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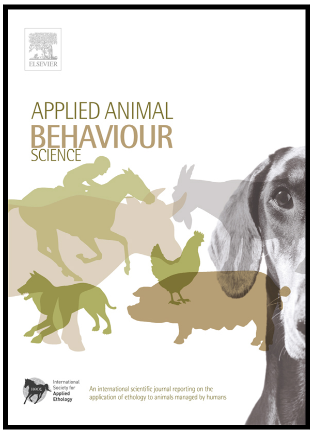

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The Effect of Visitors on the Behaviour of Zoo-Housed Primates: a test of four hypotheses

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Abstract

The effects of human visitors on the behaviour and welfare of zoo-housed primates have been extensively studied, and we know more about these effects in primates than in any other taxon. Nevertheless, it has proved difficult to detect an overall pattern in the responses of primates to visitors, as the presence of people can be stressful to the animals, but in some circumstances can be enriching, and in other circumstances the animals appear to be largely unaffected. Several potential causal factors have been suggested, namely that variability is due to species-specific differences, differences in visitor characteristics and behaviour, differences in housing and husbandry, or differences in individual characteristics of the animals, and these can be treated as four hypotheses to account for this variability in response. Here we test these four hypotheses using published data. A significant association was found between animal response and ecological category, such that small arboreal primates were most likely to be affected negatively. Visitor characteristics showed a significant association with animal response with noisy visitors having the most stressful effect.

There was no significant effect of enclosure size or group size, though there was a significant association with enclosure type, such that animals in walk-through and semi-free range enclosures were more likely to show positive responses, though the small number of examples of these suggests treating this result with caution. Finally, individual differences were tested with gorillas, where there were sufficient data to look at individuals rather than animal groups. There was no significant effect of age or sex, but regression using all of the potential causal variables produced a significant model in which no individual predictor was significant, suggesting that it is the combination of predictors which influences the form of the response.

Keywords:

animal welfare, human-animal interactions, primate, visitor effect, zoo animals

1. Introduction

We have known for a number of decades that the presence of the public is associated with changes in the behaviour of zoo-housed primates (the visitor effect), and that these changes appear to suggest that the welfare of the primates is often, though not always, adversely affected (Hosey 2000, Davey 2007, Hosey 2017, Ward & Sherwen 2019, Sherwen & Hemsworth 2019, Edes et al. 2023). Zoo visitors are essential to the achievement by zoos of their conservation missions (Fernandez et al. 2010, Ward & Sherwen 2019), not only because of the funding they provide through donations and entry fees, but also because raised conservation awareness and knowledge of the public is fundamental to the way conservation organisations work (Moss & Esson 2010, Sherwen & Hemsworth 2019). For example, zoos can play a significant role in motivating pro-environmental behaviours in the visiting public (Grajal et al 2016). We also know that zoo visitors prefer to see active animals (Bitgood et al. 1988, Altman 1998) and they perceive animals as unhappy or experiencing poor care if they see behaviours such as pacing (Godinez et al. 2013, Miller

2012). This potentially creates a conflict between the needs of the visitors and the needs of the animals, and it is therefore important that we understand the visitor effect and exactly what causes it, as a necessary step towards resolving this conflict (Carr 2016).

One of the earliest studies, at Rotterdam Zoo, showed that cotton-top tamarins *Saguinus oedipus* held in enclosures with public access showed significantly less social behaviour than those held off-show (Glatston et al. 1984). An early study observing primates with large or small groups of visitors at Chester Zoo showed apparently negative responses across a range of primate species (Hosey & Druck 1987), and a subsequent replication of this at Sacramento Zoo (Mitchell et al. 1992a), using a different range of species, confirmed the presence of this effect. These early studies were correlational, and Mitchell et al (1992a) pointed out that an alternative explanation could hold true, that visitors did not cause the changes in behaviour, but were attracted to enclosures where animals were displaying these behaviours, presumably for some other reason. In another study with golden-bellied mangabeys *Cercocebus chrysogaster* Mitchell et al. (1991) established, by translocating animals from high-visitor visitation enclosures to low-visitation enclosures and vice versa, that visitors were indeed causing the changes. Since then, many more studies have been undertaken on a variety of primate taxa, and indeed on several non-primate taxa. Some of these involve a manipulation of some sort, such as asking visitors to change behaviour (Birke 2002, Chamove et al. 1988, Sherwen et al. 2014), moving animals to new enclosures (Ross et al. 2011), using a barrier to regulate visitor proximity (Chiew et al. 2019), or using screening to alter the visibility of visitors and animals to each other (Blaney & Wells 2004, Sherwen et al. 2015). Furthermore, in many studies physiological measures have been used (Amrein et al. 2014, Davis et al. 2005), or the behavioural changes measured are ones that would be unlikely to draw visitor attention, such as scratching or vigilance (Amrein et al.. 2014, Carder & Semple 2008, Lewis et al. 2020). Consequently, there now seems little doubt that zoo visitors can cause behavioural changes in a range of primate and other species.

Interpreting these changes, however, has proven difficult, as they show considerable variability and lack of consistency, not only in primates but also in other taxa that have been studied (Hosey 2017, Rose et al. 2020, Sherwen & Hemsworth 2019). Thus, although the majority of studies appear to show a negative influence of visitors on animal behaviour, some animals conversely show apparent attraction towards visitors (Cook & Hosey 1995, Fa 1989, Polgár et al. 2017, Williams et al. 2022), and others don't show any obvious response at all (Bonnie et al. 2016, Collins et al. 2017, Kuhar 2008, Sha et al. 2012). That these effects, or lack of effects, may be shown by different animals within the same enclosure (eg Carder & Semple 2008, Vrancken et al. 1990), and may or may not occur in the same species in different studies (eg Lewis et al. 2020, Miller et al. 2021), suggests that a range of other variables, other than just mere presence of visitors, may influence this response. An early study (Chamove et al. 1988) suggested that small-bodied arboreal primates may perceive humans as more of a threat, and would thus be more susceptible to negative responses to visitors. Other possible variables which have been suggested, in addition to this ecological variable, are the behaviour and other characteristics of the visitors, differences in housing and husbandry, and individual differences between the animals (Hosey 2017, Sherwen & Hemsworth 2019), and possibly also the quality of relationship the animals have with their caretakers (Hosey 2017).

