ZOO ANIMALS AND THEIR HUMAN AUDIENCES: WHAT IS THE VISITOR EFFECT?

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The presence of human visitors has been shown to affect the behaviour of several different mammalian species in a number of different zoos, but the behavioural changes observed are not always consistent with a simple 'stressful influence' explanation. Data for non-primate species are too sparse to draw meaningful conclusions; but for primates, the evidence reviewed in this paper allows several hypotheses to be tested. Neither a social facilitation nor an audience attraction hypothesis can be generally supported by the available studies. However, these studies are consistent with a general stressful influence hypothesis, although the extent of this influence is itself affected by other variables, notably species and housing differences. There is some evidence that chronic exposure to human audiences may lessen this stressful influence in some species; and in certain circumstances (notably where some members of the public throw food) the effect of the audience is almost an enriching one.

Keywords: *animal welfare, audience effect, humans, primates, zoo visitors*

Introduction

It would seem to be intuitively obvious that the presence of human visitors must have some effect on the behaviours of captive animals in the zoo. Every day the animals are confronted with groups of people who may passively watch, but may also stare, point, vocalize, or in some other way try to interact with the animal. When zoos are crowded the noise and visual disturbance levels become particularly high, and if this is so noticeable to us, then surely it must be affecting the animals even more strongly.

Surprisingly, the assumption that there was a 'visitor effect' was not systematically investigated until comparatively recently. However, earlier commentators did have views on what this effect might be. For example, Hediger (1970), drawing on a wealth of experience with zoo animals, suggested that they perceived humans as being significant as an enemy, a prey, a symbiont, a piece of inanimate environment, or a member of their own species. Morris (1964) considered that zoo visitors provided a welcome variability which some animals could exploit by provoking reactions; in other words, they could be a source of enrichment. There was also a view (Snyder 1975) that the animals become habituated to the public under most conditions, and their behaviour was thus not affected. These three views more or less present three alternative hypotheses: that zoo visitors are stressful, enriching, or of no consequence.

It is important to know if a visitor effect exists, and what it is, for at least three reasons. First, there are clear welfare implications – particularly if human visitors are stressful to animals. Although most zoos see their mission primarily as the support of conservation, and secondarily as educational, their survival still depends upon an ability to draw crowds. If these crowds adversely affect the animals' welfare, then solutions would have to be sought as a matter of urgency. Second, it could be important in designing a positive 'zoo experience' for people. People probably visit zoos for a number of reasons, but a very powerful one is the possibility of interacting with animals (Kreger & Mench 1995). Such interaction, particularly touch, is in turn instrumental in fostering positive attitudes towards animals and conservation (Kidd *et al* 1995). If human-animal interactions were enriching to the animals as well, then zoo experiences could move away from the passive viewing of an animal in a cage. This might help dispel the largely negative attitudes that many people have towards zoos (Finlay *et al* 1988; Reade & Waran 1996). Finally, a possible visitor effect will be significant to researchers, particularly those studying the behaviour of animals in zoos. The impact of zoo variables, including the presence of human visitors, must be understood for the correct interpretation of behavioural studies (Hosey 1997).

Recently, a number of studies have attempted to identify and quantify the visitor effect. The purpose of this paper is to review these studies and evaluate how well they support different hypotheses about the role of zoo audiences in modifying animal behaviour.

Non-primate studies

Published studies on visitor effects on non-primate species are virtually non-existent. O'Donovan *et al* (1993) studied a group of cheetah, *Acinonyx jubatus,* mothers and cubs at Fota Wildlife Park (Eire), and found no significant visitor effects on behaviour. The only other substantial report appears to be Thompson's (1989) study of behavioural responses to the presence of a zookeeper in 12 ungulate species. Data were collected both in the presence and absence of a human audience. Some behavioural changes, particularly in vigilance, were noted, and interpreted as being due to interruption of the spatial cohesiveness of the group. The changes were subtle, but it was not clear whether they implied a stressful effect.

A study on a single long-billed corella, *Cacatua tenuirostris*, at Adelaide Zoo (Nimon & Dalziel 1992) suggested that the bird was motivated to interact with human visitors, particularly because some behaviours were only performed in the presence of people.

There is a clear need for more studies to be undertaken on interspecies interactions and possible visitor effects on zoo animals, utilizing as wide a range of species as possible.

Primate studies

Virtually all zoo visitor studies have been done with captive primates. In addition, there are a number of studies which have examined the responses of monkeys and apes to human audiences in laboratories and primate research centres (both hereafter referred to as 'laboratories'), where the 'audience' may or may not correspond to that found in zoos – namely a heterogeneous assemblage of individuals unfamiliar to the animals. Some studies have looked across a range of different species, whereas others have concentrated on just one or two. A substantial number of studies concern chimpanzees, *Pan troglodytes*, and these will be considered separately because they represent a number of different situations applied to the same species.

Multi-species studies

A study by Hosey and Druck (1987) considered the behaviours of 12 different species of primate at the old Monkey House at Chester Zoo. The species comprised two lemurs (*Lemur catta* and *Eulemur fulvus*), two New World monkeys (*Ateles paniscus* and *Cebus albifrons*) and eight Old World monkeys (*Cercopithecus mitis, C. neglectus, Erythrocebus patas, Miopithecus talapoin, Macaca nigra, M. sylvanus, M. silenus* and *Papio hamadryas*). The cages varied from wire-fronted to glass-fronted in 'traditional' 1950's style (they no longer exist). Audiences were deemed to be active or passive, depending upon whether at least one person was attempting to interact with the animal. Across the 12 species it was found: that locomotory activity increased (there was a mean 25% increase in locomotory score) when audiences were active (but not passive); the frequency of intra-group interactions was unchanged by the presence of any audience; and animals directed more behaviours at the audience, if the audience was active.

