Visitor effects on zoo-housed Sulawesi crested macaque (Macaca nigra) behaviour: can signs with ‘watching eyes’ requesting quietness help?

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Abstract

Visiting public can cause changes in the behaviour of zoo-housed primates. These effects, if indicative of stress, can be of welfare concern. However, few options to mitigate visitor effects through modulating visitor behaviour have been explored. Here we evaluated the effects of visitor number and visitor noise level on the behaviour of five UK groups of Sulawesi crested macaques. We also investigated whether visitor behaviour can be effectively modulated through targeted signage requesting visitors to be quiet, and assessed the use of signs incorporating salient ‘watching’ human eyes, novel to a zoo setting, alongside ‘control’ signs lacking eyes.

We used scan sampling to collect over 100 h of behavioural observation data, analysis of which indicated that Sulawesi crested macaques were significantly affected by both visitor number and noise level at all five zoos. We found that active behaviours, such as locomotion or foraging, and behaviours identified as negative for welfare, such as vigilance, increased with increasing visitor number and noise levels, whereas resting and social huddling decreased. The extent to which these behavioural changes reflect welfare, particularly the increase seen in active behaviours, is not clear. We also found that both sign treatments, with and without salient eyes, slightly but significantly reduced visitor noise levels compared with no sign, although signs displaying human eyes were not more effective than the control signs.

Our results highlight a need for further research into active behaviours to assess whether increases in these behaviours are associated with stress. While we found signage to be a promising tool to mitigate against these visitor effects, our results also suggest areas in which signs incorporating salient human eyes could be adapted for the zoo environment in order to realise their full potential.

Keywords: Primates, Animal behaviour, Animal welfare, Visitor effects, Noise effects, Zoo animals
Highlights

- Activity and vigilance in *Macaca nigra* increased with visitor numbers at five zoos.
- Louder visitor noise also increased activity and vigilance in *Macaca nigra*.
- Signs requesting visitors to be quiet slightly but significantly reduced noise.
- Signs with ‘watching eyes’ appeared no more effective than control signs.

Introduction

Education, awareness raising and fundraising, in which the visiting public play an integral role, are amongst the primary goals of many zoos. Yet the daily influx of unfamiliar visitors can cause concern for the well-being of the animals within. Indeed, the effect of visiting public on the welfare of zoo-housed primates has been of research interest for decades. Behavioural and physiological changes can occur in primates on show to visiting public (see supplement S1 for a summary of relevant literature). However, the potential impact on welfare has been in contention, with findings suggesting primate lives may be enriched (Cook and Hosey, 1995), unaffected (Hosey, 2000), or be negatively impacted (Birke, 2002). Despite these conflicting findings, a review suggested that more often than not visitors influence changes for the worse, including changes indicative of stress (Davey, 2007), although evidence of this being severe may be rare (Hosey, 2017). Behavioural change in zoo-housed primates has been observed in response to a variety of visitor-variables, including visitor density, number, noise, position, activity and presence (Hosey, 2005; Davey, 2007), and impacts on behaviour vary both between visitor-variables and between species (Davey, 2007).

One of the more frequently studied visitor-variables has been visitor number, which has consistently been shown to affect the behaviour of zoo-housed primates. For example, in Diana monkeys (*Cercopithecus diana*) visitor group size displayed a positive correlation with frequency of active-type behaviours, such as foraging or playing, and a negative relationship with relaxed behaviours, such as resting, sleeping or grooming (Todd et al., 2007). In male white handed gibbons (*Hylobates lar*) larger visitor group sizes resulted in increases in communicative behaviours interpreted as responses to threats, such as ‘look at mate’, ‘look at visitors’ and open mouth displays (Cooke and Schillaci, 2007). Physiological responses can also occur due to higher visitor number; for example, Davis et al. (2005)
recorded increased cortisol levels (a hormone used as a marker for stress, although it can reflect activity and arousal more generally) in Columbian spider monkeys (*Ateles geoffroyii rufiventri*) with increased visitor numbers.