These possible influences on the visitor effect have not, however, been systematically tested against the results of different studies. Primates is the taxon that has been most studied with respect to visitor effects, and sufficient studies are now available to attempt such a test, and that is what we do in this paper. There are insufficient data to examine the role of primate-caretaker relationships in modulating the visitor effect, though there are one or two studies which suggest that good relationships can help ameliorate negative responses to visitors (Carrasco et al. 2009, Smith 2014), although some results are more ambiguous (Chelluri et al. 2013). Therefore, we do not consider this any further here. The remaining four suggested variables we treat as hypotheses to account for the observed variability in the visitor effect across published studies. In each case the hypotheses derive from a subset of papers which often have contradictory results, so we make no predictions about the direction in which these variables will affect primate responses to visitors:

Hypothesis 1: Species-specific differences: Although differences among species should probably be expected, it is not always easy to provide a rationale for what those should be. For example, we might consider that as powerful large-bodied primates, great apes might see visitors as less of a threat and consequently not be adversely affected; contrarily, however, great apes share many behavioural signals with us, not to mention general body form, and so may be more threatened by our presence and possible inadvertently hostile signals. Chamove et al. (1988) suggested that small-bodied arboreal primates might show a more negative response to visitors, especially if they were housed in enclosures where they could not move to be above visitor level. This was supported by their experiment in which they asked visitors to crouch, reducing their apparent size at the viewing window, which resulted in a weaker negative response by the primates. However, two related species of small-bodied arboreal callitrichids, *Saguinus bicolor* and *Leontopithecus chrysopygus*, showed opposite responses to visitors at Jersey Zoo (Wormell et al. 1996).

Hypothesis 2: Behaviour and characteristics of visitors: In laboratory studies, primates respond to the mere presence of unfamiliar people (Clarke & Mason 1988, Thomsen 1974), but we might expect zoo-housed primates to undergo some degree of habituation to unfamiliar people, given the extent of visitor exposure they experience. The study by Hosey & Druck (1987) showed that the primates showed a more negative response to visitors when visitor crowds were large and active rather than small and passive, perhaps suggesting some habituation to mere presence of people, but not when they are active or when there are lots of them. In that paper active crowds were defined in terms of attempted interaction with the animals, but again, interpreting that can be difficult as some interactions, for example proffering food (Jones et al. 2016, Choo et al. 2011), may be positive for the animals, whereas others, such as teasing (Mallapur et al. 2005, Mitchell et al. 1992b), are negative. Noise has also been identified as a notable stressor (Birke 2002, Quadros et al. 2014), and is probably related to both size and activity of visitor groups.

Hypothesis 3: Differences in housing and husbandry: Husbandry is such an integral feature of the welfare of captive animals that it would be surprising if it had no influence on the visitor effect, but once again it is difficult to predict in which direction that influence will be. Large naturalistic enclosures, for example, conceivably contain more opportunities for animals to avoid visitors or even hide themselves, so we might expect a less stressful effect of visitors. However, it might equally be the case that animals in these circumstances are less habituated to people, and therefore experience a more stressful response. Transferring chimpanzees *Pan troglodytes* and gorillas *Gorilla gorilla* at Lincoln Park Zoo in Chicago from indoor hardscape-type exhibits to outdoor naturalistic enclosures resulted in less visual monitoring of visitors in both species (Ross et al. 2011), supporting the first of those possibilities. Housing and husbandry can also change visitor behaviour, which can in turn influence animal behaviour (Chiew et al 2020).

Hypothesis 4: Individual differences between the animals: The fact that different individuals within the same enclosure can show quite different responses to visitors suggests that individual variables modulate the visitor effect. In a group of 12 gorillas at Port Lympne Zoo, for example, only two animals showed a positive correlation between self-scratching and visitor numbers, and four different animals showed a correlation with visual monitoring, and yet pooled data for the group showed a significant negative visitor effect (Carder & Semple 2008). A study of 18 gorillas in four social groups at Zoo Atlanta revealed that two of the groups showed more and two showed fewer undesirable behaviours when visitors were present (Stoinski et al. 2012). Boyle et al (2020) found that differences between individuals were important in producing visitor responses across 16 different species of mammals and fish. A number of individual variables could be implicated in these different responses, including age, sex, social status and personality, but unfortunately some of these are not routinely reported in studies, largely because they are not known, so testing this is more of a challenge.

It is important to tease apart these different variables and how they modulate the response of captive primates to visitors, not only because it increases our understanding of the visitor effect, but also because it potentially offers a means of predicting which species, which groups and which individuals are most likely to be affected, and whether that effect will be positive or negative. Different ways of reducing the negative effects of visitors on primates have been suggested, such as the use of visual barriers (Blaney & Wells 2004, Bloomfield et al. 2015) or signage (Dancer & Burn 2019), and clearly it would be beneficial to be able to anticipate which animals would most benefit from these measures. In this paper we attempt to test the four influential variables discussed above, using data gained from published primate visitor effect studies, in a first step towards achieving that understanding.

Finally, it has been suggested (Hosey 2017, Goodenough et al. 2019, Edes et al. 2023) that the negative effects of visitors may not be as great as earlier papers have led us to believe, or even that there has been an increase recently in studies which report no effect or a positive effect, and this can also be tested in our database.

2. Methods

2.1 Database

We have systematically collected publications on visitor effects since 1984, using *Proquest*, *Biological Abstracts*, and *Animal Behaviour Abstracts*, as well as the individual journals and contacts with authors to find them. A final search was made in February 2023, using *Google Scholar* and different journal websites to ensure we had captured all relevant publications. Information (explained below) was retrieved from each publication and used to make up a database in Microsoft Excel. Most studies gave results for a study group, with data for all individuals pooled, so groups were used in our database, even when not all animals in the group had been studied. Some studies contained results for more than one group, so these were entered as separate studies. Thus 'study' here refers to results from a group of primates, not to a publication. This database was used to test the first three hypotheses (species-specific, housing/husbandry and visitor variables). In the case of the gorilla, where there were more studies than for any other single species, several studies gave results for the individuals in the group, so a separate database was made up from these. This database was used to test the third (enclosure-related variables) and fourth (individual differences) hypotheses together.

2.2 Response variables

A great variety of variables has been used to measure primate responses to visitors, ranging from changes in different behaviours to use of different enclosure zones and estimates of glucocorticoid levels, making it impossible to have a single quantitative measure of response across all the studies. Here we categorise primate responses as 'positive' (typically including changes such as increases in social behaviour, increases in positive interaction with visitors, such as curious inspection, or increased proximity to viewing areas), 'unaffected' (where there is no change), or 'negative' (typically including changes such as increases in aggression, threatening visitors, self-directed behaviours or vigilance, or increases in excreted glucocorticoid metabolites), using the conclusions reached by the authors within their publication as a guide.

