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How does the zoo environment affect the behaviour of captive primates?

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Abstract

It is important for us to be able to understand the behaviour of primates in zoos for at least three reasons: firstly as a means towards ensuring their welfare, secondly to use that understanding to ensure a positive zoo experience for zoo visitors, and thirdly so that results of basic research undertaken on zoo primates can be properly evaluated. Often, however, the results of studies of how the zoo environment affects primate behaviour are not easy to interpret. We should recognize that the zoo environment is only one of a number of environments in which primates live, and should identify in which ways the zoo environment is different from those other environments. Here, it is suggested that the zoo environment may be defined in terms of three dimensions: regular presence of large numbers of unfamiliar humans, restricted space, and being managed. Individually all three of these can also be found in other, non-zoo environments, but all three together are characteristic of zoo environments. This paper is an initial attempt to compare studies of primate responses to the variables associated with each of these three dimensions across different primate environments. It is concluded that there is a need for at least two different types of study in future: comparisons across a range of primate environments using the same species and measures, and studies of the interactions between the three dimensions identified for zoo environments.
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1. Introduction

We now know quite a lot about the behaviour of captive primates. The last 20 or so years have seen a great growth in the number of behavioural studies undertaken in zoos; some of this is basic research designed to test theories from ethology and behavioural ecology, but most of it is more applied and designed to tell us something about how captive environments influence behaviour (Hosey, 1997). However, interpreting the results of these studies, particularly those on the influence of the captive environment, can be difficult, for a number of reasons, which are explored below.

One of the difficulties is that it is by no means clear what our benchmark should be for evaluating the behaviours we see in captivity. Early attempts to increase the activity, and decrease the abnormal behaviours, of captive animals, notably by Markowitz (Markowitz et al., 1978; Markowitz and Stevens, 1978; Markowitz and Spinelli, 1986) often involved presenting the animals with operant tasks for a food reward, a process generally referred to as ''behavioural engineering''. This approach was open to criticism that, amongst other things, it did not encourage natural behaviours (Hutchins et al., 1978a,b, 1984), and instead an approach was advocated based on making cage structures and furnishings more ''naturalistic'' in order to promote naturalistic behaviours (Hancocks, 1980; Forthman Quick, 1984; Maple and Finlay, 1989). Clearly, the maintenance of a naturalistic profile of behaviour by captive animals was an important goal (McGrew, 1981; Tilson, 1986), especially if captive-bred animals were ultimately to be released into the wild (Van Hooff, 1986; Redshaw and Mallinson, 1991a,b). However, an associated assumption, that the behaviour of their wild-living counterparts should be a yardstick for us to assess the well-being of captive animals, has been questioned (Veasey et al., 1996) on the grounds, among others, that non-performance by captive animals of some of the behaviours shown by wild-living animals does not necessarily indicate reduced welfare. Thus, evaluations based on the welfare of the animals should be used in conjunction with wild-captive comparisons if evaluation of well-being is our goal.

This potentially leads us to a further difficulty, which is about separating out the possible effects of different environments. The problem of defining exactly what ''wild'' means for primates was noted by Bernstein in the first ever International Primatological Society Congress (Bernstein, 1967), and the continuing impact of human activity on primate habitats has probably meant that many of the habitats where studies of wild primates are currently carried out are not really equivalent to each other in terms of the way the animals behave within those environments. At the other end of the wild-captive continuum, we find a common assumption that primates kept in laboratories or primate centres show responses to the captive environment which are equivalent to those shown by primates in zoos. This assumption has not been tested. Somewhere within this wild-captive continuum we also have to accommodate a variety of conditions variously referred to as ''feral'', ''free-range'' or ''semi-free range'', and which might include rhesus monkeys on Cayo Santiago (Zorpette, 1995), lion-tailed macaques on St. Catherine's Island (Fitch-Snyder, 1993), and lemurs in large wooded enclosures at the Duke University Primate Centre (Simons, 1986).

The point has often been made that primates show great flexibility and adaptability (see, for example, Lee, 1991) and that zoo environments for them should be somewhere within their range of adaptability (Poole, 1991). However, separating out the effects of the zoo

environment, and comparing them with the effects of the other environments that free-living and captive primates might find themselves in, has not been attempted in any systematic way, but is necessary if we are to establish any kind of theoretical framework in which to evaluate the results of our studies on the zoo environment. This paper is a first attempt at making such a comparison.

2. Why this question is important

There are at least three reasons why it is important for us to know exactly how the zoo environment, as opposed to other primate environments, affects primate behaviour, and for us to be able to interpret that knowledge within a theoretical framework.

