA
- Markowitz H and Aday C** 1998 Power for captive animals. In: Sheperdson DH, Mellen JD and Hutchins M (eds) *Second Nature: Environmental Enrichment for Captive Animals* pp 47-58. Smithsonian Institution Press: Washington DC, USA
- Markowitz H and Line S** 1990 The need for responsive environments. In: Rollin B and Kesel ML (eds) *The Experimental Animal in Biomedical Research* pp 153-170. CRC Press: Boca Raton, Florida, USA
- Markowitz H and Line S** 1989 Primate research models and environmental enrichment. In: Segal EF (ed) *Housing, Care and Psychological Well-being of Captive and Laboratory Primates* pp 203-212. Noyes Publications Inc: New Jersey, USA
- Marks D, Kelly J, Rice T, Ames S, Marr R, Westfall J, Lloyd J and Torres C** 2000 Utilizing restraint chair training to prepare primates for social housing. *Laboratory Primate Newsletter* 39: 9-10
- Marriner LM and Drickamer LC** 1994 Factors influencing stereotyped behavior of primates in a zoo. *Zoo Biology* 13: 267-275
- Mason G** 1991a Stereotypies: A critical review. *Animal Behaviour* 41: 1015-1037
- Mason GJ** 1991b Stereotypies and suffering. *Behavioural Processes* 25: 103-115
- McCormack K and Megna NL** 2001 The effects of privacy walls on aggression in a captive group of rhesus macaques (*Macaca mulatta*). *American Journal of Primatology* 54 (Suppl 1): 50-51 (Abstract)
- McDermott J and Hauser M** 2004 Are consonant intervals music to their ears? Spontaneous acoustic preferences in a non-human primate. *Cognition* 94: B11-B21
- McGrew WC, Brennan JA and Russell J** 1986 An artificial gum-tree for marmosets (*Callithrix j. jacchus*). *Zoo Biology* 5: 45-50
- McIntyre DT and Petto AJ** 1993 Effect of group size on behavior of group-housed female rhesus macaques. *Laboratory Primate Newsletter* 32: 1-5
- McKenzie SM, Chamove AS and Feistner ATC** 1986 Floor-coverings and hanging screens alter arboreal monkey behavior. *Zoo Biology* 5: 339-348
- Mendoza SP** 1999 Squirrel monkeys. In: Poole T (ed) *The UFAW Handbook on the Care and Management of Laboratory Animals* pp 591-600. Blackwell Science: Oxford, UK
- Menzel EW Jr** 1991 Chimpanzees (*Pan troglodytes*): problem seeking versus the bird in hand, least effort strategy. *Primates* 32: 497-508
- Michels AM** 1998 Sex differences in food acquisition and aggression in captive common marmosets (*Callithrix jacchus*). *Primates* 39: 549-556
- Mineka S, Gunnar M and Champoux M** 1986 Control and early socioemotional development: infant rhesus monkeys reared in controllable versus uncontrollable environments. *Child Development* 57: 1241-1256
- Mistlberger RE** 1994 Circadian food-anticipatory activity — formal models and physiological-mechanisms. *Neuroscience and Biobehavioral Reviews* 18: 171-195
- Mitchell GD, Raymond EJ, Ruppenthal GC and Harlow HF** 1966 Long-term effects of total isolation in behaviour of rhesus monkeys. *Psychological Reports* 18: 567-580
- Murchison M** 1995 Forage feeder box for single animal cages. *Laboratory Primate Newsletter* 34: 1-3
- Murchison MA and Nolte RE** 1992 Food puzzle for singly caged primates. *American Journal of Primatology* 27: 285-292
- Nelson RJ and Mandrell TD** 2005 Enrichment and nonhuman primates: "First, do no harm." *ILAR Journal* 46: 171-177
- Newberry RC** 1995 Environmental enrichment — increasing the biological relevance of captive environments. *Applied Animal Behaviour Science* 44: 229-243