2.3 Species-specific variables

Different species were categorised as 'small' if they typically had a body weight of <3kg, medium if they were 3-12kg, and large if they were >12kg. They were further categorised as 'arboreal' or 'terrestrial', using categorisations provided in Mittermeier et al. (2013), but with their categories 'semiterrestrial' and 'terrestrial' combined. This source also provided the body weights used. This gave us six ecological categories: small arboreal, small terrestrial, medium arboreal, medium terrestrial, large arboreal, and large terrestrial.

2.4 Visitor interaction variables

Again, the range of measures used in different studies is great, and includes visitor group size, density, presence, activity and noisiness, proportion of viewing area covered, number of people in the zoo (i.e. gate numbers), and sometimes combinations of several of these. We have categorised these in four groups, in an assumed ascending order of intrusiveness upon the primates: 'presence', 'number', 'activity' and 'noisiness'. In cases where the primates respond to one but not other measures in the same study, we have taken the highest of these four categories that the primates responded to.

2.5 Housing variables

We have taken two measures of housing which can most accurately be compared between studies: size in m^2, and enclosure type. Size is often not reported, so there are missing data in the database for some studies. Descriptions of enclosure type are very variable, so we have categorised them as 'indoor', 'outdoor', 'indoor and outdoor', 'semi-free range', 'walk through' or 'unknown' according to the information provided in the papers and the authors' knowledge of the zoos and enclosures. Semi-free range included housing where animals were free to roam throughout much of the zoo, and not restricted by enclosure barriers i.e. the ring-tailed lemurs housed at Fota Wildlife Park, Cork, Ireland. By contrast walk-throughs included enclosures which were expansive and enabled animals to roam, within a boundary usually restricted to one or few species i.e. the lemur wood enclosure at Wild Planet Project, Paignton, UK. We have also taken the number of primates in the group ('group size') as an additional housing variable, as this is a fairly consistently reported measure, though once again this information is not always given by authors.

2.6 Individual primate characteristics – gorilla database only

Age and sex are the only individual primate variables which are normally given by authors, so we have used these when available. Again, they are sometimes not given, so again there are missing data for these variables.

2.7 Year of study

Studies were categorised into half decade categories (1985-89, 1990-94 etc), and the proportion of studies shown in each half decade calculated.

2.8 Statistical analysis

Neither of the two continuous independent variables (enclosure size and group size) was normally distributed, and the other independent variables were all categorical, so non-parametric tests were used. Associations between the response variables and categorical independent variables were carried out using χ^2 tests of association. Differences between response variables for the continuous independent variables were undertaken with Kruskal Wallis tests for independent samples. The gorilla data were analysed with regression to determine whether any of the independent variables predicted the response variable. The proportion of studies showing a negative response was correlated against the half decade in which the study was done using Spearman's rank correlation coefficient. Analyses were undertaken with SPSS version 27.

3. Results

3.1 Database

Seventy-nine publications were found, but five of these were excluded because they were reviews, and a further four were excluded because they were concerned with indirect effects of visitor presence. Of the remainder, 13 were excluded because they contained data pooled for several species, or because they used animals which had already been studied in a previous paper. This left a database of 106 groups, using information and data from 57 different publications, with several publications containing results from more than one group. This was used for testing hypotheses 1-3. A second database for the Western lowland gorilla *Gorilla gorilla gorilla*, represented the responses to visitors of 30 individual primates, using data gained from seven different studies, and was used to test hypothesis 4. All of the species included in the database, together with their allocation to an ecological category, and the publications from which data were obtained, are listed in Table 1.

3.2 Hypothesis 1: Species-specific differences

The database contains studies on 44 different primate species belonging to ten families. The distribution of groups showing the positive, neutral and negative response to visitors by the families is shown in Figure 1. It can be seen that the majority of studies reveal a negative response by the primates to zoo visitors, and that appears to be the case in all families except Lemuridae and Cebidae. However, because the studies are heavily biased towards apes, the data for most families are too sparse for statistical analysis. Amalgamating the families into higher taxa (Strepsirrhini, Platyrrhini, Cercopithecoidea, Hominoidea) permits statistical analysis but shows no significant association between taxon and animal response (χ^2=6.58, 3df. ns; 'positive' and 'unaffected' categories combined).

Allocating species to ecological groups results in the distribution of response categories shown in Figure 2. Negative responses make up the largest response category in all ecological groups except 'small terrestrial' and 'large arboreal'. The association between response category and ecological group is significant (χ^2=12.65, 5df, $p<0.05$; 'positive' and 'unaffected' combined because of low frequencies in some cells). Examination of the residuals shows that the greatest contribution to the overall effect is through more than expected negative responses, and fewer than expected positive/unaffected responses among small arboreal primates. Considering body size and degree of arboreality separately, there is no significant association between response categories and weight categories ($\chi2$ =1.97, 2df, ns), and no significant association between degree of arboreality and response category (χ^2=2.21, 1df, ns); so, it is the combined effect of body size and degree of arboreality which appears to be important.

3.3 Hypothesis 2: Behaviour and characteristics of visitors

The distribution of different visitor characteristics across response categories is shown in Figure 3. This association is significant (χ^2=8.74, 3df, p<0.05, ns, 'positive' and 'unaffected' were combined because of low frequencies in some cells and thought to be more similar to one another compared to negative responses). Examination of the residuals shows that the greatest contribution to the overall effect is due to more than expected negative responses, and fewer than expected positive/unaffected responses to noisy visitors.

3.4 Hypothesis 3: Housing and group size

Figure 4 shows primate response categories plotted as a function of enclosure size. There is no significant difference between categories (Kruskal Wallis test, H=0.996, N=61, p=0.61). Primate response categories are shown in Figure 5 as a function of enclosure type. This association is significant (χ^2=9.58, 3df, p<0.05, positive and unaffected, and semi-free range and walk-through combined to avoid low cell counts), and examination of the residuals suggests that the greatest contribution to this association is from more than expected 'positive' and 'unaffected' responses, and fewer negative responses, in semi-free range and walk-through enclosures. If the category 'semi-free range/walkthrough', for which there are only 5 cases, is removed from the analysis, then there is no significant association between enclosure type and response category (χ^2=2.31, 2df, ns). The response variables are plotted as a function of group size in Figure 6. There is no significant difference in group size between the three response variables (Kruskal Wallis test, H=2.11, N=92, p=0.348).

3.5 Hypothesis 4: Individual primate characteristics

This was tested using the second database comprising data on individual gorillas. The number of male and female gorillas showing each type of response is shown in Figure 7. The relationship is not significant (χ^2=1.39, 2df, ns). The number of gorillas in each response category is plotted as a function of age in Figure 8. The differences between groups are not significant (Kruskal Wallis test, H=2.29, N=28, p=0.131).