2.1. Animal welfare

Maintaining the psychological as well as the physical well-being of their animals is, of course, of paramount importance to zoos. Considerable advances have been made in creating a theoretical and practical framework for understanding well-being and evaluating animal welfare (e.g. Broom and Johnson, 1993; Wiepkema and Koolhaas, 1993; Fraser et al., 1997; Fraser and Duncan, 1998; Appleby and Sande, 2002). Nevertheless, interpreting observations and experimental results remains difficult (Mason and Mendl, 1993), and it seems reasonable that welfare should be assessed in terms of what individual species have evolved to be able to cope with (Barnard and Hurst, 1996). This perspective recognizes that wild-living animals face stressors too, and can experience compromised welfare. Indeed, there is growing awareness that human impact on animal environments and habitats is not just a conservation concern but also a welfare concern (Kirkwood et al., 1994; Sainsbury et al., 1995).

What does this mean for zoo primates? It is generally assumed that the zoo environment is a more extreme one than the other environments in which primates live (with the likely exception of laboratories); this assumption needs to be tested, and in any case we need to know in which particular aspects or variables the zoo environment is extreme. At their most extreme, captive environments can cause abnormal behaviours that are rarely if ever seen in wild environments, such as regurgitation and re-ingestion in gorillas (Akers and Schildkraut, 1985; Lukas, 1999) and stereotyped body rocking in chimpanzees (Pazol and Bloomsmith, 1993). But for at least some abnormal behaviours, it is not captive environments per se which cause the behaviour, but particular aspects of particular captive environments. For example, autoaggression (self-mutilation) can be a significant problem in laboratory-housed primates (Chamove et al., 1984), but in zoo primates does not seem to occur very frequently (Hosey and Skyner, in preparation). Similarly, the effects of maternal deprivation in human-reared chimpanzees can be ameliorated to some extent by bringing the animals into a social group in a zoo environment (Martin, 2002). So to be able to understand how zoo environments affect captive primate welfare, we must identify the particular variables involved and make comparison with a range of other situations.

The other side of this particular coin, of course, is to understand better how variables in the zoo environment can be manipulated to improve the welfare of captive primates.

There is now an enormous literature on environmental enrichment for primates (see, for example, Reinhardt and Roberts, 1997; Dickie, 1998). For laboratory primates, the aim of enrichment is often to increase the activity of the animals and decrease their abnormal behaviours, and a range of techniques is used which varies from manipulation of the social group to the provision of toys (Kessel and Brent, 1998; Reinhardt, 1990, 2002). Objects may be given to zoo primates for similar reasons (e.g. Rooney and Sleeman, 1998; Renner et al., 2000), but much enrichment for zoo primates is intended to increase their foraging time and associated behaviours (e.g. Shepherdson, 1988; Howell and Fritz, 1999; Vick et al., 2000). Here again, promotion of a behavioural profile similar to that seen in the wild is often identified as the aim of the enrichment (e.g. Lambeth and Bloomsmith, 1994; Britt, 1998). This, however, should ideally be done within a framework which recognizes the behavioural adaptability of many primates and the variety of wild and captive environments in which they live. For example, Melfi and Feistner (2002) found that activity budgets of Sulawesi macaques *Macaca nigra* were different in different zoos, but were not significantly different from the wild. Therefore, the assumption that zoos represent an extreme environment for primates may not be correct, and should be tested for each species.

2.2. The zoo visitor experience

Most zoos, in their mission statements, identify conservation and education as their priorities, and, certainly in Europe and North America, actively pursue those goals. These goals are much wider than just, on the one hand breeding rare species with a view to eventual re-introduction to the wild, and on the other hand providing the public with information about exotic species. For both goals, awareness-raising and attitude changing are also important, as the perceptions many people have of zoos are often negative (Finlay et al., 1988; Reade and Waran, 1996). Attitudes to conservation and awareness of the lives of animals can be improved when people have a positive zoo experience, ideally including close contact with animals (Kidd et al., 1995; Kreger and Mench, 1995; Swanagan, 2000). Providing naturalistic, well-designed cages (Coe, 1985) and suitable environmental enrichment (Robinson, 1998) can play a large part in this process, by making it more likely that zoo visitors will see active animals doing natural behaviours in an appropriate habitat. Allowing close contact and even interaction between zoo visitors and free-ranging primates is now a feature of several zoos, notably Apenheul (Mager and Griede, 1986) and Vallee des Singes (Vermeer, 2000), and on a smaller scale has been introduced in otherwise conventional zoos like Blackpool (Webster, 2000). Zoo visitor attitudes can become more positive and people's interest in the animals increased when they encounter free-ranging primates (Price et al., 1994), and in this respect the animals act as ''ambassadors'' furthering the conservation cause (Vermeer, 2000). Primates have also been used as living demonstrations (Povada, 2000), and those that promote live animal presentations in zoos also use the term ''ambassadors'' (Gates and Ellis, 1999) to describe them. Live demonstrations do have educational benefits (Heinrich and Birney, 1992). Mixing animals and people need not conflict with the need to maintain for future re-introduction viable naturalistic populations with behavioural profiles like those seen in the wild, as managed captive breeding can lead to production of surplus or non-breeding animals (Glatston,

1998), and provided that their welfare is not compromised, it is perhaps less necessary that these animals maintain a wild-type profile of behaviour. Again, comparison with a range of other primate habitats will help us to evaluate the behaviour of primates used by zoos as ambassadors, and perhaps allow zoos to provide an experience which is enriching for both the human and non-human primates.