This study was replicated by Mitchell *et al* (1992a) at Sacramento Zoo, using essentially the same measures and audience conditions but a different range of species, comprising three lemurs (*Lemur catta, Eulemur mongoz* and *Varecia variegata*), one New World monkey (*Saimiri sciureus*), four Old World monkeys (*Presbytis francoisi, Cercopithecus ascanius, C. neglectus* and *Cercocebus galeritus*) and three apes (*Hylobates lar, Pongo pygmaeus* and *Pan troglodytes*). These researchers found virtually the same effects as Hosey and Druck (1987), but pointed out that neither study had actually demonstrated the direction of causality, only an association between the variables of behavioural change and features of the audience. Thus, although Hosey and Druck (1987) inferred that the observed changes in primate behaviour were caused by the presence of the audience, an alternative explanation, that changes in animal behaviour caused the formation of large active crowds around the cage, was equally plausible.

Further shortcomings of the Hosey and Druck (1987) study were that interspecific differences in responsiveness were not investigated (although they were alluded to); and that the category 'intra-group interactions' did not allow agonistic behaviours to be distinguished from affiliative behaviours, although there were grounds for believing that these two types of behaviour might change frequency in different directions. These issues were addressed in a series of studies, all published as one paper (Chamove *et al* 1988). The first two studies, undertaken at Edinburgh Zoo on three quite different species (*Lemur catta, Saguinus oedipus* and *Cercopithecus diana*), showed that in all three the presence of visitors was associated with a decrease of about 55 per cent in inactivity and of 80 per cent in grooming, and an increase (by a factor of over 5) in agonism. The differences were still there, but reduced to a 25 per cent fall, 30 per cent fall and factor of 2 increase respectively, when the audience was asked to crouch, making the people look smaller to the animals. Once again, the direction of causality was inferred, but the inference was supported by the crouching experiment. The third study reported in this paper, showed that increases in glancing at visitors and in activity were associated with an increase in the number of observers in a group of mandrills, *Mandrillus leucophaeus*, at Schoenbrunn Zoo in Vienna. Finally, the individual species data from the Hosey and Druck (1987) study were analysed to test the hypothesis that small arboreal species were more affected by visitors than large terrestrial species. None of the correlation coefficients obtained were significant, but they were in the predicted direction.

In all of these studies there were clear behavioural differences in the animals when audiences were present compared with when they were absent. However, while the direction of causality was not unequivocally established in any of them, a further change in behaviour in the predicted direction that occurred when the audience was asked to crouch (Chamove *et*

al 1988), supported the assumption that visitors caused the changes in behaviour. The results in this experiment were interpreted as evidence that primates find audiences stressful.

Single species studies

A number of studies have looked for visitor effects in single species, rather than across a range of different species. The earliest of these studies appears to be the comparison by Glatston *et al* (1984) of the behaviour of on-show and off-show groups of cotton-topped tamarins, *Saguinus oedipus oedipus*, at Rotterdam Zoo. They found that the animals on display to the public showed significantly less social behaviour than those off display. Exchanging the groups led to changes in both groups' behaviour, with the on-show animals again showing less social behaviour than the off-show animals. Cage design was also a variable; in the on-display animals, those in a small glass-fronted cage showed less amicable behaviour than those in a large mesh cage.

A similar comparison was undertaken by Wormell *et al* (1996) on three groups of pied tamarins, *Saguinus bicolor bicolor*, at the Jersey Wildlife Preservation Trust. One of the groups lived in a cage with a large outside but small inside area (the 'squirrel cage'), and was not only on show to the public but located close to areas of high public density and activity. This group showed more threats, piloerection and approaching than both an off-show group and an on-show group in a cage which was termed 'new style' by the authors (although it is not clear from their description how it differed from the 'squirrel cage'). The average number of threats in the 'squirrel cage' group increased from 1.28 animal^{-1} h^{-1} under no visitor conditions to 7.63 when visitors were present.

Similarly, the average number of approaches increased from 0.14 to 16.4 animal^{-1} h^{-1}. The authors' conclusion was that greater exposure to visitors was stressful to the animals, supporting their impression that some pied tamarins 'treat close approaches to their cages as a threat'. Interestingly, a group of black lion tamarins, *Leontopithecus chrysopygus*, included for comparison showed no threats or piloerection, and appeared a much 'more relaxed' species when visitors were present.

No other New World primate species appear to have been studied from this viewpoint, other than those in the multi-species studies listed above. However, several species of Old World primates have been studied, in a variety of captive contexts. Fa (1989) investigated the behaviour of green monkeys, *Cercopithecus aethiops sabaeus*, at Mexico City Zoo. The animals were housed in an open-topped pit with a rocky island in the middle, so that visitors could look over the wall and watch the monkeys climbing the rocks on the island (John Fa personal communication 1999). He found a significant positive correlation between visitor density and the number of interactions between visitors and animals (characterizing interactions as feeding, touching or throwing objects). As the zoo was closed to the public for 2 days every week, Fa was also able to compare the monkeys' behaviour on visitor and non-visitor days. On visitor days, the monkeys spent more time around enclosure edges where they were fed by visitors; however, there was no difference in the amount of agonistic behaviour shown by the animals on visitor and non-visitor days. Fa (1989) identified similarities between the caged green monkeys and the free-ranging but food-provisioned barbary macaques, *Macaca sylvanus*, on Gibraltar, which also experience heavy human visitor pressure and interact extensively with people, particularly for food. His data showed that the macaque groups subjected to the most severe visitor pressure had the lowest birth rates, which leads one to speculate whether the same might be true for zoo primates. Fa considered the additional feeding by the public to be the main intervening variable between visitor number and birth rate, rather than any stressful effect of visitor presence. In Gibraltar,

the close animal-human interaction in a context of increased food competition is associated with visitor-directed aggression (ie monkeys biting humans), and while this is an unlikely outcome of visitor presence in traditional zoos, it is, as Fa (1992) points out, a possible risk in the current trend among zoos of allowing more primate species to be free-ranging.