Finally, linear regression of the individual gorilla data using response category as the dependent variable and age, sex, group size, enclosure size and enclosure type as predictors, produced a significant model accounting for 40.4% of the variance ($F_{5,22}$=2.976, p=0.034). However, none of the predictor variables individually showed a significant effect, implying that all variables in combination are contributing to the animals' responses.

3.6 Year of Study

There was no significant correlation between the proportion of studies showing a negative effect and the half decade in which the study took place (r_s=0.29, df=5, p=0.53).

4. Discussion

Although it may at first seem disappointing that so few clear significant effects come out of this analysis, it is perhaps not surprising that this is the case. We are, after all, considering an order of ecologically diverse species, a captive environment which is very variable in type, and a stimulus which has a number of components. Nevertheless, the analysis presented here permits us to start to make sense out of what is clearly a complex issue.

Perhaps the clearest effect here is that the responses of captive primates to zoo visitors are related to species-specific differences in ecological type, in particular body size and degree of terrestriality/arboreality. Small-bodied arboreal primates appear to be negatively affected the most, and small terrestrial primates the least. This possibility was first suggested in one of the earliest studies of the visitor effect (Chamove et al. 1988), but the correlation those authors presented of changes in activity as a function of body size, although showing a trend, was not statistically significant. From our results here it appears that it is the combination of body size and degree of arboreality which is important, rather than just one singularly. Small-bodied primates are at greater risk of predation than larger bodied species, and that is particularly the case for arboreal species living at forest margins and tops of canopies, where they are most exposed (Isbell 1994). Presumably, however, other factors are also involved in species-specific differences, as similar species may sometimes show different responses to visitors. Black lion tamarins *Leontopithecus chrysopygus*, for example, showed a less intense response to visitors at Jersey Zoo than the ecologically and similarly sized pied tamarins *Saguinus bicolor* (Wormell et al. 1996). Differences in average temperaments between closely related species appear to be linked to species differences in social behaviour (Clarke & Boinski 1995; Sussman et al. 2013), and potentially this could cast light on species differences in response to zoo visitors. Comparison of three macaque species found that rhesus monkeys *Macaca mulatta* were particularly aggressive and unsociable towards humans, whereas long-tailed macaques *Macaca fascicularis* were more cautious and fearful, and pigtailed macaques *Macaca nemestrina* were more sociable and less aggressive to humans than the other two species (Sussman et al. 2013). Anubis baboons *Papio anubis* in another test were more active than long-tailed and pigtailed macaques in establishing or terminating contact with the tester (Heath-Lange et al. 1999). These studies have generally taken place in laboratories, and the tests are not easy to perform in zoos. Anecdotally, however, Mitchell et al. (1990), who carried out an extensive series of investigations of visitor effects on golden-bellied mangabeys at Sacramento Zoo, characterised this species as "emotionally volatile". If there are such systematic differences in temperament across different primate species, these may go some way to explaining part of the variability we see in responsiveness to human visitors, but currently there are not enough data to be able to do this. The low incidence of negative responses in small terrestrial primates is more puzzling, but may be a consequence of the small number of these in our sample being skewed in favour of lemurids in walk=through enclosures.

Apart from ecological category, the only other variable which came close to helping explain negative responses to visitors was the noisiness of visitors. The association between visitor noise and negative responses by the animals was significant. Noise in zoos can arise from a number of sources, including construction projects (Powell et al. 2006; Sulser et al. 2008) and concerts and other events (Harley et al. 2022; Readyhough et al. 2022) as well as from visitors, and there is evidence that animals will seek out quieter places to escape the noise (Wark et al. 2022). At Belo Horizonte Zoo, the mean sound pressure level was 46.75 dB(A) on days when the zoo was closed to the public, but that rose to 60.42 dB(A) on public days (Quadros et al. 2014), and this had a detrimental impact on animals in the zoo. We should point out, however, that noise is usually correlated with other measures of visitor pressure such as visitor number and activity (Quadros et al. 2014; Hashmi & Sullivan 2020), so disentangling the individual effects of these variables is not easy.

So far we have been considering variables that promote a negative response to zoo visitors, but in thirteen of the groups in our database (13.27%) the response was positive, and in 20 groups (20.41%) the animals were unaffected, so in one third of the studies there was no apparent negative effect. The only significant effect we have found which potentially helps explain these is that positive and unaffected responses occur more frequently than expected in semi-free range or walk-through enclosures. A positive response is sometimes associated with the provision of food. For example, green monkeys *Chlorocebus sabaeus* at Mexico City Zoo responded positively to food being thrown into the enclosure by visitors (Fa 1989), and the crowned lemurs *Eulemur coronatus* showing a positive response at Newquay Zoo were part of an animal feeding experience offered to visitors by the zoo (Jones et al. 2016). For other animals it appears to be an enriching effect of being able to interact with people that generates a positive response (Cook & Hosey 1995; Polgár et al. 2017). However, a note of caution is necessary, as none of these examples was in a walk through or semi-free range enclosure. Only two of our studies, both involving ringtailed lemurs *Lemur catta*, were in walk-through enclosures (Pollastri et al. 2022; Goodenough et al. 2019), and only three, involving baboons *Papio anubis* (Williams et al. 2022), orangutans (Choo et al. 2017) and, again, ringtailed lemurs (Collins et al. 2017), were in semi-free range, and the significant association is based on none of them showing a negative response. It is, of course, possible that animals are chosen for these sorts of enclosures primarily because they do not respond negatively to visitors, and more studies of these would help clarify this.

Our final hypothesis was that individual differences between animals might help to explain their different responses to visitors. Clearly this can only be tested if there are enough data from a number of individuals, rather than groups, within the same species, and at the moment this is only feasible for gorillas. Data were available for 30 individual animals in seven different studies (Carder & Semple 2008; Clark et al. 2012; Quadros et al. 2014; Collins & Marples 206; Lewis et al. 2020; Boyle et al. 2020; Miller et al. 2021). Analysis of these data revealed that there were neither sex nor age differences in the gorillas according to the different responses they gave. Interestingly, a regression which included both of these, as well as housing and husbandry variables, did generate a significant model, accounting for 40.4% of the variance, though no single predictor was significant on its own. Four different groups of gorillas, all housed at Zoo Atlanta, showed different responses to visitors, and the authors of that study (Stoinski et al. 2012) suggested that both intrinsic (eg personality, sex and rearing history) and extrinsic (kind of group) factors might be involved in these different responses. This could certainly be an avenue for future research, but at the moment the data to test these ideas are not available.