2.3. Behavioural research

Despite the popular myth that worthwhile behavioural research is not possible in zoos because they are such an artificial environment, in reality not only is a substantial amount of good research undertaken on zoo-housed animals, but much of it has made important contributions towards developing and testing theory in behavioural biology. An advantage of zoo primates is that the observer can detect subtle behaviours which may well be missed in the wild. For example, long-term studies of chimpanzees at Arnhem (de Waal, 1978, 1982, 1984; de Waal and Van Hooff, 1981; Preuschoft et al., 2002), and Japanese macaques at Rome Zoo (D'Amato et al., 1982; Scucchi et al., 1988; Schino et al., 1993) have been instrumental in refining our knowledge of group dynamics, post-conflict behaviour, alliances and coalition formation in primates. Similarly, unusual behaviours such as tool use by gorillas (Nakamichi, 1998), bonobos (Gold, 2002) and orangutans (O'Malley and McGrew, 2000); predation by woolly monkeys (Stearns et al., 1988) and lemurs (Jolly and Oliver, 1985; Glander et al., 1985); and fruit smearing by chimpanzees (Fernandez-Carriba and Loeches, 2001) may represent behaviours which also occur but are rarely seen in the wild.

Undoubtedly, the results of behavioural studies on zoo primates must be interpreted in the context of the possibility that the zoo environment has affected the animals' behaviour. That such effects on behaviour can contaminate behavioural studies is just an assumption, and needs to be tested. Testing the assumption can show, as with the Sulawesi macaques studied by Melfi and Feistner (2002), that zoo groups may not differ from wild ones in their overall activity budgets. Nevertheless, there may be other ways in which zoo groups do differ from wild ones, and it is important to compare zoos with a range of other primate habitats so that these differences can be evaluated within an appropriate framework.

3. Defining the zoo environment

The first step in comparing primate responses to the zoo environment with their responses to other environments is to identify exactly what are the independent variables associated with the zoo environment. It is possible, probably likely, that primate behaviour is affected not by any single variable, but by a number of zoo-related independent variables acting together. For this reason, we need to distinguish the zoo environment from other environments in which primates live. This is not as easy as it might at first seem. Some primate research centres, for example, have many superficial similarities to zoos, but might differ from them in some important variables. I propose the following three dimensions to define the zoo environment and distinguish it from other primate environments:

1. The chronic presence of human visitors. By this, I mean the frequent (usually daily) arrival of large numbers of people who are unfamiliar to the animals. This, then, would exclude most primate centres, where the animals are routinely exposed only to humans who are more-or-less known to them, and groups of unknown visitors are rare.
2. Restricted space. The physical space available to even the most naturalistic groups of zoo primates is usually much less than they would range over in the wild.
3. Being managed. Most aspects of the life histories of zoo primates are managed to some extent by humans. Group membership, spatial accommodation, feeding routine, health and reproduction are all largely outside the animals' control.

Having identified these three dimensions, we can now look more closely at some of the variables associated with each one in comparison with non-zoo primate environments.

4. Presence of zoo visitors

In order to achieve their mission objectives and also to be financially viable, zoos must not only admit the public but must also give them an enjoyable and positive experience based upon seeing and perhaps even interacting with active, healthy animals. If the presence of those visitors causes an animal to retreat, become hidden or immobile, become stressed, or start to show abnormal behaviours, then there is a very clear problem.

Research of the past 20 or so years has not given a completely consistent picture of what effect zoo visitors have on captive primates, but in general the results of most studies can be interpreted that most zoo primates find the presence of large active groups of visitors to be stressful (Hosey, 2000). Thus, for example, across a range of primate species housed in traditional cages, the animals increased their locomotory activity and audience-directed behaviours when active audiences were present (active audiences being those where at least one person attempted to interact with or draw the animals' attention), but were not significantly affected by passive audiences (Hosey and Druck, 1987; Mitchell et al., 1992c). If intra-group interactions were examined, it was generally found that agonistic behaviours increased and affiliative (e.g. grooming) behaviours might increase or decrease under audience conditions (Glatston et al., 1984; Chamove et al., 1988; Perret et al., 1995; Wormell et al., 1996; Birke, 2002). However, such changes have not been seen in all studies (Fa, 1989; Lukas et al., 2002). A detailed series of studies undertaken by Mitchell et al. (1990, 1991a,b, 1992a,b) on golden-bellied mangabeys showed that the animals increased visitor-directed and within-group aggression when audiences were present, but affiliative behaviours were largely unchanged. Furthermore, the male and female monkeys directed their aggression to different targets among the human audience, implying that the animals viewed humans as agonistic competitors.