Probably the most detailed and extensive series of studies on any species faced with human visitors is that of Mitchell and his co-workers on golden-bellied mangabeys, *Cercocebus galeritus chrysogaster*, at Sacramento Zoo (Mitchell *et al* 1987; 1990; 1991a, b; 1992b, c). The mangabeys were very reactive, often responding with threats to the presence of people (Mitchell *et al* 1987). The presence of several groups of mangabeys at Sacramento Zoo allowed Mitchell *et al* (1990) to determine whether the animals experienced different levels of visitor pressure because of their different cage locations. They found that there were significant differences in visitor attendance at three cages that differed only in their location and the particular mangabeys they contained, and these differences persisted even when animals were moved between cages. If the differences in visitor pressure bring about predictable changes in the behaviours of the monkeys (eg more visitors result in more visitor-directed behaviour), then moving the animals to a different cage should result in corresponding systematic changes in their responses. This was indeed the case (Mitchell *et al* 1991a; 1992b). Moving the group from the medium visitor number (M) cage to the low visitor number (L) cage led not only to decreased visitor-directed aggression in that group, but also increased displays towards neighbours and decreased within-group aggression. The group moved from the L to the M cage showed exactly the reverse changes, with, for example, a doubling of intra-group aggression. However, grooming, sexual behaviour and play increased in both groups, and seemed unaffected by visitor pressure.

In a further series of observations, Mitchell *et al* (1991b; 1992c) discovered age- and sex-related differences in threat behaviour in both the mangabeys and their human audiences. Adult male monkeys threatened more than females – except to other monkeys in neighbouring cages. There were, however, intriguing differences in the frequencies of threats directed at different categories of human. This led the authors to conclude that keepers were treated like familiar conspecifics, observers (ie the experimenters) like familiar neighbours, and visitors like interlopers (Mitchell *et al* 1991b). The mangabeys also differentiated between their targets even within the category 'visitors', such that male monkeys mostly threatened men and female monkeys mostly threatened women. Toddlers and senior citizens were rarely threatened by monkeys of either sex. Similarly, adult male human visitors mostly threatened (harassed) male mangabeys, whereas female visitors harassed both male and female monkeys (Mitchell *et al* 1992c). Once again, Mitchell *et al* interpreted these results as indicating that mangabeys treat humans (and indeed humans treat mangabeys) as interlopers. What is not clear from their data is how much of the threatening in either species was initiated by that species, and how much was a response to the threats of the other.

The behaviour of the human audience, as opposed to its mere presence, is clearly an important variable, but it is one that is difficult to manipulate in the zoo setting. In the laboratory, however, mere presence effects can be investigated. In a study by Clarke and Mason (1988) three species of macaque were subjected to the passive presence of a single observer, who also scored the data. For this experiment, the animals were housed in individual cages in a room with other primates at the California Primate Center, although before the experiments they were housed in groups in outdoor enclosures. A number of behavioural measures were recorded, and then aggregated into two composite scores, 'fear' or 'hostility'. Consistent species differences were found, with crab-eating macaques, *Macaca fascicularis*, showing higher fear scores than hostility ones; rhesus macaques, *M. mulatta*,

showing higher hostility than fear scores; and bonnet macaques, *M. radiata*, showing very low scores for both fear and hostility. These results were consistent with other behavioural and physiological measures which (broadly) allowed crab-eaters to be characterized as reactive and fearful, rhesus as aggressive, and bonnet macaques as affiliative.

Returning to the zoo studies, Nimon and Dalziel (1992) investigated possible interactions between zoo visitors and siamangs, *Hylobates syndactylus*, at Adelaide Zoo. In this study, an 'initiation' constituted any behaviour performed while the two species (human and siamang) were present. There were significant associations between some of the siamang behaviours and the subsequent behaviours of humans, and vice versa. People generally responded with behaviours resembling those of the siamangs: for example, hostile behaviours were responded to with hostile behaviours, and reaching out or staring was followed by people attempting to make physical contact with the animals. Siamang responses to humans, however, were consistent with the explanation that the animals responded to apparently hostile humans as if they were hostile siamangs, but that the mere presence of people did not lead to increases in siamang activity.

Vrancken *et al* (1990) investigated whether the presence of the public influenced the amount of time spent in the cage zone next to the viewing glass by eastern lowland gorillas, *Gorilla gorilla graueri*, at Antwerp Zoo. Four of the five animals were unaffected; the fifth, a young, adult, hand-reared female, spent more time next to the glass when an audience was present. She appeared to seek interactions, particularly eye contact, with the public.

Finally, a detailed study of orangutans, *Pongo pygmaeus*, was carried out by Mather (1999) using three different groups at different zoos (Chester, Jersey Wildlife Preservation Trust and Rotterdam). She found virtually no changes in behaviour that could confidently be ascribed to the presence of an audience, and showed that the levels of behaviour shown by the orangutans was comparable with published data from wild animals. There was an association between visitor presence and animal activity, but when differences between zoos and individuals were taken into account, the most plausible explanation was that visitors were attracted to view active orangutans.