- Nieuwenhuijsen K and de Waal FBM** 1982 Effects of spatial crowding on social behavior in a chimpanzee colony. *Zoo Biology* 1: 5-28
- Novak MA** 2003 Self-injurious behaviour in rhesus monkeys: new insights into its etiology, physiology and treatment. *American Journal of Primatology* 59: 3-19
- Novak MA and Drewsen KH** 1989 Enriching the lives of captive primates: issues and problems. In: Segal EF (ed) *Housing, Care and Psychological Well-being of Captive and Laboratory Primates* pp 161-182. Noyes Publication Inc: New Jersey, USA
- Novak MA and Suomi SJ** 1991 Social-interaction in nonhuman-primates — an underlying theme for primate research. *Laboratory Animal Science* 41: 308-314
- Ogden JJ, Lindburg DG and Maple TL** 1994 A preliminary study of the effects of ecologically relevant sounds on the behavior of captive lowland gorillas. *Applied Animal Behaviour Science* 39: 163-176
- O'Neill P** 1989 A room with a view for captive primates: issues, goals, related research and strategies. In: Segal EF (ed) *Housing, Care and Psychological Well-Being of Captive and Laboratory Primates* pp 135-160. Noyes Publications Inc: New Jersey, USA
- Overmier JB, Patterson J and Wielkiewicz RM** 1980 Environmental contingencies as sources of stress in animals. In: Levine S and Ursin H (eds) *Coping and Health* pp 1-38. Plenum Press: New York, USA
- Owen S, Thomas C, West P, Wolfensohn S and Wood M** 1997 Report on primate supply for biomedical scientific work in the UK. *Laboratory Animals* 31: 289-297
- Parks KA and Novak MA** 1993 Observations of increased activity and tool use in captive rhesus monkeys exposed to troughs of water. *American Journal of Primatology* 29: 13-25
- Poole T, Hubrecht R and Kirkwood JK** 1999 Marmosets and tamarins. In: Poole T (ed) *The UFAW Handbook on the Care and Management of Laboratory Animals* pp 559-574. Blackwell Science: Oxford, UK
- Pines MK, Kaplan G and Rogers LJ** 2002 Comparison of behavior changes and cortisol levels of common marmosets (*Callithrix jacchus jacchus*) to indoor and outdoor cages. *Caring for Primates Abstracts of the XIXth Congress*. The International Primatological Society, Beijing: Mammalogical Society of China: 267
- Poole TB, Costa P, Netto WJ, Schwarz K, Wechsler B and Whittaker D** 1994 Non-human primates. In: O'Donoghue PN (ed) *The Accommodation of Laboratory Animals in Accordance with Animal Welfare Requirements*. Bundesministerium für Ernährung, Landwirtschaft und Forsten: Bonn, Germany
- Prescott MJ and Buchanan-Smith HM** 2003 Training nonhuman primates using positive reinforcement techniques: Guest editors' introduction. *Journal of Applied Animal Welfare Science* 6: 157-161
- Price EC and McGrew WC** 1990 Cotton-top tamarins (*Saguinus o. oedipus*) in a semi-naturalistic captive colony. *American Journal of Primatology* 20: 1-12

- Pyle DA, Bennett AL, Zarcone TJ, Turkkan JS, Adams RJ and Heinz RD** 1996 Use of two food foraging devices by singly housed baboons. *Laboratory Primate Newsletter* 35: 10-15
- Reinhardt V** 1990 Social enrichment for laboratory primates: a critical review. *Laboratory Primate Newsletter* 29: 7-12
- Reinhardt V** 1991 Serum cortisol concentrations of single-housed and isosexually pair-housed adult rhesus macaques. *Journal of Experimental Animal Science* 34: 73-76
- Reinhardt V** 1992 Improved handling of experimental rhesus monkeys. In: Davis H and Balfour AD (eds) *The Inevitable Bond: Examining Scientist-Animal Interactions* pp 171-177. Cambridge University Press: Cambridge, UK