Our study raises a number of further questions, an important one of which is whether these changes observed in the animals have consequences for their welfare. The data reported in most studies are changes in the frequencies of behaviour when visitors are present, compared to either when no visitors or fewer visitors are present. These often look like substantial changes, but in absolute terms may still represent low frequency behaviours. For example, in a bachelor group of gorillas the mean proportion of scans showing aggressive behaviour changes from just less than 0.01 when small groups of visitors are present to just less than 0.04 when large groups are present (Figure 1 in Kuhar 2008). This is a significant increase, but it nevertheless means that there were a large number of observation sessions when no aggression was seen at all. A related issue is about whether all of the measures used in different studies are actually measuring effects that impact on welfare at all. Whereas the rationale for using self-scratching (Carder & Semple 2008), self-injury (Skyner et al. 2004) and other abnormal behaviours (eg Mallapur et al. 2005; Hashmi & Sullivan 2020; Sherwen et al. 2015) is convincing, the interpretation of vigilance, inactivity and proximity to the visitors needs more care (Sherwen & Hemsworth 2019), as they could denote positive arousal (interested vigilance and coming forward in the enclosure to interact with people) or negative arousal (fearful vigilance and coming forward in the enclosure to threaten people).

Finally, our data show that the proportion of studies showing a negative effect has not declined over recent years. It was thought possible that the increased emphasis on positive rather than negative welfare in recent years, coupled with the evolution of larger and more naturalistic enclosures, might result in visitors having a less adverse, or even no effect on primate behaviour (Hosey 2017, Edes et al. 2023). It was, furthermore, suggested that results attributed to the presence of visitors might sometimes be due to confounding variables, such as the weather (Goodenough et al. 2019). All of these may be true, but unfortunately are not reflected in our database, possibly in part because of a reluctance both by authors and by journal editors to publish results showing no significant effect.

In summary, while we are a long way from predicting which primates will be most affected in which ways by human visitors, we can say that small arboreal primates appear to be particularly likely to respond negatively, and that visitor noise might be the main aspect of visitor behaviour that we might try to change. It is also encouraging that semi-free range and walk-through enclosures appear not only to not produce negative responses, but might actually be positive for the animals, although we should also note that these enclosures may not be appropriate for many primate species. Exactly how animals will respond to visitors appears to be a consequence of the combined effects of a lot of different factors, and it is likely that we will only reach a fuller understanding of this when we have more studies examining individual differences in responses. As always, more research is needed, particularly on the latter two kinds of enclosure. And finally, can we urge those who will do those studies to provide full details of their study groups and enclosures, as these are missing in a surprising number of papers, but are essential for this kind of analysis.

5. Conclusion

This paper set out to test four hypotheses regarding the impact of visitors on primates housed in zoos using already published data. Test of the first hypothesis found that small arboreal primates are more likely to be affected negatively by visitors than larger or terrestrial primates. For the second hypothesis, the behaviour and characteristics of visitors, and in particular visitor noise, were found to significantly impact the behavioural responses of primates. Housing design (hypothesis three) was found to significantly impact primate responses with walk-through and semi-free range enclosures allowing for more positive or neutral behaviours. Group size however did not impact on the behaviour of the primate groups. Testing the final hypotheses (individual and enclosure characteristics) found that age, sex, group size, enclosure size and enclosure type combined contributed significantly towards the negative behaviours of gorillas. Whilst results are still difficult to tease apart, we can make recommendations for further research within this area including a focus on semi free range and walk-through exhibits of different species as well as further data on small arboreal primates.

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Table 1. Taxa represented in the database, together with the ecological group for each species, and the publications in which data were obtained. For ecological categories SA: small arboreal; ST: small

terrestrial; MA: medium arboreal; MT: medium terrestrial; LA: large arboreal; LT: large terrestrial.

Information on typical body sizes and arboreality/terrestriality from Mittermeier et al. 2013.

Species	Ecological category	Reference
Lemuridae		
Lemur catta	ST	Chamove et al. 1988; Collins et al. 2017; Goodenough et al. 2019; Pollastri et al. 2022
Eulemur coronatus	ST	Jones et al. 2016; Cairo-Evans et al. 2022
Galagidae		
Otolemur garnetti	SA	Boyle et al. 2020
Callitrichidae		
Leontopithecus rosalia	SA	Farrand 2007
Leontopithecus chrysomelas	SA	Quadros et al. 2014; Ingram 2009
Leontopithecus chrysopygus	SA	Wormell et al. 1996
Saguinus oedipus	SA	Glatston et al. 1984; Chamove et al. 1988
Saguinus bicolor	SA	Wormell et al. 1996
Aotidae		
Aotus trivirgatus	SA	Boyle et al. 2020
Atelidae		
Ateles geoffroyii rufiventris	MA	Davis et al. 2005
Alouatta guariba	MT	Quadros et al. 2014
Pitheciidae		
Callicebus donacophilus	SA	Cairo-Evans et al. 2022
Cebidae		
Saimiri sciureus	ST	Farrand 2007; Polgar et al. 2017
Sapajus xanthosternos	SA	Quadros et al. 2014
Sapajus apella	ST	Sherwen et al. 2015
Cercopithecidae		
Macaca fuscata	MT	Woods et al. 2019
Macaca nigra	MT	Dancer & Burn 2019; Snider 2016
Macaca mulatta	MT	Das Gupta et al. 2019 ; Sharma et al. 2023
Macaca nemestrina	MT	Das Gupta et al. 2019
Macaca silenus	MT	Mallapur et al. 2005
Papio hamadryas	LT	Farrand 2007; Bortolini & Bicca-Marques 2011
Papio anubis	LT	Das Gupta et al. 2019; Williams et al. 2022; Snider 2016
Mandrillus sphinx	LT	Chamove et al. 1988
Allenopithecus nigroviridis	MT	Cairo-Evans et al. 2022
Cercopithecus diana	MT	Chamove et al. 1988; Todd et al. 2007
Cercopithecus mona	MA	Boyle et al. 2020
Cercopithecus neglectus	MT	Cairo-Evans et al. 2022
Chlorocebus sabaeus	MT	Fa 1989
Cercocebus atys lunulatus	MT	Fragata 2010
Cercocebus chrysogaster	MT	Mitchell et al. 1991
Trachypithecus pileatus	MA	Das Gupta et al. 2019
Trachypithecus auratus	MA	Roth & Cords 2020
Nasalis larvatus	LA	Sha et al. 2012
Colobus guereza	MA	Cairo-Evans et al. 2022
Hylobatidae		
Hylobates pileatus	MA	Skyner et al. 2004; Hashmi & Sullivan 2020
Hylobates lar	MA	Cooke & Schillaci 2007
Nomascus leucogenys	MA	Lukas et al. 2002; Smith & Kuhar 2010; Boyle et al. 2020
Symphalangus syndactylus	MA	Smith & Kuhar 2010