If any conclusion can be drawn from these studies, it is probably that associations between human presence and primate behaviour are themselves influenced by a number of other variables. Species differences are clearly important in this respect, and housing differences may also play a role. It also appears that (some) primates distinguish different categories of people, and respond to them in different ways.

Chimpanzee studies

Because there have been several studies on chimpanzee responses to humans, we can use this species to try to identify situational variables that might affect the responses. The studies have been undertaken in zoos, laboratories and primate centres. Therefore, they differ not just in housing but also in the extent to which the animals are exposed to human contact.

The first study was carried out at a research colony in Texas (Maki *et al* 1987). In this case the visitors were not the public, but visiting scientists and students touring the facility. Aggressive behaviours by the chimpanzees were significantly higher when these unfamiliar people were present. This aggression was directed at both conspecifics and humans but most of the aggression was directed at other group members. When the laboratory records were analysed, it was found that wounding episodes among the chimpanzees were, on average,

more than three times higher on weekdays, when there was more human activity at the colony, than on weekends (Lambeth *et al* 1997).

Laboratory chimpanzees characteristically display vigorously to unfamiliar humans (Rumbaugh 1988), the display being one which, in the field, is interpreted as indicating high arousal and a willingness to fight intruders. Although Rumbaugh's study did not explicitly measure the behavioural change in the chimpanzees, it mentioned that the chimpanzees became calmer and less likely to display if the cage design was altered to prevent some of the more physical aspects of the display, such as shaking the cage.

Given these results from the laboratory colonies, we might expect zoo colonies of chimpanzees to be very dangerous places indeed. At Krefeld Zoo (Germany), Perret *et al* (1995) found that while relatively passive groups of observers had little effect on the behaviour of the chimpanzees, active human groups led to an increase in virtually all categories of chimpanzee behaviour, including not only agonistic and visitor-directed aggressive behaviours, but also affiliative behaviours. The authors considered that these changes might reflect mechanisms by which the animals compensated for the negative, disruptive effects of visitors.

Other studies, however, imply that the relationship between zoo chimpanzees and their human audiences is more complex than this. The study by Cook and Hosey (1995) did not look particularly at intra-group behaviour, but concentrated on what appeared to be audience-directed behaviours by the chimpanzees, and chimpanzee-directed behaviours by the human audience. The chimpanzees constituted a large group (24 individuals) in an open air, moated enclosure at Chester Zoo. A number of interaction sequences were observed, with repeated behaviours directed towards the other member of the dyad within the same human-chimpanzee dyad. Many of the chimpanzee behaviours involved eye-fixation, approach and begging, which often ended with people throwing food to the animal. The data supported an interpretation that both humans and chimpanzees were motivated to interact with one another. However, not all chimpanzees engaged in this interaction, and it is possible that non-interactors were affected differently by audiences, although no data were collected on this.

Unravelling the complexities of chimpanzee-human interaction and the situational variables that influence it has barely begun. Wood (1998) examined the relationship between the number of human visitors and the presence of new or old (one-day-old) enrichment. She found that changes in chimpanzee activity were influenced by the visitor and enrichment variables acting together. Thus, for example, new enrichment and low (weekday) crowds mostly increased foraging and object use, whereas no consistent pattern of crowd influence was apparent on feeding behaviour when the enrichment was new. However, high (weekend) crowds were associated with lowered frequencies of foraging, object use, grooming and play across both enrichment conditions. Public orientation took up a small part of the animals' time, and was mostly composed of watch/idle and food-begging behaviours. Again, there was evidence (from analysis of visitors' spoken comments) that people were motivated to try to interact with the chimpanzees.

On the basis of these studies we might conclude that zoo chimpanzees find human audiences a less stressful, and possibly more rewarding, experience than those housed in laboratories and primate facilities. At any rate, some zoo chimpanzees seem to come to regard human visitors as a source of mild interest or even food. We do not know whether the same is true of other zoo primates.

Discussion

How do we interpret what these different studies are telling us? The earlier studies suggested that human visitors exerted a stressful effect on captive primates. Yet anyone visiting a zoo such as Apenheul in the Netherlands, where some species of primates are allowed to range freely among the human visitors, may gain the impression that some of the animals seek out (and even follow) large crowds of visitors. At the very least, the primates do not avoid or hide from human visitors as would be expected if they were causing stress.

One of the problems is that the papers reviewed here do not, as a rule, adopt a theoretical position or make clear predictions to test an explicit hypothesis. In this section, I will present some explicit hypotheses about how visitor presence and primate behaviour could be linked, and test them against the findings of those papers. The first step is to discriminate between two alternative hypotheses about the direction of causality, accepting the accumulated evidence that there is a demonstrated association between visitor presence and changes in primate behaviour. These hypotheses are:

i) *Visitor effect hypothesis.* For our purposes we can state this as, 'the presence of human audiences causes changes in the behaviour of captive primates'. Although not explicitly stated as a hypothesis, it is the position implicitly adopted in many earlier papers, including Hosey and Druck (1987), Chamove *et al* (1988), Fa (1989) and Mitchell *et al* (1991a; 1992b).

ii) *Visitor attraction hypothesis.* This hypothesis was put forward by Mitchell *et al* (1992a) as a possible alternative explanation for the results of their own and Hosey and Druck's (1987) study. We can state it as, 'changes in the behaviour of caged primates cause crowds to gather'.

The visitor attraction hypothesis is plausible because the behavioural change most often associated with large visitor groups is increased activity and increased aggression by the animals, and there is indeed good evidence that visitors spend more time with and attend more to active animals (Bitgood *et al* 1988; Altman 1998). This hypothesis has not been explicitly tested, but Mather (1999) considered it provided the best explanation for her observations on captive orangutan behaviour.