It was suggested long ago by Morris (1964) that visitors might provide zoo animals with welcome variability in an otherwise monotonous existence, but the possibility that audiences might be enriching for some zoo primates has not really been tested. However, the green monkeys in Fa's (1989) study, which showed no visitor-related increase in agonism, were extensively thrown food by members of the public; similarly Cook and Hosey (1995) found that chimpanzees were willing to enter into fairly long interaction

sequences with members of the public, when the only apparent reward was an occasional piece of food being thrown.

There is a clear need for more audience studies to be undertaken with primates in more modern naturalistic cages, and indeed with those allowed to free-range in the zoo; in both cases, we might expect from casual observation that the animals would find the presence of people less stressful. We must also recognise that audience presence is a condition rather than a variable, and must try to identify what particular variables of the human audience cause which, if any responses. Data so far implicate audience activity (Hosey and Druck, 1987; Mitchell et al., 1992a) and noisiness (Birke, 2002).

We should also note that exposure to a human audience, both in terms of chronic large crowds and in terms of occasional short exposure, is by no means a condition that only zoo primates experience. On Gibraltar, non-captive barbary macaques *Macaca sylvanus* are exposed at one site to visitor densities of 238,000/ha/year and are routinely fed by visitors as well as being provisioned by the army (Fa, 1991, 1992). There are few data on changes in the animals' behaviour when the public are present, but levels of visitor-directed aggression are high, mostly as a consequence of people being bitten by monkeys they have provoked (Fa, 1992). In comparison, Fa (1992) reports that people-directed aggression is very low in semi-natural macaque enclosures elsewhere in Europe; he also points out that feeding by the public has had an adverse effect on the reproduction of the Gibraltar macaques, and warns of the possibility of this as well as visitor-directed aggression in zoo primates (Fa, 1989).

Other places where non-captive primates are exposed to large numbers of human visitors include some temples in Asia. For example, Small (1998) compared long-tailed macaques *Macaca fascicularis* at three different tourist temples in Bali, and found differences between them in the amount of aggression they showed to humans; they were particularly aggressive at a temple where ''tourist guides'' acted aggressively towards them. In Indian cities, the rhesus macaques *Macaca mulatta* scrounge and beg for food, and are generally tolerated by the human population (Southwick and Siddiqi, 1998). The lesson from Gibraltar, Bali and India would seem to be that close proximity between human and non-human primates need not be stressful for either, but that the introduction of feeding by the audience has the potential, unless properly managed, of resulting in increased intra-group and visitor-directed aggression, not to mention possible long-term reduction of the animals' fertility and impairment of health.

Non-captive primates who do not live in proximity to human settlements may also receive regular human visitors, but not in the numbers seen at zoos and tourist sites. Few studies have collected systematic data on the responses of these animals to human visitors. Tutin and Fernandez (1991) found that gorillas responded to sudden human presence mostly with curiosity, and chimpanzees mostly with flight; they interpreted the animals as perceiving humans initially as unfamiliar species rather than as potential predators or competitors. Subsequent encounters with humans could be negative or neutral, but were not positive. A later study by Werdenich et al. (2003) found virtually the opposite response pattern for the two species, but pointed out that other variables, such as the activity of the observers, could influence this. In general, however, gorillas appear to habituate more readily than chimpanzees to the presence of human observers in wild populations when provisioning is not used (Tutin and Fernandez, 1991). The meagre data from wild primates

do not, unfortunately, allow us to make any worthwhile comparisons which would give us insights into the habituation of zoo primates to their human visitors.

There are, however, a small number of studies on responses of primates to humans in captive, non-zoo conditions. In one study (Clarke and Mason, 1988), three different macaque species were subjected to the passive presence of a single human observer, with a number of different behavioural measures being taken. The animals, normally housed in groups in outdoor enclosures were housed in individual cages in a primate room for the experiment. The results, along with the results from physiological studies (Clarke et al., 1988) allowed the three species to be characterised as reactive and fearful (crab-eating macaques), aggressive (rhesus macaques) or affiliative (bonnet macaques). What this tells us is that different species are likely to respond to a stressor in different ways, so we should not expect a uniform response pattern to human audiences across all the different primate species that are kept in zoos.

Primates housed in research facilities, like those in zoos, are exposed to chronic human contact from familiar humans, but, unlike zoos, do not daily encounter large groups of unfamiliar humans. Thus, there is less opportunity than in zoos for the animals to habituate to unfamiliar visitors, so a comparison between zoos and research centres would be an ideal way of looking at the extent to which captive primates do habituate to their audiences. Unfortunately, such a comparison has yet to be made, though there are some data from chimpanzee colonies which suggest that zoo animals do habituate to some extent. Maki et al. (1987) found that intra-group and visitor-directed aggression were high among the chimpanzees at a research centre in Texas on days when visiting scientists and students were touring the centre. Subsequent analysis of laboratory records showed that there were, on average, three times as many episodes of wounding among the chimpanzees in periods (weekdays) when human activity was greatest, compared to weekends (Lambeth et al., 1997). Others have observed that laboratory chimpanzees show vigorous aggressive displays to unfamiliar intruders, and that these can be reduced by changing the design of the cage (Rumbaugh, 1988). Data from these studies do not permit direct comparison with zoo chimpanzees, but in those studies where zoo chimpanzee responses to human visitors have been examined (Cook and Hosey, 1995; Perret et al., 1995; Wood, 1998) such high levels of aggression have not been seen.

