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What factors should determine cage sizes for primates in the laboratory?

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Abstract

It is imperative to provide adequate quantity and quality of space for all captive animals. Yet practically all guidelines on the housing of primates in the laboratory specify minimum cage sizes based solely on body weight. We argue that no single factor, such as body weight, is sufficient to determine cage size. Instead a suite of characteristics should be used that include morphometric, physiological, ecological, locomotor, social, reproductive and behavioural characteristics. Ideally, the primate's age, sex and individual history should also be taken into account. In this paper we compare this suite of characteristics for some commonly used primates whose weights overlap, to illustrate important differences amongst them. For good animal welfare and good quality science it is necessary to be sensitive to such species differences when determining suitable cage sizes.

Keywords: *animal welfare, arboreality, breeding success, colony management, primate, species-specific needs*

Introduction

A wide range of primate species is used in research and testing, including representatives from the prosimians, New and Old World monkeys, and apes. There are considerable variations in the physiology, behaviour, ecology and locomotion of these species: a result of their adaptation to different environments. Despite these variations, practically all guidelines on the housing of primates in the laboratory specify minimum cage sizes based on a single factor — body weight. What is more, there is considerable variation between the different guidelines in the amount of space specified for a given body weight. For example, the UK Home Office (Home Office 1989, 1995) specifies greater space allowances than the Council of Europe (1986), whose allowances are in turn greater than those of the Institute of Laboratory Animal Resources (ILAR 1996). Guidelines from the International Primatological Society (IPS 1993), the Primate Vaccine Evaluation Network (Poole & Thomas 1995) and the Australian National Health and Medical Research Council (NHMRC 1997) do not set minimum cage sizes. The IPS guidelines list those set by other bodies but criticise them for failing to allow for the different space requirements of different species.

Whilst it is important to set minimum standards, conforming to these legal guidelines is no guarantee for meeting the needs of species in terms of space. This is particularly true for primates in minimum-sized cages, since legal minima are the results of compromises between, on the one hand, animal welfare and, on the other hand, economic and practical issues such as the desire to sanitise cages in automatic cage washers. Yet the provision of an adequate quantity and quality of space for all captive animals is a requisite for psychological well-being. Cage size not only influences behaviour, but also determines whether there is sufficient room for the provision of suitable environmental enrichment. Appropriate cage size also permits captive animals to be housed in socially harmonious groups and to fulfil their reproductive potential.

It is not our intention in this paper to specify what minimum cages sizes should actually be for the different primate species used in laboratories. Instead we intend to illustrate that no single factor, such as body weight, is sufficient to determine minimum cage size. In this paper we present published data to demonstrate that various primate species, whose weights overlap, differ in a number of important ways and can therefore show quite different responses to the laboratory environment. For good animal welfare and good quality science it is necessary to be sensitive to such species differences.

Species comparisons

Since the majority of primates used in research and testing are marmosets and macaques, we focus on these two groups. Specifically, we explore relevant differences between the common marmoset (*Callithrix jacchus*), the red-bellied tamarin (*Saguinus labiatus*) and the cotton-top tamarin (*S. oedipus*), all of which fall into the <1 kg weight category, and between five macaque species (rhesus macaque — *Macaca mulatta*, long-tailed or cynomolgus macaque — *M. fascicularis*, bonnet macaque — *M. radiata*, pig-tailed macaque — *M. nemestrina* and stump-tailed macaque — *M. arctoides*) and the vervet monkey

Table 1 A selection of primates used in the laboratory with overlapping adult body weights. M = male, F = female.

Weight category (kg)				
<1	1–3	3–6	6–9	9–15
M,F Common marmoset	F Vervet monkey	M,F Vervet monkey	M Vervet monkey	
M,F Cotton-top tamarin	F Long-tailed macaque	M,F Long-tailed macaque	M Long-tailed macaque	
M,F Red-bellied tamarin		M,F Bonnet macaque	M Bonnet macaque	
		M,F Rhesus macaque	M,F Rhesus macaque	M,F Rhesus macaque
		F Pig-tailed macaque	M,F Pig-tailed macaque	M,F Pig-tailed macaque
			F Stump-tailed macaque	M,F Stump-tailed macaque

(*Chlorocebus aethiops*), whose weights also overlap (see Table 1). It is necessary to state at the outset that comparisons between species are difficult since there are few experimental studies that systematically compare their behaviour, reproduction and physiology in same- and different-sized cages. Furthermore, of the few studies of this type, some have compared primates in cages so small that the results are meaningless.