Visitor noise is less frequently studied, but it has been associated with behavioural responses in primates (Hosey, 2005). When sound levels outside orang-utan (*Pongo pygmaeus*) enclosures were experimentally manipulated by verbally asking visitors to be either silent or loud, the orang-utans responded negatively to higher noise levels, with increases in adults looking at visitors, and infants holding on to adults (Birke, 2002). Furthermore, a study of the effect of noise on a range of zoo-housed mammals found that noise levels outside certain enclosures, such as western lowland gorillas (*Gorilla gorilla gorilla*) and golden-bellied capuchin monkeys (*Cebus xanthosternos*), at times exceeded 70dB (the recommended limit for human well-being (WHO, 1999)), and concluded that as a consequence these species were experiencing negative welfare (Quadros et al., 2014).

Zoo-housed primates may experience reduced welfare due to their inability to escape visiting public or exert control over their environment (Wells, 2005). For example, larger, more naturalistic enclosures, which afford increased refuges and distance from visiting public, could lessen visitor effects (Davey, 2007), although providing larger enclosures may not always be feasible due to financial and space constraints. Alternatively, to mitigate the effect of noise level specifically, signage could be used to encourage visitors to be quieter outside enclosures. Signs have previously been effective at modulating visitor behaviour in a zoo setting. For example, three signs displaying different messages were tested to discourage visitors from banging on aquarium windows, and all three signs significantly reduced the level of banging compared to when no sign was displayed (Kratochvil and Schwammer, 1997).

An option previously untested in a zoo setting is to modulate visitor behaviour by using signage which incorporates salient human eyes as if ‘watching’ the reader. This method has been applied successfully in non-zoo settings to promote cooperative behaviour in people. For example, people gave more generously to a donation box when asked to via a sign showing salient eyes than via a sign showing a control image (Bateson et al., 2006). This effect is assumed to work by giving people the impression they are being watched (Bateson et al., 2006; Ernest-Jones et al., 2011).
The effect of visitor number and noise level on the behaviour of the Sulawesi crested macaque (Macaca nigra) is examined in the present study. Currently listed as critically endangered, they are semi-terrestrial and frugivorous, and native to north-eastern Sulawesi (Supriatna & Andayani, 2008). At the time of the present study there were approximately 167 Sulawesi crested macaques housed in 21 zoos across Europe (ZIMS, 2015), and the species is part of the European Endangered species Programme. Sulawesi crested macaques have previously been part of a multi-species study into the effect of visitor activity on behaviour, but not visitor number or noise level (Hosey and Druck, 1987). Locomotion increased in all species, including Sulawesi crested macaques, in the presence of more active visitors.

The aims of this study are to provide an understanding of how visitor number and noise level affect the behaviour of Sulawesi crested macaques, and whether visitor noise can be mitigated through signs, especially those with salient eyes. If results suggest visitor numbers and noise impact negatively on the macaques then recommendations could be made for how signage could be adapted to improve welfare. This study tested two overarching hypotheses. Firstly, and based on previous findings of a range of primate species, if individuals are affected by visitors, they would carry out more active (e.g. locomotion, play, foraging, interacting with furniture, begging, mounting and social behaviour) or negative (e.g. aggression, vigilance, stereotypy, hiding) behaviours and fewer relaxed (e.g. resting, grooming, huddling) behaviours in the presence of larger groups of visitors or higher noise levels. Secondly, that visitor noise would be highest when no sign is present and lowest when a sign requesting them to be quiet and including salient eyes is present.

Methods

Sites and subjects

Five UK zoos, each with an on-exhibit group of Sulawesi crested macaques, participated in the study, which took place in 2015, including a pilot study at one of the zoos from 13th to 15th May 2015. The number, age and sex ratio of macaques in each zoo differed, as did the size of macaque enclosures (Table 1).
Prior to commencing data collection a short questionnaire was sent to the appropriate keeper at each zoo, to record zoo-specific husbandry details. Questions included diet, feeding times, times of restricted access to parts of enclosure, types and times of enrichment, and whether keepers had noticed any undesirable behaviours in the macaques (e.g. self-biting, body-slamming, over-grooming or begging to visitors), or behaviours expressed by the macaques when either stressed or relaxed. The answers to these questions helped with ethogram design.