- Reinhardt V** 1994a Caged rhesus macaques voluntarily work for ordinary food. *Primates* 35: 95-98
- Reinhardt V** 1994b Effective environmental enrichment for caged rhesus macaques. *In Touch* 1: 1-5
- Reinhardt V** 1994c Pair-housing rather than single-housing for laboratory rhesus macaques. *Journal of Medical Primatology* 23: 426-431
- Reinhardt V** 1995 Arguments for single-caging or rhesus macaques: are they justified? *Animal Welfare Information Centre Newsletter* 6: 7-8
- Reinhardt V** 1997b Species-adequate housing and handling conditions for Old World primates kept in research institutions. In: Reinhardt V (ed) *Comfortable Quarters for Laboratory Animals* pp 84-93. Animal Welfare Institute: Washington DC, USA
- Reinhardt V** 1997a Lighting conditions for laboratory monkeys: are they adequate? *Animal Welfare Information Centre Newsletter* 8: 3-6
- Reinhardt V** 1999 Pair-housing overcomes self-biting behavior in macaques. *Laboratory Primate Newsletter* 38: 4
- Reinhardt V** 2002 The myth of the aggressive monkey. *Journal of Applied Animal Welfare Science* 5: 321-330
- Reinhardt V and Cowley D** 1990 Training stump-tailed monkeys (*Macaca arctoides*) to cooperate during in-homecage treatment. *Laboratory Primate Newsletter* 29: 9-10
- Reinhardt V, Cowley D, Scheffler J, Verstein R and Wegner F** 1990 Cortisol response of female rhesus-monkeys to venipuncture in homecage versus venipuncture in restraint apparatus. *Journal of Medical Primatology* 19: 601-606
- Reinhardt V, Liss C and Stevens C** 1995 Restraint methods of laboratory non-human primates: a critical review. *Animal Welfare* 4: 221-238
- Reinhardt V and Reinhardt A** 2000a The lower row monkey cage: an overlooked variable in biomedical research. *Journal of Applied Animal Welfare Science* 3: 141-149
- Reinhardt V and Reinhardt A** 2000b Meeting the 'social space' requirements of pair-housed primates. *Laboratory Primate Newsletter* 39: 7
- Reinhardt V, Reinhardt A, Eisele S, Houser D and Wolf J** 1987 Control of excessive aggressive disturbance in a heterogeneous troop of rhesus monkeys. *Applied Animal Behaviour Science* 18: 371-377
- Rennie AE and Buchanan-Smith HM** 2005 Report on the extent and character of primate use in scientific procedures across Europe in 2001. *Laboratory Primate Newsletter* 44: 6-12
- Rennie AE and Buchanan-Smith HM** 2006 Refinement of the use of non-human primates in scientific research. Part I: the influence of humans. *Animal Welfare* 15: 203-213
- Roder EL and Timmermans PJA** 2002 Housing and care of monkeys and apes in laboratories: adaptations allowing essential species-specific behaviour. *Laboratory Animals* 36: 221-242
- Rothe H and Darms K** 1993 The social organization of marmosets: a critical evaluation of recent concepts. In: Rylands AB (ed) *Marmosets and Tamarins: Systematics, Behaviour and Ecology* pp 176-199. Oxford University Press: Oxford, UK
- Ruppenthal GC** 1992 Effects of rearing conditions on behavioural development: indices of stress? XIVth Congress of the International Primatological Society pp 236 (Abstract) IPS, Strasbourg, France
- Russell WMS and Burch RL** 1992 *The Principles of Humane Experimental Technique*. Universities Federation for Animal Welfare: Wheathampstead, Herts, UK
- Sainsbury AW** 1997 The humane control of captive marmoset and tamarin populations. *Animal Welfare* 6: 231-242