Body weight and size

In determining absolute minimum cage size (eg for short-term holding of experimental animals), one important consideration should be that the animal is able to sit or stretch out without any of its body parts touching the enclosure sides. In hens and rabbits, restricted space has been shown to affect bone structure (Knowles & Broom 1990; Drescher & Loeffler 1991). Although we know of no quantitative data to support this point in primates, the National Research Council (1996) state that for arboreal primate species, the cage height should allow the animal to rest on a perch without its tail touching the ground.

Whilst body weight is clearly *one* factor that will give an indication of the space required to meet these considerations, it does not necessarily bear any direct relation to head, body or tail length. Using data presented in Table 2, on the body weights, head and body lengths and tail lengths of six primate species, there is no significant correlation between the mean body weight (mean of mid-point of range from male and female) and mean head and body length (mid-point of range) of the macaque and vervet group (Pearson's $r = 0.73$, $P > 0.05$, n = 6). Indeed there is a highly significant negative correlation between the mean body weight and the combined head, body and tail length (sum of mid-points of their ranges) of this group (Pearson's $r = -0.96$, $P = 0.002$, n = 6). On the basis of this analysis, body weight alone is an inappropriate factor for specifying minimum cage size; body dimensions should also be taken into account. This is particularly important in considering the housing of long-tailed macaques and vervet monkeys who possess a noticeably longer tail than the other macaque species examined here.

Physiological and behavioural responses to cage size and novelty

For both marmosets and tamarins, increasing cage size and/or complexity in the laboratory has been shown to increase exploratory and play activities and reduce stereotyped and stress-related behaviour (see Prescott & Buchanan-Smith 2004). Data on this issue are inconsistent for macaques. Crockett and colleagues (1995, 2000) and Bayne and McCully (1989) did not find significant differences in the prevalence of abnormal behaviour for rhesus macaques, long-tailed macaques or pig-tailed macaques housed in larger cages compared with smaller ones. However, the cages used in the studies of Crockett and co-workers ranged from 20% to 148% of the United States Department of Agriculture (USDA) regulation floor area; even the largest cage used was smaller than the UK legal minimum cage size for macaques of 4–6 kg (Home Office 1989), and therefore was unlikely to allow for suitable expression of species-typical behaviours. Furthermore, the cages contained no enrichment such as perches or manipulanda. One can hardly expect an animal's behaviour or physiology to change significantly when given a few extra cubic centimetres of dead space. Where a significant increase in useable space has been provided for macaques, a reduction in abnormal behaviour and an increase in the amount or complexity of normal behaviours have been seen (eg Paulk *et al* 1977; Bayne *et al* 1992).

The studies of Crockett and co-workers are important, however, as they demonstrate species differences amongst the macaques. Rhesus, long-tailed, bonnet and pig-tailed macaques show distinct and consistent differences in behavioural and adrenocortical responses to stress induced by brief confinement in a transport cage, and by a cage and room change (Clarke *et al* 1988; Crockett *et al* 1995, 2000). Long-tailed macaques showed the greatest increase in corticosteroid levels in response to novelty and physical restraint, whereas rhesus macaques showed the smallest increase, and bonnet macaques exhibited levels intermediate between the other two species (Clarke *et al* 1988). Similar studies examining heart rate in macaques have found consistent differences between species. Clarke and co-workers (1994) found that long-tailed macaques had the greatest overall heart rate in response to a novel environment and physical restraint, while rhesus macaques showed the lowest rate, and bonnet macaques exhibited a heart rate intermediate between the other two species. In summary, it would appear that long-tailed macaques show a greater stress response to the laboratory environment and to laboratory procedures than do other commonly used macaque species.