Table 1. Dates of study and macaque details for each of the five participating zoos.

<table>
<thead>
<tr>
<th></th>
<th>Zoo A</th>
<th>Zoo B</th>
<th>Zoo C</th>
<th>Zoo D</th>
<th>Zoo E</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dates of study, 2015</td>
<td>1st to 6th July</td>
<td>24th to 29th June</td>
<td>20th to 25th May</td>
<td>10th to 15th June</td>
<td>3rd to 8th June</td>
</tr>
<tr>
<td>Number of macaques</td>
<td>20</td>
<td>5</td>
<td>8</td>
<td>12</td>
<td>10</td>
</tr>
<tr>
<td>Male:Female</td>
<td>8:12</td>
<td>2:3</td>
<td>5:3</td>
<td>5:7</td>
<td>7:3</td>
</tr>
<tr>
<td>Age range of macaques</td>
<td>1 - 15 yrs</td>
<td>3 - 10 yrs</td>
<td>10 mths - 19 yrs</td>
<td>2 - 16 yrs</td>
<td>2 - 17 yrs</td>
</tr>
</tbody>
</table>

Behavioural Observations and Recordings of Sound Levels and Visitor Numbers

A 3 day pilot was conducted to test the study design, ethogram and sampling method, and allowed for necessary changes to be made. A total of 6 days (Wednesday to Monday) were then spent at each zoo, with the same observer (AMMB) conducting all observations. The first day was spent habituating the macaque group to the observer’s continuous presence outside the enclosure and for determining the most suitable locations for observation. Data collection took place over five days at each zoo, with a mixture of weekdays (Thursday, Friday and Monday) and weekend days (Saturday and Sunday) representing a range of visitor numbers. These days were kept consistent across zoos.

Behavioural observations were collected using instantaneous scan sampling with 5 min intervals and one-zero sampling. The group was scanned from left to right of the enclosure at each 5 min sample point and the behaviour of each macaque was recorded using a pre-designed ethogram (adapted from published ethograms, see Baker, 2012; Nickelson and Lockard, 1978; Thierry et al., 2000)
Between sample points, during sample intervals, event behaviours relevant to the study were also captured using one-zero recording. The macaques were observed for three 1h 30min sessions per day (10:00 – 11:30, 12:00 – 13:30, 14:30 – 16:00), totalling 4h 30min of observation per day, per zoo. Times when keepers fed or were otherwise interacting with the macaques were also recorded.