- Sales GD, Milligan SR and Khirnykh K** 1999 Sources of sound in the laboratory animal environment: a survey of the sounds produced by procedures and equipment. *Animal Welfare* 8: 97-115
- Sambrook TD and Buchanan-Smith HM** 1996 What makes novel objects enriching? A comparison of the qualities of control and complexity. *Laboratory Primate Newsletter* 35: 1-4
- Sambrook TD and Buchanan-Smith HM** 1997 Control and complexity in novel object enrichment. *Animal Welfare* 6: 207-216
- Schapiro SJ and Bushong D** 1994 Effects of enrichment on veterinary treatment of laboratory rhesus macaques (*Macaca mulatta*). *Animal Welfare* 3: 25-36
- Schapiro SJ, Bloomsmith MA, Porter LM and Suarez SA** 1996 Enrichment effects on rhesus monkeys successively housed singly, in pairs, and in groups. *Applied Animal Behaviour Science* 48: 159-171
- Schapiro SJ, Stavisky R and Hook M** 2000 The lower-rank cage may be dark, but behavior does not seem to be affected. *Laboratory Primate Newsletter* 39: 4-6
- Schimi PA, Mendoza SP, Saltzman W, Lyons DM and Mason WA** 1996 Seasonality in squirrel monkeys (*Saimiri sciureus*): social facilitation by females. *Physiology and Behavior* 60: 1105-1113
- Schino G, Scucchi S, Maestriperi D and Turillazzi PG** 1988 Allogrooming as a tension-reduction mechanism: a behavioural approach. *American Journal of Primatology* 16: 43-50
- Scott L** 1991 Environmental enrichment for single housed common marmosets. In: Box HO (ed) *Primate Responses to Environmental Change* pp 265-274. Chapman and Hall: London, UK
- Scott L, Pearce P, Fairhall S, Muggleton N and Smith J** 2003 Training nonhuman primates to co-operate with scientific procedures in applied biomedical research. *Journal of Applied Animal Welfare Science* 6: 199-208
- Seay B, Hansen E and Harlow HF** 1962 Mother-infant separation in monkeys. *Journal of Child Psychology and Psychiatry* 3: 123-132
- Shepherdson DJ** 1998 Tracing the path of environmental enrichment. In: Shepherdson DH, Mellen JD and Hutchins M (eds) *Second Nature: Environmental Enrichment for Captive Animals* pp 1-12. Smithsonian Institution Press: Washington DC, USA
- Shively CA, Laberlaid K and Anton RF** 1997 Behavior and physiology of social stress and depression in female cynomolgus monkeys. *Biological Psychiatry* 41: 871-882
- Smith JA and Boyd KM** 2002 (eds) *The Use of Non-Human Primates in Research and Testing*. The British Psychological Society: Leicester, UK
- Smith TE, McGreer-Whitworth B and French JA** 1998 Close proximity of the heterosexual partner reduces the physiological and behavioral consequences of novel-cage housing in black tufted-ear marmosets (*Callithrix kuhli*). *Hormones and Behavior* 34: 211-222

- Snowdon CT** 1991 Naturalistic environments and psychological well-being. In: Novak MA and Petto AJ (eds) *Through the Looking Glass: Issues of Psychological Well-Being in Captive Non-Human Primates* pp 103-115. Washington DC: American Psychological Association, USA
- Snowdon CT and Savage A** 1989 Psychological well-being of captive primates: general considerations and examples for callitrichids. In: Segal EF (ed) *Housing, Care and Psychological Well-being of Captive and Laboratory Primates* pp 75-89. Noyes Publications Inc: New Jersey, USA
- Spector MR, Kowalczyk MA, Fortman JD and Bennett BT** 1994 Design and implementation of a primate foraging tray. *Contemporary Topics in Laboratory Animal Science* 33: 54-55