From all of these studies, we can make some tentative conclusions about audience presence, though we should at the moment regard these as no more than working hypotheses. Clearly more studies are needed to test these and establish them more firmly:

(a) Different species of wild-living primates probably respond to humans in different ways, perhaps reflecting different social organisations and different typical species responses to environmental events;
(b) In some situations, some wild-living primates live in close proximity to humans and may encounter and interact with them regularly. Often food appears to be the motivation for contact in these situations;
(c) Both captive and non-captive primates appear to habituate to humans they encounter regularly, and perhaps also in some situations (e.g. zoos, tourist areas) to those they do not. The extent of this habituation may also depend as much on species-typical response patterns as on the amount of exposure to humans.

We can perhaps add that altering the conditions of captivity (e.g. through naturalistic enclosures, allowing free range, etc.) to give the animals more control over their encounters with humans is likely to make the whole process of habituating to, interacting with, and coping with humans a much easier and less stressful one for the animals, though currently there are no direct data to support this suggestion.

5. Restricted space

For many people, one of the most negatively perceived features of the zoo environment is the restricted space afforded to the animals, a perception often expressed in terms of the confinement of the animals and their inability to roam as they do in the wild (Rhoads and Goldsworthy, 1979; Finlay et al., 1988). Again, as with the presence of human visitors, a comparison of different primate environments shows that the effects of physical space are more complex than this suggests, and interpretation of studies can be difficult. Here again, we must recognise that captive and non-captive primates can live in a variety of situations and that not all of them afford the animals unrestricted space. For example, ring-tailed lemurs *Lemur catta* have now been studied at the Berenty Reserve in southern Madagascar for some 40 years. However, during that time the troops have maintained virtually the same home ranges and core areas (Jolly and Pride, 1999; Mertl-Milhollen, 2000), so to that extent the animals are still constrained by boundaries of some sort. However, it is also likely that different species, with different ranging patterns in the wild, will have different responses to restricted space in captivity, as appears to be the case in carnivores (Clubb and Mason, 2003).

As with audiences, there are a number of variables associated with the space that primates occupy. Early studies considered that crowding, which could be achieved experimentally by reducing the physical space or by increasing the number of animals, would result in elevated levels of aggression. Most of these studies were laboratory-based, although at least one (Southwick, 1967) was undertaken in a zoo, but in a restricted area where presumably the public were not allowed access. Space reduction was only one of Southwick's manipulations with his rhesus monkey group, and it did indeed result in increased aggression. However, his overall conclusion was that social changes had a much greater impact on levels of intra-group aggression than environmental changes. A similar experiment by Alexander and Roth (1971) on Japanese macaques housed at a primate centre also showed increased levels of aggression when space was reduced, but suggested that the most severe aggression was related more to the change of being put into an unfamiliar enclosure than to the space reduction per se. Novelty is an important confounding variable and is often more responsible for behavioural change than changes in the physical size of the cage (Nash and Chilton, 1986). A series of experiments on pig-tailed macaques (summarised in Erwin, 1979, 1986) at a primate centre also failed to find a simple connection between aggression and space; indeed the animals showed more aggression when two rooms were available than only one. Again, social variables seemed to interact with the spatial variables.

What about primates in zoos? Waterhouse and Waterhouse (1971) studied the rhesus macaque group in the Monkey Temple at Bristol Zoo, and found a mean of 4.4 fights per

hour when 41 animals were present, but only 1.5 fights per hour when half the animals had been removed. They considered that fighting was a social pathology in response to overcrowding. However, extensive study of the chimpanzees in the naturalistic enclosure at Arnhem showed that aggression rose only slightly when the animals were crowded, and they used other social behaviours to maintain amicable social relationships when threatened by crowding-induced stress (Nieuwenhuijsen and de Waal, 1982). We now know much more about the behaviours many primates use to avoid the damaging effects of aggression (e.g. reconciliation, consolation, avoidance) and can see that these allow captive groups to live relatively peacefully in restricted space (de Waal, 1989; de Waal et al., 2000). Other observations also imply that primates cope behaviourally with crowding; for example Kummer (1982) mentioned that hamadryas baboons, when transported in pairs in small cages, typically sat facing away from each other, which might be interpreted as a conflict avoidance strategy.