Table 2. Ethogram of behaviours for Sulawesi crested macaques. The symbol ‘↘’ denotes behaviour predicted to decrease, ‘↗’ denotes behaviour predicted to increase with increasing visitor number or noise level and ‘?’ denotes that predicted behaviour change with increasing visitor number or noise level is not known. The ethogram is adapted from published ethograms, see Baker, 2012; Nickelson and Lockard, 1978; Thierry et al., 2000.
<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Status/ Sampling method</th>
<th>Predicted direction</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allo-grooming</td>
<td>State/ Scan</td>
<td>↘</td>
<td>An individual picks through and examines the fur and skin of another individual.</td>
</tr>
<tr>
<td>Auto-grooming</td>
<td>State/ Scan</td>
<td>↘</td>
<td>An individual picks through and examines their own fur and skin.</td>
</tr>
<tr>
<td>Fighting</td>
<td>State/ Scan</td>
<td>↗</td>
<td>Aggressive behaviour towards another member of the group; chasing initiated by an individual displaying the open-mouth bared-teeth threat followed by running at another individual. This is often accompanied by the chased giving a screaming vocalisation. Fighting may include biting, hitting or one or more individuals open-mouth bared-teeth ‘threat’.</td>
</tr>
<tr>
<td>Foraging &amp; Feeding</td>
<td>State/ Scan</td>
<td>↗</td>
<td>Actively looking towards and picking through vegetation/ feeding devices, and consuming food items.</td>
</tr>
<tr>
<td>Hiding</td>
<td>State/ Scan</td>
<td>↗</td>
<td>Animal behind refuge, obscured from view of public. Not obviously carrying out other behaviours.</td>
</tr>
<tr>
<td>Interaction with furniture/ enrichment</td>
<td>State/ Scan</td>
<td>↗</td>
<td>Interaction with enclosure furniture (e.g. hammocks, swings) or with enrichment items in enclosure, e.g. mirrors.</td>
</tr>
<tr>
<td>Locomotion</td>
<td>State/ Scan</td>
<td>↗</td>
<td>Movement around enclosure. Including: walking, running, climbing, jumping and swinging, all without foraging.</td>
</tr>
<tr>
<td>Play</td>
<td>State/ Scan</td>
<td>↗</td>
<td>Wrestling, including play biting (gentle gnawing) and chasing resulting in either wrestling or reciprocal chasing. Usually occurs between younger individuals.</td>
</tr>
<tr>
<td>Resting</td>
<td>State/ Scan</td>
<td>↘</td>
<td>Individual sitting or reclining in a relaxed position, without scanning the enclosure or looking fixedly at a point or individual. May have closed or half-closed eyes.</td>
</tr>
<tr>
<td>Category</td>
<td>Type/Modes</td>
<td>Description</td>
<td></td>
</tr>
<tr>
<td>------------------------</td>
<td>------------</td>
<td>--------------------------------------------------------------------------------------------------------------------------------------------</td>
<td></td>
</tr>
<tr>
<td>Social huddle</td>
<td>State/Scan</td>
<td>Sitting in contact with other individuals, consisting of extensive contact of body trunk, possibly with arms around each other, either sitting or lying.</td>
<td></td>
</tr>
<tr>
<td>Social interaction</td>
<td>State/Scan</td>
<td>An individual interacts with another individual which is not play, aggression or allo-grooming (e.g. touching, approaching another individual whilst looking at it or retracting scalp whilst looking at another to invite an affiliative interaction).</td>
<td></td>
</tr>
<tr>
<td>Vigilant</td>
<td>State/Scan</td>
<td>Individual with alert, stiff posture, visually scanning inside or outside the enclosure, or an individual (sitting or standing).</td>
<td></td>
</tr>
<tr>
<td>Begging</td>
<td>Event/One-zero</td>
<td>Individual approaches bars or window of enclosure and holds hand/s out to a visitor.</td>
<td></td>
</tr>
<tr>
<td>Body-slamming</td>
<td>Event/One-zero</td>
<td>Slams part of own body against walls of enclosure.</td>
<td></td>
</tr>
<tr>
<td>Mounting</td>
<td>Event/One-zero</td>
<td>An individual grips legs of another with hind feet and grasps the waist with hands. May be accompanied by a thrusting action.</td>
<td></td>
</tr>
<tr>
<td>Scratching</td>
<td>Event/One-zero</td>
<td>Repetitive raking of the skin or fur using fingers or feet.</td>
<td></td>
</tr>
<tr>
<td>Self-directed behaviour</td>
<td>Event/One-zero</td>
<td>Any self-directed behaviour which can be repetitive with no obvious function, including self-touching, body shaking and hair plucking.</td>
<td></td>
</tr>
<tr>
<td>Lipsmack</td>
<td>Event/One-zero</td>
<td>Lips pursed and lower jaw moves up and down rapidly with the lips often producing an audible sound. Used during affiliative interactions, to end conflicts and as a signal to appease or reassure.</td>
<td></td>
</tr>
<tr>
<td>Open mouth bared-teeth threat</td>
<td>Event/One-zero</td>
<td>Mouth wide open, exposing teeth. Often accompanied by staring and screaming vocalisations. Occurs in agnostic contexts.</td>
<td></td>
</tr>
<tr>
<td>Other</td>
<td>State or Event</td>
<td>Any other behaviours not covered in ethogram.</td>
<td></td>
</tr>
<tr>
<td>Out of sight</td>
<td>State</td>
<td>Out of sight to the observer</td>
<td></td>
</tr>
</tbody>
</table>
We were unable to recruit a second observer to allow the assessment of inter-observer reliability, so all the results reflect the standardised interpretation of a single observer. The observer was trained to masters-level in behavioural observation research techniques. To further familiarise themselves with the species the observer spent five days shadowing macaque keepers of one of the participating zoos and, during the process of ethogram design.