Ecological and locomotor considerations

Within the order Carnivora, there is a positive relationship between natural home range size and the frequency of

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Table 2 Range of body weights, head and body lengths, and tail lengths of six primate species used in the laboratory whose weights fall into 6–9 kg weight bracket. M = male, F = female.

Species	F body weight (kg)	M Body weight (kg)	Head and body length (cm)	Tail length (cm)	References
Rhesus macaque	4.4–10.9	5.6–10.9	470–635	189–305	Fa 1989, Parker 1990
Long-tailed macaque	2.5–5.7	4.7–8.3	385–648	400–655	Fa 1989
Stump-tailed macaque	7.5–9.1	9.9–10.2	485–650	15–125	Fa 1989
Pig-tailed macaque	4.7–10.9	6.2–14.5	467–564	130–245	Fa 1989
Bonnet macaque	3.9–4.4	5.4–8.9	390–444	330–639	Fa 1989
Vervet monkey	1.5–4.9	3.1–6.4	300–600	406–764	Napier 1981

stereotypic behaviour performed in captivity (Clubb & Mason 2003). Although such a study has not been conducted for primates, it is known that they develop behavioural locomotor and self-directed abnormalities if housed inadequately (Capitanio 1986), and that there is large variation in home range sizes in the wild (see Rowe 1996). For example, tamarins have larger mean daily path lengths and home ranges than marmosets, and may be more predisposed to develop stereotypies in captivity (see Prescott & Buchanan-Smith 2004).

When assessing the spatial requirements of a primate and constructing a cage to suit, consideration should be given to both the horizontal and vertical dimensions of the cage to allow performance of species-typical locomotor behaviour on and above the ground (Poole 1991). Confinement of primates in small cages and the resultant lack of adequate physical exercise has been shown to lead to atrophy of the muscles and decreased joint mobility (Faucheux *et al* 1978; Turnquist 1985). If animals are to be housed in a restricted space for extended periods of time, an adjacent exercise enclosure is a practical addition to provide opportunities for natural locomotor behaviour.

There is a significant difference in the activity levels of macaque species. Petto and colleagues (1992) studied rhesus and long-tailed macaques in an indoor–outdoor housing enclosure. Rhesus macaques showed higher levels of activity than long-tailed macaques. It may be that the rhesus macaque should be provided with a greater area to satisfy its requirements for high levels of locomotion and activity.

Amongst the macaque species used in the laboratory, long-tailed macaques are primarily arboreal (Crockett & Wilson 1980; van Noordwijk *et al* 1993), rhesus and stump-tailed macaques are primarily terrestrial (Seth & Seth 1986), and pig-tailed macaques are partly terrestrial and partly arboreal (Caldecott 1986). In line with this natural adaptation, Crockett and colleagues (2000) found that long-tailed macaques spent more time suspended above floor level than pig-tailed macaques (although note that cage height varied only from 0.43 m to 0.84 m). Shimoji and colleagues (1993) found that long-tailed macaques in lower level cages spent more time on an elevated perch than those in upper level cages. This reluctance to approach the floor, combined with their long tails, emphasises the importance of the vertical dimension for this species. What is more, long-tailed macaques exhibit less self-directed stereotypy in vertically enhanced cages compared to standard cages (Watson & Shively 1996). However, consistent findings for increased perch use in lower-level compared to upper-level cages, or for a preference for the upper part of the cage, have also been reported in rhesus macaques (eg Woodbeck & Reinhardt 1991), thus demonstrating the need for vertical space for even the most terrestrial of macaques. This may be related to the fact that all macaques show a vertical flee response (Crockett & Wilson 1980) and require a vertical escape route to reduce the impact of potentially stressful laboratory routines (Reinhardt 1997). Even amongst the highly arboreal marmosets and tamarins, there are species differences in cage usage. Tamarins show a greater predisposition than marmosets to avoid the lower half of their enclosures (Prescott & Buchanan-Smith 2004). This effectively reduces the cage volume available to them and must be taken into account when deciding space allowances. If cage height cannot be increased because of ceiling height, cage cleaning requirements or ease of capture, the only way to increase useable cage space is to increase the cage floor area.