The physical dimension of the space is not the only variable associated with space that has any significance for primates. Several studies have shown that the complexity of the space is more important than its size. Wilson (1982), for example, measured the activity of animals in 43 groups of gorillas and 68 groups of orangutans in 41 different zoos. The best predictors of activity in the groups were number of animals and the presence of objects rather than enclosure size, usable area or feeding frequency. A further study by Perkins (1992) looked only at orangutans and used multiple regression to identify important variables. She concluded that providing large enclosures which contained a lot of movable objects and provided social opportunities for the animals promoted higher levels of activity in the orangutans.

Complexity of space is usually increased by the provision of structures, with the naturalistic environment being the clearest attempt to provide structural complexity similar to that seen in the wild. This can result in spatial use of the enclosure very similar to the use of space seen by animals in the wild. For example, in a naturalistic enclosure with high moulded trees and vines but a flooded floor, orangutans spent most time sitting and reclining in the upper canopy and avoided the floor (Hebert and Bard, 2000). Surprisingly, few studies have tried to identify exactly how much use animals make of the space or structures in their enclosures, and sometimes the results can be surprising. Gorillas, for example, often prefer to spend time close to their holding buildings (Ogden et al., 1993; Stoinski et al., 2001a,b), and in one zoo have been estimated to spend 50% of their time in less than 15% of the exhibit (Stoinski et al., 2001a,b). Nevertheless, in both these studies the gorillas showed strong preferences for areas near structures, such as trees and rocks. Among four female chimpanzees on a zoo island exhibit, each had a preferred site where they spend most time (Bettinger et al., 1994). Even in laboratory cages, which usually have less space and structural complexity than zoo enclosures, animals' use of cage space is often not uniform. Chimpanzees in laboratory cages, for instance, prefer levels above the cage floor (Goff et al., 1994) and may also prefer perimeter areas and even smaller cages (Traylor-Holzer and Fritz, 1985).

If cage complexity is so important to captive primates, then increasing the complexity of their enclosures should have measurable effects on their behaviour consistent with both improved welfare and a more naturalistic profile of behaviour. A very large literature suggests that this is the case, with complexity being increased by structural changes to cage

furnishings and substrates (e.g. Anderson and Chamove, 1984; McGrew et al., 1986; McKenzie et al., 1986; Zucker et al., 1991; Bayne et al., 1992; Brent, 1992; Ludes-Fraulob and Anderson, 1999), by moving animals from indoor to outdoor enclosures (e.g. Clarke et al., 1982; Macedonia, 1987; Chamove and Rohrhuber, 1989; O'Neill et al., 1991; Jensvold et al., 2001), by moving animals into more naturalistic enclosures (e.g. Goerke et al., 1987; Ogden et al., 1990; Chang et al., 1999) and by releasing animals into free-range (Price et al., 1989; Price, 1992; Garrison and White, 1993).

What these and other similar studies tell us is that restricted space per se need not be a welfare problem and need not lead either to the loss of species-typical behaviours or the acquisition of abnormal behaviours provided that the components of the space (particularly structural complexity) are appropriate and give behavioural opportunities. Thus, we may question, in terms of restricted space being a dimension of the zoo environment, whether the best zoo enclosures are particularly different at all from non-captive environments, at least in terms of the behaviour of the animals that occupy them. Certainly, the Sulawesi macaque groups studied in zoos by Melfi and Feistner (2002) did not differ significantly in their activity budgets from animals in the wild. Similarly Little and Sommer (2002), who studied a group of Hanuman langurs *Presbytis entellus* in a traditional cage and again after a move to a new style naturalistic enclosure, found that while there were behavioural changes, in fact the activity patterns in both kinds of housing were within the range of variation seen in the wild. More direct wild-captive comparisons of this sort are needed, over a variety of captive and non-captive environments, and using additional measures, since some behavioural change is not reflected in activity budgets.

6. Being managed

Most aspects of the lives of zoo primates are managed to some extent by humans, and this can have considerable impact on their behaviour. Being managed, of course, is also a significant feature of the lives of laboratory primates, and it is likely that the impact of management on their behaviour is somewhat different from that of zoo primates because of the differences in the other two dimensions, presence of public and amount of space. It should, however, be remembered that many populations of primates that are regarded as wild or free-range are also managed to some extent, because they are pests, or of conservation importance, or of tourist interest, or of research interest. Examples of management of these populations include provisioning of macaques for tourist and research purposes (e.g. Fa, 1991; O'Leary, 1996; Hill, 1999), capture of animals for marking and measurement (e.g. Altmann, 1962) and veterinary procedures (Laudenslager et al., 1999) and maintenance of free-living or provisioned populations in areas where they may or may not be native (e.g. Peignot et al., 1999; Dierenfeld and McCann, 1999).