At each sample point sound level in decibels (dB) was also recorded using a sound level metre with data logger (CEM DT-815, CEM Instruments Ltd). The observer stood quietly approximately in the middle of the visitor viewing area, one metre back from the enclosure barrier. If there was both an indoor and outdoor viewing area the observer stood in the viewing area approximately in between the two. The sound level metre was held at arm’s length towards the enclosure. At each sample point the number of visitors outside the enclosure (indoor and outdoor) was also recorded, excluding the observer.

Sign Treatments

Sign treatments were applied at four of the five zoos (Zoos B - E). Zoo A did not permit visitor manipulation due to an existing behavioural study. Two signs were designed, both with the same message “Please be as quiet as possible outside the Sulawesi crested macaque enclosure. Thank you”. One sign displayed an image of salient human eyes, the other a control image of flowers (Fig. 1).

The text was agreed in advance to meet zoo requirements. Zoos were permitted to apply final formatting and branding to encourage participation. Zoos C - E all agreed on the formatting shown in Figure 1; Zoo B added a border and logo to each sign. The signs were printed size A2 and displayed in an A-frame.
Figure 1. The two designs of sign. (a) ‘Eyes’ sign: sign with image of salient human eyes; and (b) Control sign with image of flowers.

For each 90 min session either the sign with the image of salient eyes, the sign with the control image, or no sign was present. The order of treatments was balanced across the five days per zoo to control for time of day. During each treatment two identical signs were displayed; one outside the outdoor enclosure and one outside the indoor enclosure. At Zoo B, which had no indoor enclosure, a sign was placed at each end of the outdoor enclosure. Only one sign was displayed at Zoo C, due to restricted space, placed outside the outdoor enclosure. However, visitors approached via a one-way route passing first the outdoor and then indoor enclosure, so all visitors passed the sign. Signs were positioned in front of enclosure barriers where paths joined visitor viewing areas.

Statistical Analysis

Behavioural observations

Behaviours were analysed if they showed sufficient variation in performance, being neither too rare nor too frequent (recorded on 10-90% of observations). Begging, Body-slamming, Fighting, Hiding, Lip-smacking, Mounting, Scratching, Self-directed behaviour and Teeth-baring were too rare for analyses, even when combined into meaningful categories (e.g. Body-slamming and Self-directed
behaviour being summed to comprise ‘abnormal behaviour’). Other and Out of Sight were also excluded due to their ambiguity. This left 11 behaviours for analysis.

Relationships between behaviours and visitor number or noise level were assessed by fitting Generalised Linear Mixed Models (GLMM, SPSS, with significance at the p<0.05 level) to the data, with each behaviour in turn as the binary response variable, using a binomial link function. Visitor noise and number were included as explanatory variables in separate models, because of their correlation with each other. Also included in every model were Observation day (a random categorical variable), Observation time-point (a continuous fixed factor), and Zoo (a fixed categorical variable, because there were too few zoos to constitute a random factor). Models were checked for inflated standard errors that could indicate autocorrelation problems, but no such problems were observed.

Sample points with potential confounding factors were removed before analysis, including those points where a keeper was present and attracting begging or vigilance from macaques, and immediately after a group had been fed and >50% of macaques were consequently feeding. For the latter, points were removed until the proportion of individuals feeding dropped below 50% for >1 sample point.

Sign treatment

Data from the four zoos in the treatment study were analysed using a GLMM as above, but noise level as the continuous response variable meant that an identity link function was appropriate. Model assumptions were checked via examination of the residuals. The explanatory variables included Treatment, Weather and Visitor number, in addition to those included above as before (Observation day, Observation time-point, and Zoo).