Discriminating between these hypotheses requires manipulation of the audiences or of the animals' behaviours. In the study by Glatston *et al* (1984) the audiences were manipulated to the extent that tamarin groups were allocated to on-show or off-show conditions. The visitor attraction hypothesis predicts that the behaviours of the on-show and off-show groups would not differ significantly, which was clearly not the case. Similarly, the cage exchange experiments with mangabeys by Mitchell *et al* (1991a; 1992b) showed results counter to this prediction – in this case, when the animals were swapped between cages of different attendance pressure. It could be argued that the physical translocation of the animals led to changes in their behaviour, making them more attractive to visitors, but such effects would have influenced all groups equally, and the prediction would still stand. Finally, in one of the experiments described in Chamove *et al* (1988), the audience was made to look smaller. The result was a change in the behaviour of the animals, but the visitor attraction hypothesis would have predicted no change.

Clearly the evidence supports the visitor effect hypothesis. Having said that, it is probably the case that the visitor attraction hypothesis is also true sometimes – as the two are not mutually exclusive – but it cannot account for most of the observed effects. The next step, is to formulate different variants of the visitor effect hypothesis, and test each against the literature. We shall do that by considering three alternative hypotheses.

Hypothesis 1: The visitor effect is one of simple social facilitation

This has not been suggested anywhere in the literature, but should be considered as possibly the simplest kind of social influence on behaviour. Social facilitation refers to changes in the performance of a behaviour caused by the mere presence of an observer (Atkinson *et al* 1996). (This is often referred to as the 'audience effect', but social facilitation also includes 'coaction effects', which are to do with performance increments when undertaking a task with others.) The changes, demonstrable in humans and a variety of other animals, are generally increments in performance (ie facilitation) of simple, highly practised or instinctive responses, and impairment in performance of complex or newly learned responses (Zajonc 1965). In captive primates these changes should be measurable as increases or decreases in the frequencies or durations of behaviours. Strictly, 'mere presence' should mean literally that, with no attempt at interaction by the audience. However, in the two studies I have found where non-human primates have been experimentally put in this condition (and with a human rather than conspecific observer), data were not collected for the 'no observer' condition, and, therefore, *changes* in behaviour could not be inferred (Thomsen 1974; Clarke & Mason 1988). In the zoo, of course, the audience is more than a 'mere presence', and can be noisy, distracting and interactive. Nevertheless, we can test whether the observed audience effects could be due merely to social facilitation.

A problem here is to identify, a priori, which behaviours are simple and which complex, and, therefore, to make predictions about which should increase and which should decrease. In the study by Perret *et al* (1995), for instance, the chimpanzee behaviours which increased under audience conditions were affiliation, mother-child contact, displacement behaviour, locomotion, agonistic behaviour and visitor-directed aggression. However, play behaviour decreased, and there is no obvious reason why play should be regarded as a more 'difficult' behaviour than the others. Similarly, in the three species studied by Chamove *et al* (1988), agonistic behaviour and activity increased, while grooming and affiliative behaviour decreased. Not only would this result be difficult to predict, but it would also imply that affiliation has a different behavioural status in chimpanzees than in monkeys and lemurs. One prediction that can be made, however, is that at least the direction of behavioural change should be the same under all audience conditions, regardless of audience size; furthermore, no correlation is usually posited between size of audience and extent of social facilitation. At least one experiment, where mangabeys were moved between cages experiencing different audience pressures (Mitchell *et al* 1991a; 1992b), does not support these predictions.

We can conclude that social facilitation effects cannot explain the pattern of responses of non-human primates to human observers. Without further studies it is unclear whether the presence of humans has any general facilitatory effect on primate behaviour.

Hypothesis 2: Visitors are a stressful influence on behaviour

Some of the earliest studies (eg Glatston *et al* [1984]; Chamove *et al* [1988]) interpreted visitor presence as stressful to captive primates, and this is probably now generally felt to be true. However, no studies have made predictions about what specific effect such a stressful influence should have, but have inferred stress from the observed pattern of behaviour. Nevertheless, one prediction might be that all species of primates should show broadly the same response. An increase in agonistic behaviours and a decrease in affiliative ones is often seen as consistent with this interpretation, and indeed this was what was found by Chamove *et al* (1988). As we have seen, however, this pattern is not found in all studies. For example, Perret *et al* (1995) found increases in affiliative as well as agonistic behaviours in their chimpanzees, as did Mitchell *et al* (1991a; 1992b) in some of their translocated mangabeys.

Perhaps specific behavioural changes can be predicted. For example, Broom and Johnson (1993) identify some short-term (orientation, startle, reflex responses) and long-term (increase in aggression, stereotypies, apathy and unresponsiveness) behavioural indicators of poor welfare. The short-term measures listed above are not commonly used in audience studies, although one of the experiments in Chamove *et al* (1988) demonstrated an increase in glancing (visual orientation) at the audience by mandrills as audience size increased. However, as Broom and Johnson (1993) point out, these measures alone do not necessarily mean that the animal is encountering a problem. Thus, for instance, Perret *et al* (1995) interpreted the behavioural change seen in their chimpanzees as the result of 'stressful excitement' caused by the visitors, but also regarded the pattern of change as indicating behavioural mechanisms adopted by the chimpanzees to compensate for this effect.