For many people, the most obvious way in which zoo and laboratory primates lead different lives from their wild counterparts is in the fact that they are supplied with regular food, and therefore do not need to spend time finding food. Traditionally food has been presented to captive primates in a ready-processed form, and low foraging and feeding times are often found in their activity budgets compared to those in the wild (e.g. Britt,

1998). Changing the way food is presented, for example by supplying whole rather than chopped fruit (Smith et al., 1989), scattering food in the substrate (Anderson and Chamove, 1984) and providing opportunities that the animals get in the wild (McGrew et al., 1986), can significantly change behaviour in a more naturalistic direction. Another behavioural change in captive primates related to feeding is pre-feeding agonism, for example in baboons (Wasserman and Cruikshank, 1983) and chimpanzees (Howell et al., 1993). Attempts to manage pre-feeding agonism include the use of unpredictable feeding schedules (Bloomsmith and Lambeth, 1995) and positive reinforcement training (Bloomsmith et al., 1994), though these techniques have generally been tried with laboratory rather than zoo primates. Zoo primates may also be exposed to foods that are not a part of their normal natural diet (Nijboer and Dierenfeld, 1996; Campbell et al., 2001), which may have consequences for their behaviour. Finally, diets in captivity may lead to obesity, resulting in animals that are heavier than their wild counterparts (Schwitzer and Kaumanns, 2001), which again may have behavioural consequences. As with the other variables we have considered, these aspects of feeding management can also be found in non-captive primates. For example, vervet monkeys living in Entebbe who have access to human food show more time resting and less time feeding than their ''wild'' counterparts (Saj et al., 1999); provisioned groups of Japanese macaques show greater agonism and differences in other social behaviours compared to unprovisioned groups (Hill, 1999), but also show more innovative behaviours (Huffman and Hirata, 2003); and ring-tailed lemurs and lion-tailed macaques living free-range on St. Catherine's Island eat a variety of native plants that they would not encounter in their original environments (Dierenfeld and McCann, 1999).

Another way in which zoo primates are managed, and may therefore show behavioural change, is through changes to cages, changes to group composition, and proximity to other species. The effects of changes to cage furnishings or design, or moves to new enclosures, are most studied when they involve enrichment or a move from a traditional to a naturalistic enclosure (see previous section). Recently, several studies have advocated regular moving of animals between enclosures as a way of increasing activity and enclosure use. This can involve different groups of the same species, for example gorillas (Lukas et al., 2003), where the regular alternation of enclosures may simulate, among other things, ranging behaviours seen in the wild; or different species may be rotated, as in the study by White et al. (2003), which involved orangutans and siamangs as well as tapirs, tigers and babirusa. More species-typical behaviours were seen, and the animals were affected by whoever had previously been in the enclosure. Thus, animals may, for example, be exposed to scents of their predators or their prey, and the effects and welfare implications of this have hardly been studied. In laboratory conditions, cotton-top tamarins *Saguinus oedipus* show elevated anxiety responses to faecal scents of predators compared to scents of non-predators, which may have welfare implications for how these animals are housed in zoos (Buchanan-Smith et al., 1993). It has, however, also been suggested that captive tamarins, again in laboratories, may benefit from brief threatening events; for example they may show increased affiliation and new behaviour patterns when confronted with occasional stimuli such as a model bird flying overhead (Moodie and Chamove, 1990). Here again, we do not have sufficient data to know if zoo and laboratory primates are affected in different ways by such stimuli.

Zoo primates are, however, often maintained in mixed species groups, sometimes other primates but often non-primate species which they may or may not encounter in the wild. Few studies have been undertaken on these groups, but Ziegler (2002) surveyed mixed species exhibits in German zoos and found that although in some of them the different species appeared to ignore each other, in others there were inter-species interactions which included: baboons riding on and grooming elephants, Japanese macaques riding on and grooming barbary sheep, an owl monkey building up a relationship with a male sloth, tamarins attacking viscachas and agoutis, baboons stealing eggs from ostriches, and young barbary macaques and barbary sheep playing together. How to interpret these responses in terms of the welfare of the animals concerned, let alone the naturalism of their behaviour, is not easy.

Changes to the composition of captive primate groups can also have profound effects on behaviour. In laboratories and primate centres, pair or group housing has long been advocated as a social enrichment and a number of studies have documented the behavioural changes associated with a change in the social environment (Reinhardt et al., 1988, 1995). But changes to group membership may be carried out both in laboratories and zoos for other reasons, and sometimes these may reflect social processes that also occur in the wild, such as seasonal separation and subsequent re-integration of males and females (Williams and Abee, 1988: squirrel monkeys). Captivity imposed changes can include merging of groups (Araguete et al., 1998; Seres et al., 2001), introducing new individuals into existing groups (Scruton and Herbert, 1972; Inglett et al., 1989; Pfalzer and Ehert, 1995; Hoff et al., 1996; Brent et al., 1997) and introducing individuals to each other prior to putting both into an existing group (Meshik, 1999). Such introductions are often accompanied by initial aggression, and have varying levels of success. Clearly, a good knowledge of the behavioural biology of the species in the wild is needed before undertaking social manipulations (Visalberghi and Anderson, 1993).