Results

Effects of visitor number on behaviour

Visitor numbers ranged from a median (IQR) of 4 (0-8) at the least visited of the five zoo enclosures (Zoo D) to 13 (7-23) at the most visited (Zoo A). As the number of visitors increased, the likelihood of active behaviours being observed significantly increased: Autogrooming, Foraging, Furniture use, Locomotion, and Vigilance (Table 3). Correspondingly, with more visitors, Resting and Huddling
decreased in likelihood. All effects were relatively subtle as indicated by odds ratios close to one for each additional visitor.

Table 3. Statistically significant effects of visitor numbers and noise levels on Sulawesi macaque behaviour. The behaviour category reflects suggested behavioural interpretations, although other interpretations are possible as outlined in the Introduction.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Behaviour category</th>
<th>Behaviour</th>
<th>Effect direction</th>
<th>Odds Ratio</th>
<th>s.e.</th>
<th>F (DF)</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of visitors</td>
<td>Active</td>
<td>Foraging</td>
<td>↗</td>
<td>1.02</td>
<td>1.01</td>
<td>8.472 (1, 1179)</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>Furniture use</td>
<td></td>
<td>↗</td>
<td>1.03</td>
<td>1.01</td>
<td>10.464 (1, 1179)</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Locomotion</td>
<td></td>
<td>↗</td>
<td>1.02</td>
<td>1.01</td>
<td>11.404 (1, 1179)</td>
<td>0.001</td>
</tr>
<tr>
<td>Relaxed</td>
<td>Autogrooming</td>
<td></td>
<td>↗</td>
<td>1.02</td>
<td>1.01</td>
<td>4.922 (1, 1179)</td>
<td>0.027</td>
</tr>
<tr>
<td></td>
<td>Huddling</td>
<td></td>
<td>↘</td>
<td>0.98</td>
<td>1.01</td>
<td>8.875 (1, 1179)</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td>Resting</td>
<td></td>
<td>↘</td>
<td>0.98</td>
<td>1.01</td>
<td>10.920 (1, 1179)</td>
<td>0.001</td>
</tr>
<tr>
<td>Negative</td>
<td>Vigilance</td>
<td></td>
<td>↗</td>
<td>1.07</td>
<td>1.01</td>
<td>78.890 (1, 1179)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Noise (dB)</td>
<td>Active</td>
<td>Foraging</td>
<td>↗</td>
<td>1.03</td>
<td>1.01</td>
<td>7.105 (1, 1169)</td>
<td>0.008</td>
</tr>
<tr>
<td></td>
<td>Furniture use</td>
<td></td>
<td>↗</td>
<td>1.03</td>
<td>1.01</td>
<td>5.890 (1, 1169)</td>
<td>0.015</td>
</tr>
<tr>
<td></td>
<td>Play</td>
<td></td>
<td>↗</td>
<td>1.04</td>
<td>1.01</td>
<td>8.767 (1, 1169)</td>
<td>0.003</td>
</tr>
<tr>
<td>Relaxed</td>
<td>Resting</td>
<td></td>
<td>↘</td>
<td>0.97</td>
<td>1.01</td>
<td>8.149 (1, 1179)</td>
<td>0.004</td>
</tr>
<tr>
<td>Negative</td>
<td>Vigilance</td>
<td></td>
<td>↗</td>
<td>1.07</td>
<td>1.01</td>
<td>39.401 (1, 1169)</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Effects of visitor noise on behaviour

Visitor noise ranged from a mean ± s.e. of 52.5 ± 0.4 dB at the quietest zoo enclosure (Zoo D) to 61.5 ± 0.4 dB at the loudest (Zoo E). Noise levels outside enclosures reached as high as 90dB. As the noise level increased, certain active behaviours were significantly more likely to be observed: Foraging, Furniture use, Play, and Vigilance (Table 3; Figure 2a). Resting, on the other hand, was significantly less likely to be observed with louder visitor noise (Figure 2b).

Figure 2. Effects of visitor noise on Sulawesi macaque (a) vigilance and (b) resting behaviour, taking zoo into account. The white bars represent the absence of the behaviour and the grey bars represent its presence.