Of course, visitor presence is a long-term variable, and we might expect changes in the animals' responsiveness to visitors through long-term failure to cope (eg an increase in stereotypies) or through long-term habituation (eg a decrease in the extent to which agonistic behaviours increase under visitor conditions). Unfortunately, no such longitudinal studies have been performed. An alternative way of approaching this question might be to compare chronically exposed animals (ie in a zoo) with acutely exposed animals (eg in a laboratory or primate centre). If exposure to human audiences is stressful, then we might predict that the zoo animals would show different baseline measures of some of these behaviours (eg higher rates of agonism) than the laboratory animals. Furthermore, we might also predict that the responses of the acutely exposed animals to the infrequent visitors would be quantitatively greater than the responses of the chronically exposed animals to sustained high levels of visitor pressure. Again, such studies have yet to be performed. In the case of chimpanzees, where several studies in laboratories and zoos are available, the quantitative data presented do not permit comparison between conditions. However, studies such as those of Cook and Hosey (1995) and Wood (1998) imply that the chimpanzees' responses to humans in zoos are at least milder, and maybe qualitatively different, from those in laboratories.

Perhaps the most appropriate conclusion here is that the studies are largely consistent with the interpretation that at least *some* stressful effects are brought about by the presence of audiences, but that it is not a simple case of increasing aggression and decreasing affiliation. In other words, other variables are also at work, and these mediate the form of the response. Candidates for these variables include species temperament, the animals' perceptions of categories of human visitor, and differences in housing.

Effects of species temperament

The concept of a 'species temperament' is not one that has received any great treatment in the literature, but is familiar at an anecdotal level to many people who work with primates. Several of the authors reviewed here comment on what their species is like, although without necessarily using the term 'temperament'. For instance, Mitchell *et al* (1990) characterized the golden-bellied mangabeys as 'emotionally volatile', and elsewhere (Mitchell *et al* 1991b) as 'aggressive and irascible'. Wormell *et al* (1996) considered black lion tamarins to be 'a much more relaxed species with visitors present' than pied tamarins. The concept, applied to primates, is based upon observed behavioural dispositions across a range of situations (Clarke & Mason 1988). The differences in responses to an observer that Clarke and Mason (1988) found in three macaque species were consistent with the 'species temperaments' of these three species as judged using other behavioural and physiological criteria. Although we are a long way from characterizing different primate species in this way, there is a good deal of anecdotal evidence available among primate researchers and keepers which, if collected,

could help us make judgements about how particular species might respond to human visitors, and indeed to other variables of captivity.

Animals' perceptions of categories of human visitors

The notion that zoo animals might perceive and, therefore, categorize human visitors in different ways dates back at least to Hediger (1970). There is good evidence in the papers reviewed here that some primates do indeed discriminate between different categories of visitor. The clearest evidence of this comes from Mitchell *et al* (1991b), where keepers (familiar humans), observers (less familiar) and zoo visitors (unfamiliar) were treated in different ways by the golden-bellied mangabeys: as if they were, respectively, familiar conspecifics, familiar neighbours and interlopers. Although their readiness to threaten humans is perhaps related to their 'emotionally volatile' nature, the circumstances and forms of threat are probably more consistent with the ecological and behavioural characteristics of this species in the wild: such as being, 'robust, sexually dimorphic, semiterrestrial...in troops of 13–36 with one or more males, peripheral males, and solitaries' (Mitchell *et al* 1987).

Similarly, Chamove *et al* (1988), in attempting to identify a rationale for the species differences they observed, suggested that small, arboreal primates might be most affected by human visitors. There was some support for this hypothesis from experimentally reducing the height of the audience, and from performing cross-species correlations of behavioural change against body weight (none of which were significant, but which were in the predicted direction). One reason small, arboreal primates might be more affected, is that they may perceive humans as potential predators. Small species are anyway perhaps more likely to be fearful of humans than large ones, and this would result in different behavioural responses. We might predict that these responses would be avoidance and defensive threat in small species and offensive threat in large ones (perhaps accompanied by increased intra-group agonism).

Further studies on individual species would help us to test these predictions. The species which have so far been considered do seem to support this approach. Orangutans, for instance, which are large, semi-solitary species that occasionally aggregate, are largely unaffected by human visitors (Mather 1999); chimpanzees, which are large and live in multi-male:multi-female groups, appear to respond to unfamiliar humans with heightened aggression (Perret *et al* 1995; Lambeth *et al* 1997), but may also come to see humans as almost an enrichment (Cook & Hosey 1995). It also helps explain why the activity of the audience has a more profound effect than its size or mere presence (Hosey & Druck 1987; Mitchell *et al* 1992a). Audience activity is often harassment, which the animals perhaps perceive as threat.

Housing effects

Although housing variables may influence behaviour directly, there is evidence that they also interact with the visitor effect. This may be an effect on visitor density due to cage location (Mitchell *et al* 1990), or there may be features of cage design which enhance the animals' perception of harassment. For example, cotton-topped tamarins in small, glass-fronted cages showed more agonistic and less amicable behaviours than those in large, mesh cages (Glatston *et al* 1984). The studies by Hosey and Druck (1987), Chamove *et al* (1988) and Mitchell *et al* (1992a) all involved some species housed in glass-fronted cages. It is possible that the stressful effects of human audiences are less for animals in cages where the barrier between them and the visitors is more obvious; perhaps larger, more naturalistic cages produce a more naturalistic profile of behaviour which is more resistant to disruptions from

visitor presence. More importantly, some cages are designed in such a way that the animals cannot easily escape from public exposure. Where the animals are free-ranging they usually also have the ability to choose the extent of their contact with the public. Modern naturalistic cages usually also confer that choice. The point is, that the control should rest with the animal rather than the visitors. More research is needed to compare audience responses of species under different housing conditions.