Hominidae		
Pongo spp.	LA	Choo et al. 2011; Pederson et al. 2019
Pongo abelii	LA	Farrand 2007; Boyle et al. 2020
Pongo pygmaeus	LA	Birke 2002; Amrein et al. 2014; Bloomfield et al. 2015; Hashmi & Sullivan 2020
	LT	Vrancken et al. 1990
Gorilla beringei *Gorilla gorilla*	LT	Wells 2005; Farrand 2007; Kuhar 2008; Carder & Semple 2008; Clark et al. 2012; Ross et al. 2011; Stoinski et al. 2012; Quadros et al. 2014; Collins & Marples 2016; Bonnie et al. 2016; Pederson et al. 2019; Bastian et al. 2020; Hashmi & Sullivan 2020; Boyle et al. 2020; Edes et al. 2021; Lewis et al. 2020; Miller et al. 2021; O'Malley et al. 2021; Williams et al. 2022 ; Cox et al. 2023
	LT	Boyle et al. 2020; Williams et al. 2022
Pan paniscus *Pan troglodytes*	LT	Cook & Hosey 1995; Perret et al. 1995; Wood 1998; Farrand 2007; Ross et al. 2011; Quadros et al. 2014; Bonnie et al. 2016; Williams et al. 2022

Figure Legends

Figure 1. Number of studies (total N=106 in 57 publications) showing each of the primate response categories to visitors across primate families.

Figure 2. Number of studies (total N=106 in 57 publications) showing each of the primate response categories to visitors across ecological/size categories. This association is significant (χ^2=12.65, 5df, $p<0.05$; 'positive' and 'unaffected' combined because of low frequencies in some cells).

Figure 3. Number of studies (total N=106 in 57 publications) showing each of the primate response categories to visitors displaying different characteristics. This association is significant (χ^2=8.74, 3df, $p<0.05$, ns, 'positive' and 'unaffected' were combined).

Figure 4. Primate response categories as a function of enclosure size (m^2); outliers represent 4 studies from the database comprising 106 studies in 57 publications. Enclosure sizes are not significantly different between primate response categories.

Figure 5. Response categories as a function of enclosure type. The relationship between number of studies (N=106 in 57 publications) and enclosure type is significant (χ^2=9.58, 3df, $p<0.05$, positive and unaffected, and semi-free range and walk-through combined to avoid low cell counts)

Figure 6. Primate response categories as a function of group size; outliers represent 7 studies from the database comprising 106 studies in 57 publications. The difference in group size between different response categories is not significant.

Figure 7. Numbers of male and female gorillas in each response category (total number of gorillas =20). The association is not significant.

Figure 8. Number of gorillas (total number of gorillas = 20) in each primate response category as a function of age; there is one gorilla which is an outlier. The differences are not significant.