- Stevenson MF and Rylands AB** 1988 The marmosets, genus *Callithrix*. In: Mittermeier RA, Rylands AB, Coimbra-Filho AF and Fonseca GAB (eds) *Ecology and Behavior of Neotropical Primates Vol II* pp 131-222. World Wildlife Fund: Washington DC, USA
- Suomi SJ** 1978 Maternal behavior by socially incompetent monkeys: Neglect and abuse of offspring. *Journal of Pediatric Psychology* 3: 28-34
- Swallow JJ** 1999 Transporting animals. In: Poole T (ed) *The UFAW Handbook on the Care and Management of Laboratory Animals* pp 171-187. Blackwell Science: Oxford, UK
- Tardif SD and Richter CB** 1981 Competition for a desired food in family groups of the common marmoset (*Callithrix jacchus*) and the cotton-top tamarin (*Saguinus oedipus*). *Laboratory Animal Science* 31: 52-55
- Tustin GW, Williams LE and Brady AG** 1996 Rotational use of a recreational cage for the environmental enrichment of Japanese macaques (*Macaca fuscata*). *Laboratory Primate Newsletter* 35: 5-7
- Veasey JS, Waran NK and Young RJ** 1996 On comparing the behaviour of zoo housed animals with wild conspecifics as a welfare indicator. *Animal Welfare* 5: 13-24
- Vick SJ, Anderson JR and Young R** 2000 Maracas for macaca? Evaluation of three potential enrichment objects in two species of zoo-housed macaques. *Zoo Biology* 19: 181-191
- Voland E** 1977 Social play behavior of the common marmoset (*Callithrix jacchus*) in captivity. *Primates* 18: 883-901
- Waitt C and Buchanan-Smith HM** 2002 The effects of caretaker-primate relationships on primates in the laboratory. *Journal of Applied Animal Welfare Science* 5: 309-319
- Wallis J** 2002 Reproduction in baboons: The influence of environmental enhancement. *American Journal of Primatology* 57: 85 (Abstract).
- Wallis J and Valentine B** 2001 Early vs natural weaning in captive baboons: the effect on timing of postpartum estrus and next conception. *Laboratory Primate Newsletter* 40: 10-13
- Watson LM** 2002 A successful program for same- and cross-age pair-housing adult and subadult male *Macaca fascicularis*. *Laboratory Primate Newsletter* 41: 6-9
- Watson L, Cosby R and Lee-Parritz D** 1993 Behavioral effects of enrichment devices on laboratory primates with stereotypic and self-directed behavior. *American Journal of Primatology* 30: 355-356
- Watson LM and Petto AJ** 1988 Infant adoption and reintroduction in common marmosets (*Callithrix jacchus*). *Laboratory Primate Newsletter* 27: 1-4
- Weber H, Berge E, Finch J, Heidt P, Hunsmann G, Perretta G and Verschuere B** 1997 Sanitary aspects of handling non-human primates during transport. *Laboratory Animals* 31: 298-302
- Welshman M** 1999 Breeding macaques in source countries. In: Poole T (ed) *The UFAW Handbook on the Care and Management of Laboratory Animals* pp 636-642. Blackwell Science: Oxford, UK
- Westergaard GC, Izard MK and Drake JH** 2000 Reproductive performance of rhesus macaques (*Macaca mulatta*) in two outdoor housing conditions. *American Journal of Primatology* 50: 87-93
- Wolfensohn S and Honess P** 2005 *Handbook of Primate Husbandry and Welfare*. Blackwell Science: Oxford, UK
- Wolff A and Ruppert G** 1991 A practical assessment of a non-human primate exercise program. *Laboratory Animals* 20: 36-39
- Woodcock AJ** 1982 The first weeks of cohabitation of newly-formed heterosexual pairs of common marmosets (*Callithrix jacchus*). *Folia Primatologica* 37: 228-254
- Wright BW** 1995 A novel item enrichment program reduces lethargy in orangutans. *Folia Primatologica* 65: 214-218