Effects of signs and other factors on visitor noise

Visitor noise was affected by treatment (F$_2$, 1049 = 9.30; P < 0.001; Figure 3), in that it was significantly quieter with both sign treatments compared with no sign at all (Eyes: coeff ± s.e. = -0.011 ± 0.003; P < 0.001; and Control: coeff ± s.e. = -0.008 ± 0.003; P = 0.001). However, the sign showing salient eyes was not significantly more effective than the control sign (P = 0.450).

Visitor noise increased with visitor numbers (coeff ± s.e. = 0.003 ± 0.000; F$_1$, 1049 = 359.3; P < 0.001), and differed between zoos (F$_3$, 1049 = 17.62; P < 0.001). It was also affected by the weather (F$_3$, 1049 =
4.36; P = 0.005), because it was quieter during sunshine (coeff ± s.e. = -0.016 ± 0.005; P < 0.001) and sunny intervals (coeff ± s.e. = -0.011 ± 0.005; P = 0.016) than when it was raining.

Figure 3. Effect of signage on mean noise levels. The data are logged to reflect the statistical analysis. To correct for the significant effect of visitor number on sound levels, data are presented as dB per visitor. The minimum value on the y-axis was selected as the 5th percentile value (because sound was never zero).

Discussion

The results from this study indicate that the behaviour of Sulawesi crested macaques is significantly affected by increases in both visitor number and visitor noise levels, with an increase in active-type and negative behaviours, such as locomotion and vigilance, and both decreases and increases in certain relaxed-type behaviours. Although visitor noise was not significantly reduced by signs with salient eyes when compared to the control signs, visitor noise was reduced by both signs when compared with having no sign present.
Effect of visitor number

Of the seven behaviours included in the analysis categorised as active-type, three (foraging/feeding, interaction with furniture/enrichment, and locomotion) significantly increased with visitor number. This corresponds to findings from numerous other studies (Davey, 2007). Specifically, activity increased with increased visitor numbers (Todd et al., 2007), visitor activity (Hosey and Druck, 1987; Mitchell et al., 1992) and visitor presence (Mallapur et al., 2005). However, this effect is not consistent across species; for example, western lowland gorillas significantly reduced foraging and feeding with increasing visitor numbers (Clark et al., 2012).

The hypothesised decrease in relaxed-type behaviours with higher visitor numbers was only seen for resting and social huddling, as auto-grooming increased with higher visitor numbers. Previous studies have found that resting behaviour decreases in western lowland gorillas with high visitor density (Wells, 2005), and in Diana monkeys with increased visitor number (Todd et al., 2007).

The increase in grooming behaviours was not expected because we classed it as a ‘relaxed’ behaviour rather than an active behaviour. Looking at the detailed microstructure of the grooming in future studies could help to evaluate which interpretation is more appropriate because, in some species, grooming occurs as an action pattern that becomes disarranged in stressful situations (e.g. in rats: Komorowska and Pisula, 2003). Some studies have found increases in auto-grooming similar to the current study, e.g. in western lowland gorillas grooming increased with visitor density (Wells, 2005), but in other species, such as Diana monkeys, grooming behaviours decreases with increased visitor numbers (Todd et al., 2007).

The above increases in activity and decreases in inactivity are difficult to interpret in terms of macaque welfare, because they could indicate that the visitors were either stressful or providing welcome stimulation for the animals (Fureix and Meagher, 2015). In future, distinguishing between resting with eyes open versus closed could help distinguish whether this was likely to be ‘boredom’-related behaviour that the visitors relieved, or truly ‘relaxed’ sleep that the visitors disturbed. That the huddling here decreased, rather than increased, when more visitors were present suggests that it is unlikely to be a negative defensive response and may indeed be a ‘relaxed’ behaviour. If so, this suggests that visitors may have disturbed the macaques somewhat. In future, there are many other welfare relevant behaviours and physiological measurements that could help elucidate whether
visitors are stressful or enriching, as reviewed using elephants as an example by Mason and Veasey (2010).