Social and reproductive characteristics

The well-being and breeding success of primates are closely correlated (Poole *et al* 1999). Although there are similarities in the group size and social structure of marmosets and tamarins (they tend to live in small extended family groups), tamarins consistently have poorer breeding and rearing success in the laboratory than marmosets. Whilst both marmosets and tamarins require a good quantity and quality of space for successful breeding, it is particularly important for tamarins (see Prescott & Buchanan-Smith 2004). Increasing space also improves reproductive success in long-tailed and rhesus macaques (Boot *et al* 1985; Westergaard *et al* 2000).

The presence of abnormal behaviour (eg stereotypies) indicates that either currently, or at some stage in the past, the animal's environmental conditions have been sub-optimal (Mason 1991a), although there is some debate as to

whether stereotypic behaviour is an indicator of current suffering (see Mason 1991b for a review). However, it should also be noted that the absence of abnormal behaviour is not an indicator of good welfare. Macaques and vervets live in multi-male multi-female groups in the wild, but the tendency for rhesus macaques to show more abnormal behaviour than pig-tailed macaques when isolated in captivity (Sackett *et al* 1981) could be due to the fact that this species naturally lives in a social group with a higher mean number of members (Caldecott 1986; Seth & Seth 1986). However, long-tailed macaques show less abnormal behaviour than rhesus macaques (Sackett *et al* 1981), although they both live naturally in social groups of similar sizes (Wolfheim 1983). The naturally large group size of the rhesus macaque may combine with its genetic make-up to cause the increased stress response and the high rate of behavioural disturbances.

In addition, dominance style varies amongst macaque species and has been categorised as being either 'egalitarian' or 'despotic', with despotic species, such as the rhesus macaque, showing more extreme aggression and wounding than more egalitarian species, such as the stump-tailed macaque (see de Waal & Luttrell 1989). In terms of temperament, the rhesus macaque is considered to be a more belligerent species than the long-tailed macaque, which has been described as passive or reserved (Clarke & Lindburg 1993). It is not clear exactly how dominance style and temperament impacts on space requirements, but it may be that despotic, belligerent species require more spatial freedom and privacy than egalitarian species, and therefore require larger cages which provide more opportunity to avoid aggressive interactions.

Age, sex and individual characteristics

Although this paper emphasises the importance of considering differences between species when determining suitable space allocations, age, sex and individual history are also important. Juvenile animals, though smaller, are usually more active than adults and therefore require similar or greater space allowances for physical development and play (eg Wells & Turnquist 2001). Sex differences also exist in the amount of activity and play behaviour; for example, juvenile rhesus macaque males exhibit more high-energy and rough and tumble play than females (Lovejoy & Wallen 1988). These juvenile behaviours are likely to be essential for the development of normal social relationships and for physiological development. Furthermore, the temperament of each individual will affect how it expresses behaviourally the amount of stress it experiences. The temperament, or reactivity, of an adult primate depends in part on the amount of stress it experienced as an infant (see Capitanio 1986).

Conclusions and animal welfare implications

Captive primates housed in laboratories should be given extensive opportunities to satisfy their physical, behavioural (psychological) and social needs. An increase in cage space alone cannot satisfy their requirements. The space must be useable with adequate cage furnishings and complexity to prevent psychological disturbances and to minimise stress, which is a prerequisite for the collection of accurate and valid data during experimental procedures.

We conclude that decisions concerning cage volume and furnishings should always be based on a thorough understanding of the needs of the species and individual, and not just calculated from multiplication of the minimum cage volumes specified in legal guidelines. There are important behavioural, social, and physiological differences amongst primate species whose weights overlap, and who are therefore generally housed in cages of the same size. In addition, we highlight some critical age, sex and temperament differences. These factors should be taken into consideration for responsible animal management. However, extensive and dedicated research is needed to elucidate how these factors might be used in a practical way to determine cage space allowances.

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