Hypothesis 3: Visitors are an enrichment

Not all the responses captive primates show to the presence of visitors can be interpreted simply as a response to a stressor. The green monkeys observed by Fa (1989) were not stressed by visitors if agonism is a measure, because there was no difference in agonistic behaviours on days when visitor were present and non-visitor days. However, changes in the monkeys' behaviour occurred because the animals changed their activity budgets and dispersion in the enclosure to take advantage of food thrown in by the visitors. From the animals' point of view this might have been enriching, but as Fa points out, with reference to the visitor-fed Gibraltarian macaques, the effect of this was an increase in food-directed behaviours at the expense of other (eg social) behaviours. The long-term consequence on Gibraltar was a decline in the macaques' birth rate, which may, of course, also have been indicative of underlying poor welfare. Fa suggests the same might be true of the zoo-housed green monkeys.

Similarly, Cook and Hosey (1995) found sequences of interactions between chimpanzees and humans that could be initiated by either species; the main motivation of the chimpanzees to do this appeared to be to obtain food. Feeding of animals by the public was not permitted in this zoo or the one where Fa (1989) worked, but occurred nevertheless. This effect is just as disruptive of behaviour as the stressful response, and probably has different welfare implications – nutritional rather than behavioural. Whether it could be tolerated as a means of enriching the experience of zoo visitors (and perhaps the animals as well) is a question that has not been researched, and neither has the related question of whether allowing visitors to feed the animals reduces their likelihood of teasing them, and thus instigating more stressful responses.

Clearly, these two studies alone are not sufficient to support a general hypothesis that human audiences are enriching, but they do imply that, under some circumstances, visitor presence is not necessarily stressful.

Conclusions

This review has identified a number of places where research is lacking, and a number of questions whose answers could help us to reach firm conclusions. Nevertheless, from the studies included here we can draw the following conclusions:

i) The passive, mere presence of human observers, while unsettling to laboratory primates, does not generally produce significant behavioural changes in zoo primates.

ii) The presence of active human observers, ie people who try to interact with the animals, is likely to produce behavioural changes in captive primates:
   a) If these attempted interactions are aggressive or teasing they may promote returned threats, avoidance and sometimes changes in intra-group interactions; the evidence is that these encounters with humans are stressful to the animals.

b) If the attempted interactions are more benign and even involve food, it is possible that the animals would learn to respond to all such interactions as if the result will be that they are given food; such encounters with humans do not appear to be stressful to the animals.

iii) The precise way in which a group of primates responds to visitor presence within these general trends may be influenced by their housing and differ between species.

This last conclusion may seem to open up the prospect that every species in every cage needs to be assessed to see how and why they are affected, but this is not the case. In principle, testable predictions can be derived for each of these variables, based on: i) known differences in social organization (eg that large-bodied, hierarchically organized species are more likely to respond with threats and approach the audience, small bodied arboreal species are more likely to avoid the audience, and solitary species are unlikely to show any change in behaviour); ii) differences in species temperament (for which we still need basic data); and iii) observed housing differences (eg the suggestion that more obvious barriers reduce the stressful effect; perhaps giving the choice to the animal as to whether it is exposed to humans or not might change the effect). General principles seem to be emerging, and further research should test these. Then, of course, there are the non-primates...

Animal welfare implications

While it is difficult to prevent people harassing and feeding zoo primates, zoos must endeavour to reduce any stressful consequences for the animals. However, opportunities for people to interact with the animals should not necessarily be discouraged, since such interactions may be important in maintaining feelings of interest and concern for the animals by the public. It is also possible that brief threatening events are beneficial to captive primates (Moodie & Chamove 1990).

The key to reconciling these apparently conflicting considerations is perhaps related to the amount of control that the animals have over their exposure to humans. Modern naturalistic cages allow animals to move away from direct public exposure; thus, we could predict that visitor effects, and particularly stressful ones, would be less in a large enclosure where animals can comfortably spend time out of public view. We could also predict that visitor effects would be lower among primates kept in moated enclosures than among those in wire- or glass-fronted enclosures, because the moat is a more obvious barrier that keeps the public at a further distance. These predictions have yet to be tested; when they are, the results may indicate that the effects of the visiting public on captive primates need not constitute a welfare problem in the modern zoo.

References

Altman J D 1998 Animal activity and visitor learning at the zoo. *Anthrozoos 11:* 12-21

Atkinson R L, Atkinson R C, Smith E E, Bem D J and Nolen-Hoeksema S 1996 *Hilgard's Introduction to Psychology.* Harcourt Brace: Fort Worth, USA

Bitgood S, Patterson D and Benefield A 1988 Exhibit design and visitor behaviour: empirical relationships. *Environment and Behaviour 20:* 474-491

Broom D M and Johnson K G 1993 *Stress and Animal Welfare.* Chapman & Hall: London, UK

Chamove A S, Hosey G R and Schaetzel P 1988 Visitors excite primates in zoos. *Zoo Biology 7:* 359-369

Clarke A S and Mason W A 1988 Differences among three macaque species in responsiveness to an observer. *International Journal of Primatology 9:* 347-364

Cook S and Hosey G R 1995 Interaction sequences between chimpanzees and human visitors at the zoo. *Zoo Biology 14:* 431-440

Fa J E 1989 Influence of people on the behavior of display primates. In: Segal E F (ed) *Housing, Care and Psychological Well-being of Captive and Laboratory Primates* pp 270-290. Noyes Publications: Park Ridge, USA

Fa J E 1992 Visitor-directed aggression among the Gibraltar macaques. *Zoo Biology 11:* 43-52

Finlay T, James L R and Maple T L 1988 People's perception of animals: the influence of zoo environment. *Environment and Behavior 20:* 508-528