Figure 1

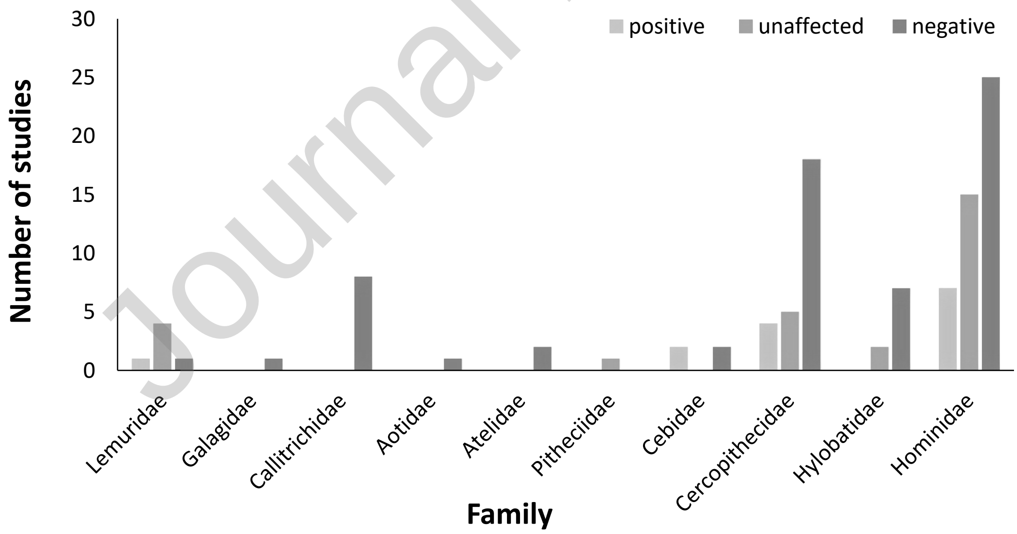


Figure 2

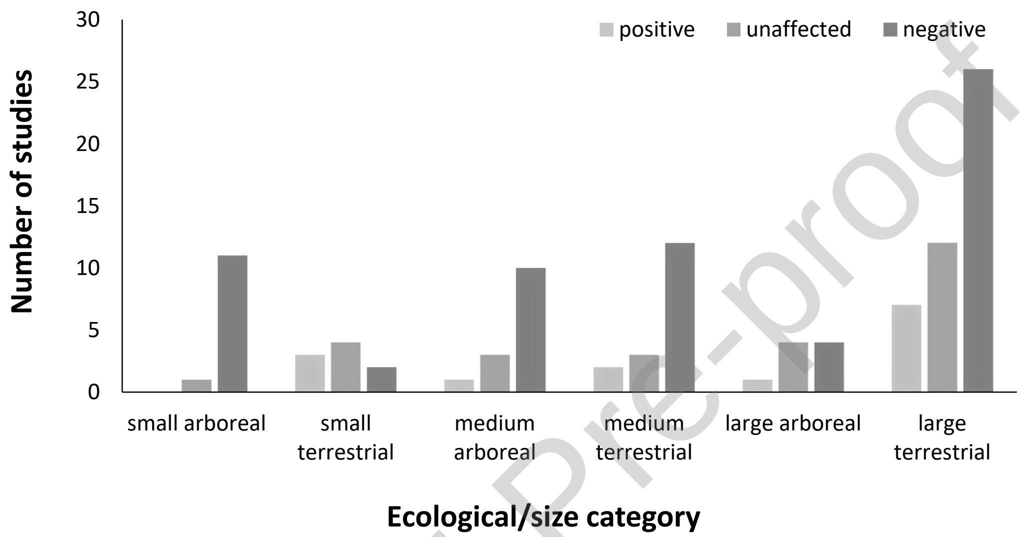


Figure 3

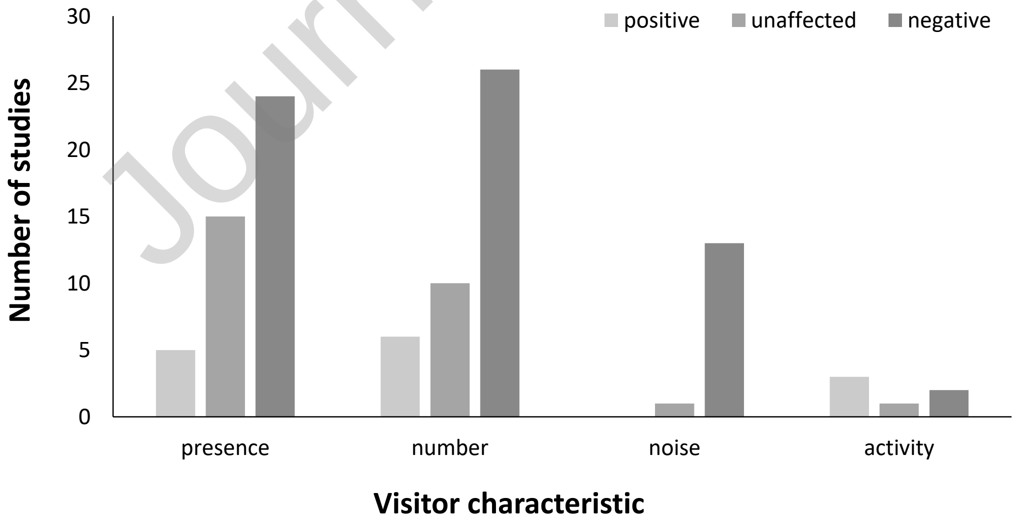


Figure 4

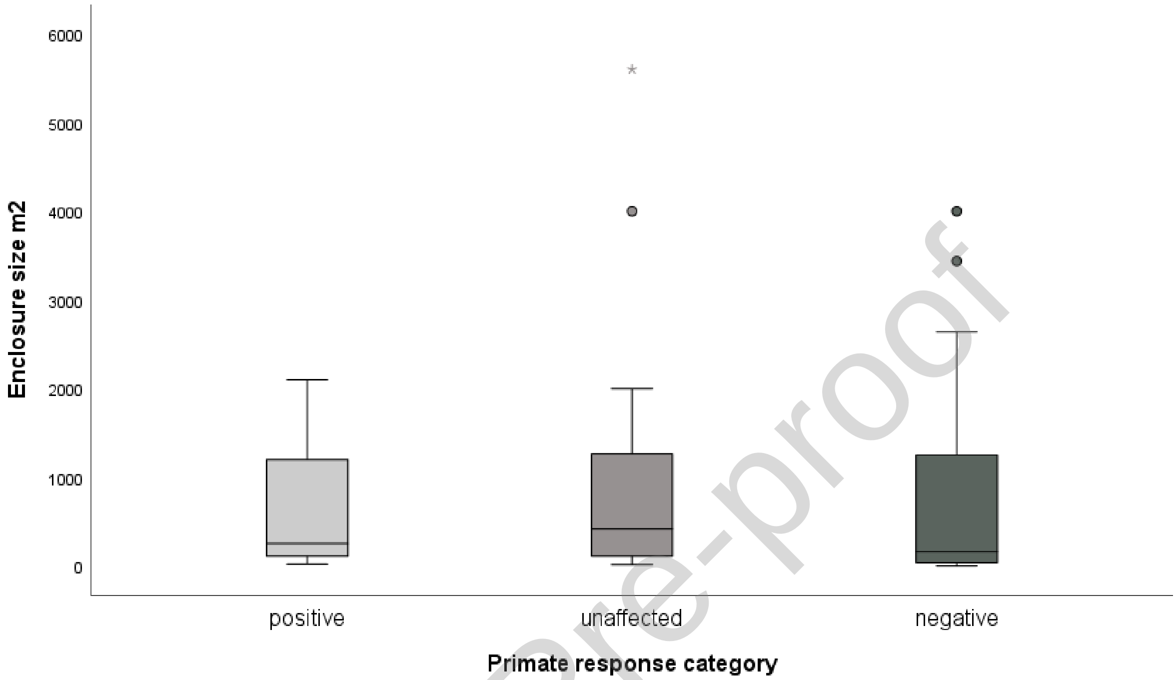


Figure 5

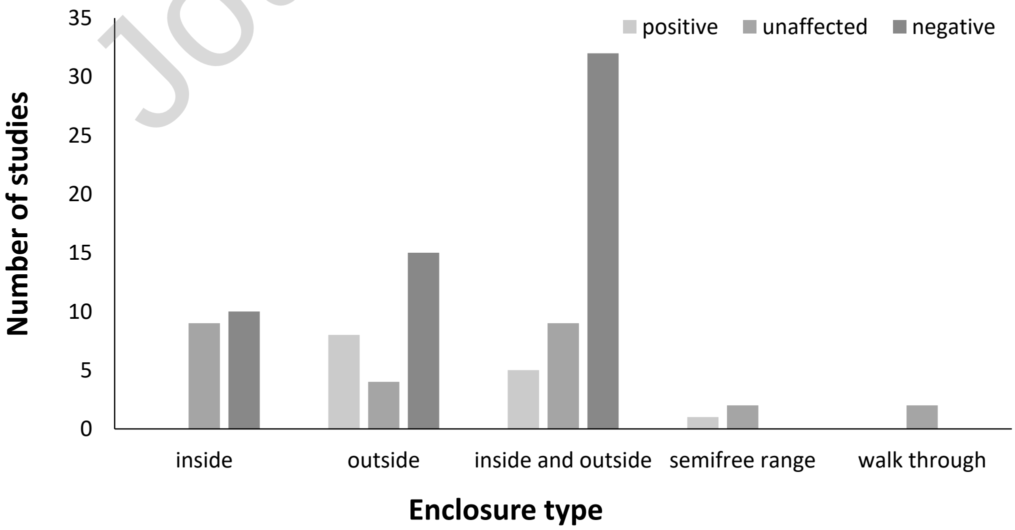


Figure 6

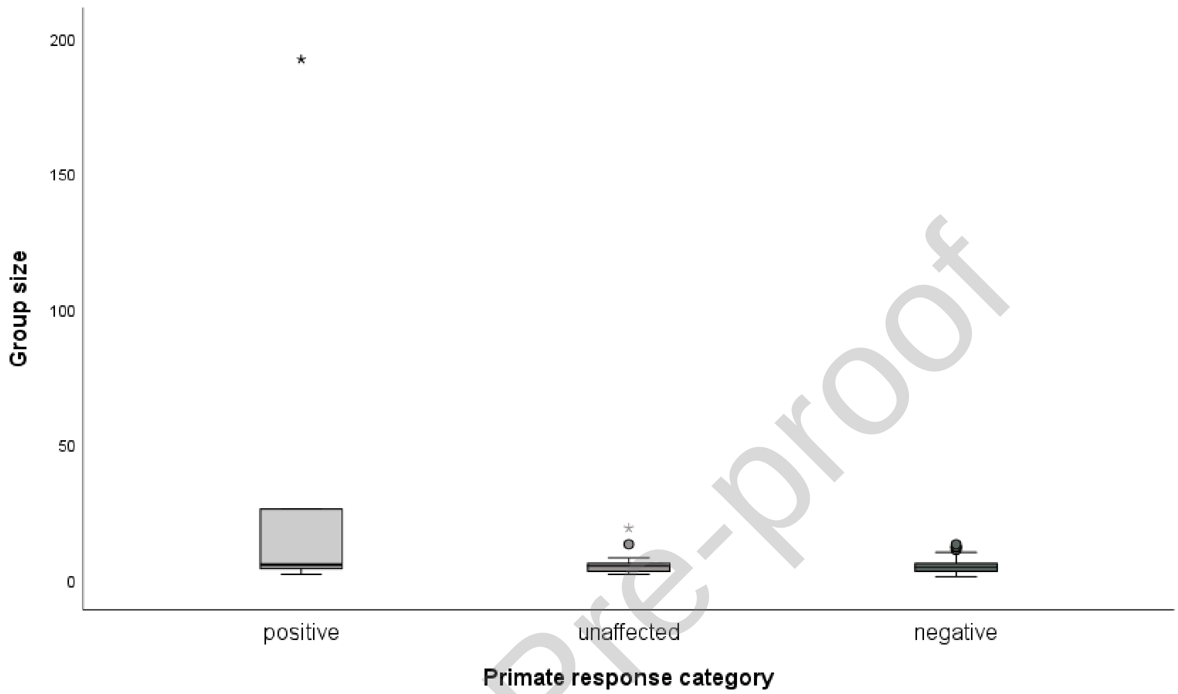


Figure 7

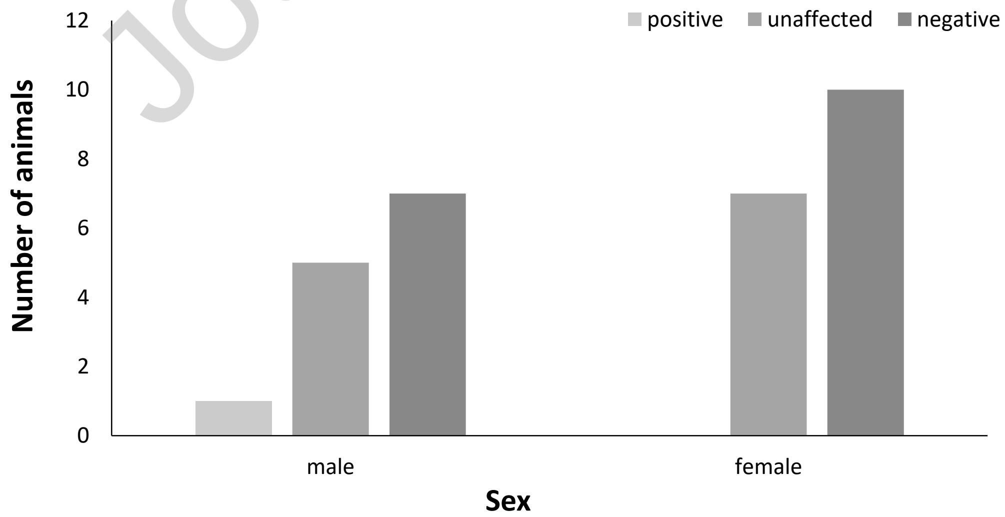
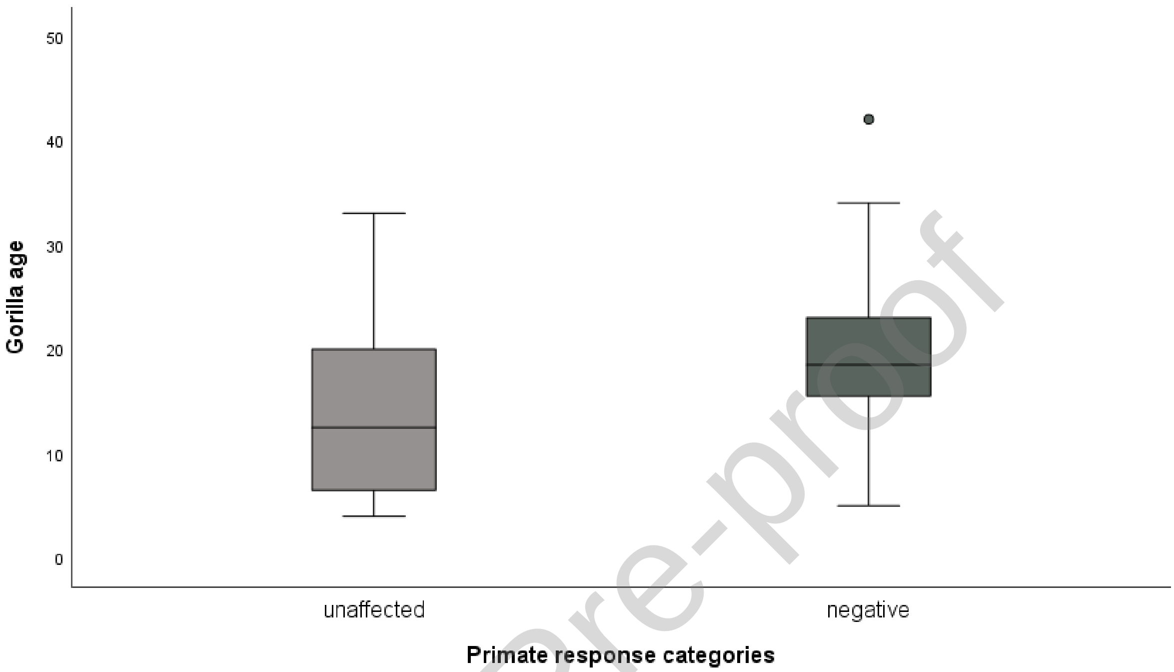


Figure 8



Declaration of Competing Interest

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Research Highlights

- Databases were created to test four hypotheses to explore the zoo primate visitor effect.
- Ecology: Small arboreal primates were more likely to be affected negatively by visitors.
- Housing: walk-through and semi-free range enclosures were associated with more positive and neutral responses by primates to visitors, but primate group size had no effect.

- Visitor noise was associated with negative responses by primates