Often introductions of animals into groups occurs because the animal in question has been hand reared and/or is asocial because of early social deprivation. There is quite a large literature on this for gorillas (Meder, 1985, 1990; Jendry, 1996; McCann and Rothman, 1999; Burks et al., 2001; Ryan et al., 2002) but also for species as diverse as chimpanzees (Pfeiffer and Koebner, 1978; Fritz, 1986), siamangs (Parker et al., 1988), orangutans (Hamburger, 1988) and ruffed lemurs (Brockman et al., 1987). Infants may also be introduced to potential foster parents as an alternative to hand rearing (Kerridge, 1999: ruffed lemurs). A further consequence of the captive management of primate populations can be surplus males, which may be kept as bachelor groups, notably in gorillas (Stoinski et al., 2001, 2001b, Pullen, this symposium), but also in species like ruffed lemurs (Romano and Vermeer, 2003) and lion-tailed macaques (Stahl et al., 2000). Understanding and evaluating the welfare and behaviour of hand reared, fostered and single-sex grouped animals may not be particularly helped by simple comparisons with the wild, but may benefit from comparisons across all the different captive and non-captive situations in which primates live.

Even in non-captive situations primates may be subjected to some of the management practices described above. As representative examples, we can point to the release of ring-tailed lemurs onto St. Catherine's Island (Keith-Lucas et al., 1999) as perhaps being similar to zoo lemurs being released into a naturalistic enclosure; release of ruffed lemurs into

Madagascar (Britt et al., 2004) as an example of integrating animals into existing groups; and proposals for translocating rhesus and hanuman monkeys for conservation purposes (Pirta et al., 1997) as being rather like some of the movements of captive primates between zoos.

As can be seen, there is evidence available about the impact on behaviour of a number of management procedures used on captive primates in zoos and laboratories. However, how the combined effects of all of these different practices lead to differences, if any, between different captive and non-captive groups of primates, is currently unclear.

7. Discussion

As we can see from the above review, there are obviously difficulties in defining exactly what the zoo environment consists of. However, it seems at least pragmatically clear that the three factors of audience presence, restricted space and being managed are crucial to furthering our understanding of this environment.

But it would be a mistake to assume that wild environments are characterised by a lack of these features. Human impact means that the space available to non-captive primates is declining all the time, and many species have to change their ecology and behaviour in order to survive (see, for example, Johns and Skorupa, 1987; Johns, 1991). Many non-captive primates already regularly encounter humans through tourism (e.g. Lee et al., 1986), or because they raid human crops and garbage (e.g. Forthman Quick, 1986; Else, 1991) or because they are hunted. Even other non-captive groups, that are not hunted, pests or tourist features, may be regularly provisioned with food by people (Hill, 1999). So, in some of these variables zoo and some wild environments are becoming more similar.

Some of this similarity can be seen in Table 1. Clearly, the features identified there each show considerable variability, as do the categories ‘‘zoo’’, ‘‘laboratory’’ and ‘‘wild’’. However, it would be simplistic to infer from this that the zoo environment can be

Table 1
Some of the variables that may affect zoo primate behaviour, and how they may also occur in other primate environments

	Zoo	Laboratory/research centre	Wild
Humans			
Regular unfamiliar audience	Yes	No	Some
Regular familiar small number of people	Yes	Yes	Some
Occasional unfamiliar people	No	Yes	Yes
Space			
Small, not naturalistic	Some	Some	No
Small naturalistic	Some	Some	Some
Large naturalistic	No	No	Some
Managed			
Food supplied	Yes	Yes	Some
Getting caught/handled	Yes	Yes	Some
Getting moved around	Yes	Yes	Some
Encountering other species	Some	Some	Yes

equivalent to the wild for captive primates. The goal of the modern zoo is to provide environments which are within the range of behavioural adaptability for the animals, as it is also clear that there can be great variability within the same species in the behaviour of primates in different non-captive environments. To do this effectively, we need to undertake more comprehensive comparisons of the behaviour of different species in a range of captive and non-captive environments.

We also need to look more closely at how the different variables associated with the zoo environment interact with each other, as there is evidence (e.g. see Wood, 1998) that they do. Thus, there is also a clear need for research into the combined effects of visitor presence, cage complexity and management processes on the behaviour of zoo primates.

However, even the limited comparison undertaken here gives some reason for optimism, because the indications are that variability within different environments may be greater than the variability between them. So, returning to the original reasons why we considered it important to do the comparison, we can suggest that the zoo environment need not, by definition, be detrimental to the welfare of captive primates; that research on zoo primates may not necessarily be affected by systematic bias in comparison with studies done in the wild; and that the zoo visitor experience can include watching animals behaving in a way which is not too dissimilar to the way they behave in the wild. With systematic comparisons across different environments, and more knowledge about the interactions between variables, we will be a step closer to providing a much-needed theoretical framework within which the behaviour of zoo primates can become more understandable.

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