Glatston A R, Geilvoet-Soeteman E, Hora-Pecek E and Van Hooff J A R A M 1984 The influence of the zoo environment on social behavior of groups of cotton-topped tamarins, *Saguinus oedipus oedipus. Zoo Biology 3:* 241-253

Hediger H 1970 *Man and Animal in the Zoo.* Routledge & Kegan Paul: London, UK

Hosey G R 1997 Behavioural research in zoos: academic perspectives. *Applied Animal Behaviour Science 51:* 199-207

Hosey G R and Druck P L 1987 The influence of zoo visitors on the behaviour of captive primates. *Applied Animal Behaviour Science 18:* 19-29

Kidd A H, Kidd R M and Zasloff R L 1995 Developmental factors in positive attitudes toward zoo animals. *Psychological Reports 76:* 71-81

Kreger M D and Mench J A 1995 Visitor-animal interactions at the zoo. *Anthrozoos 8:* 143-158

Lambeth S P, Bloomsmith M A and Alford P L 1997 Effects of human activity on chimpanzee wounding. *Zoo Biology 16:* 327-333

Maki S, Alford P L and Bramblett C 1987 The effects of unfamiliar humans on aggression in captive chimpanzee groups. *American Journal of Primatology 12:* 358 (Abstract)

Mather L 1999 *Response of Captive Orang Utans to Human Audiences.* Unpublished MPhil thesis, University of Manchester (Bolton Institute), Bolton, UK

Mitchell G, Herring F and Obradovich S 1992c Like threaten like in mangabeys and people? *Anthrozoos 5:* 106-112

Mitchell G, Herring F, Obradovich S, Tromborg C, Dowd B, Neville L E and Field L 1991a Effects of visitors and cage changes on the behaviors of mangabeys. *Zoo Biology 10:* 417-423

Mitchell G, Herring F, Tromborg C, Dowd B, Steiner S and Obradovich S 1992b Targets of aggressive facial displays by golden-bellied mangabeys (*Cercocebus galeritus chrysogaster*) at the Sacramento Zoo. *Applied Animal Behaviour Science 33:* 249-259

Mitchell G, Obradovich S D, Herring F H, Dowd B and Tromborg C 1991b Threats to observers, keepers, visitors, and others by zoo mangabeys (*Cercocebus galeritus chrysogaster*). *Primates 32:* 515-522

Mitchell G, Obradovich S, Sumner D, De Morris K, Lofton L, Minor J, Cotton L and Foster T 1990 Cage location effects on visitor attendance at three Sacramento Zoo mangabey enclosures. *Zoo Biology 9:* 55-63

Mitchell G, Soteriou S, Towers S, Kenney L and Schumer C 1987 Descriptive accounts of the behavior of breeding and nonbreeding pairs of golden-bellied mangabeys (*Cercocebus galeritus chrysogaster*). *Zoo Biology 6:* 391-399

Mitchell G, Tromborg C T, Kaufman J, Bargabus S, Simoni R and Geissler V 1992a More on the 'influence' of zoo visitors on the behaviour of captive primates. *Applied Animal Behaviour Science 35:* 189-198

Moodie E M and Chamove A S 1990 Brief threatening events beneficial for captive tamarins? *Zoo Biology 9:* 275-286

Morris D 1964 The response of animals to a restricted environment. *Symposia of the Zoological Society of London 13:* 99-118

Nimon A J and Dalziel F R 1992 Cross-species interaction and communication: a study method applied to captive siamang (*Hylobates syndactylus*) and long-billed corella (*Cacatua tenuirostris*) contacts with humans. *Applied Animal Behaviour Science 33:* 261-272

O'Donovan D, Hindle J E, McKeown S and O'Donovan S 1993 Effect of visitors on the behaviour of female cheetahs *Acinonyx jubatus*. *International Zoo Yearbook 32:* 238-244

Perret K, Preuschoft H and Preuschoft S 1995 Einfluss von Zoobesuchern auf das verhalten von Schimpansen (*Pan troglodytes*). *Der Zoologische Garten N F 65:* 314-322

Reade L S and Waran N K 1996 The modern zoo: how do people perceive zoo animals? *Applied Animal Behaviour Science 47:* 109-118

Rumbaugh D M 1988 Cage design attenuates display patterns of male chimpanzees. *Zoo Biology 7:* 177 – 180

Snyder R L 1975 Behavioral stress in captive animals. In: *Research in Zoos and Aquariums* pp 41-76. National Academy of Sciences: Washington, DC, USA

Thompson V D 1989 Behavioral response of 12 ungulate species in captivity to the presence of humans. *Zoo Biology 8:* 275-297

Thomsen C E 1974 Eye contact by non-human primates toward a human observer. *Animal Behaviour 22:* 144-149

Vrancken A, Van Elsacker L and Verheyen R F 1990 Preliminary study on the influence of the visiting public on the spatial distribution in captive eastern lowland gorillas (*Gorilla gorilla graueri* Matschie, 1914). *Acta Zoologica et Pathologica Antverpiensia 81:* 9-15

Wood W 1998 Interactions among environmental enrichment, viewing crowds, and zoo chimpanzees (*Pan troglodytes*). *Zoo Biology 17:* 211-230

Wormell D, Brayshaw M, Price E and Herron S 1996 Pied tamarins *Saguinus bicolor bicolor* at the Jersey Wildlife Preservation Trust: management, behaviour and reproduction. *Dodo Journal of the Wildlife Preservation Trusts 32:* 76-97

Zajonc R B 1965 Social facilitation. *Science 149:* 269-274