Of the behaviours which have been established to indicate stress and were categorised as negative, vigilance increased with visitor number. Similar findings have been observed in mandrills (*Mandrillus sphinx*) (Chamove et al., 1988), and orang-utans (Choo et al., 2011), both of which increased time spent in a stiff posture watching visitors with higher visitor numbers. The effect increasing visitor number has on increasing negative vigilant behaviour could suggest that the macaques are under increased stress as a result, which could have implications for Sulawesi crested macaque welfare. Visitor number showed no effect on aggression, which could have been because it was not affected by visitor number, or because there was always a visitor present in the form of the observer. Remote video analysis or use of a hide could assist with this issue in future. Also a larger sample size or more time spent observing may help, especially as the remaining negative behaviours, stereotyped behaviour and hiding, were too rare for analysis here.

In summary, Sulawesi crested macaque behaviour is significantly affected by the number of visitors outside their enclosures. The increase seen in one of the negative behaviours implies that visitors in part, are of welfare concern. However, whether increases in active-type behaviours and grooming or decreases in resting and huddling are suggestive of stress is not known, and as yet it is unclear from the literature what, if any, the implications of those changes are for welfare (Furiex and Meagher, 2015).

**Effect of visitor noise**

Visitor noise in the viewing area could be loud, regularly reaching above 70dB (the recommended limit for human well-being (WHO, 1999)). Even so, visitor noise had less of an effect on the macaque groups than visitor number, but three active-type behaviours (foraging, furniture use, and play) increased with increasing noise level. Increases in foraging and play behaviours have been observed previously in primates; Todd et al. (2007) saw increases in both behaviours with visitor group size in Diana monkeys, while increases in foraging and play was observed in both olive baboons *Papio anubis* and gorillas with visitor number and noise level (Snider, 2016). It is not clear what increases in these seemingly positive active type behaviours, such as play, may mean in terms of welfare (Held
and Špinka, 2011; Ahloy-Dallaire et al. in press, 2017). Indeed, the macaques may be enriched by increased noise levels and so stimulated to play (Hosey, 2000; Snider, 2016). However, if the noise is stressful, play may provide short term stress relief (Antonacci et al., 2011) or distraction. Conversely, it is also worth considering that playful or more active behaviours may draw in a larger crowd of visitors and subsequently higher noise levels, rather than the behaviours being a direct result of the visitors.

Vigilance increased with visitor noise level, again indicating potential welfare concern as above. In a study of 12 mammal species by Quadros et al. (2014) vigilance increased with noise in half the species. Similarly, Clark et al. (2012) observed an increase in visitor directed vigilance with increased noise levels in gorillas, an effect also found in zoo-housed orang-utans (Birke, 2002). Thus, this result is robust despite here being fairly subtle.

Resting behaviour again reduced with visitor noise level, but as explained above, it is not clear whether this was positive or negative. The fact that it seems to have been replaced with vigilance and playful active behaviour suggests that it may include negative and possibly some positive aspects, respectively. Furthermore, whether the resting behaviour was replaced by either vigilance or play could be partially dependent on the age of the individual macaques, with younger individuals more likely to play.

The effects of visitor noise levels on behaviour may have been fewer than those of visitor number because noise levels heard by the macaque groups may not have been as loud as where recording took place, although levels will still have been relatively loud or quiet. Additionally, it is likely that Sulawesi crested macaques are affected by noise outside the human frequency range (which the noise level metre is designed to pick up) as the closely-related Japanese macaque's (Macaca fuscata) upper limit is 34.5-kHz, compared to 17.6-kHz for humans (Heffner and Heffner, 2007). Therefore, the sound meter may not have recorded the sounds that most affected the animals. Future research measuring noise levels within the macaques hearing frequency and inside enclosures could help.
Mitigation of visitor effects using signs

Visitor noise was significantly quieter in the presence of both the sign treatments than with no sign present. However, the effect was subtle. This may have been partly because, when large numbers of visitors (>12) were present, the signs could get crowded and blocked from view of any new approaching visitors. This was particularly true for Zoo C, which had a small visitor viewing area where visitors could often be several people deep in front of the enclosure. Furthermore, that macaque enclosure was situated opposite the zoo’s gorilla enclosure in front of which large crowds would gather and, due to the gorillas’ popularity, high noise levels would occur. Also, the signs could not reduce other background noises from visitors at other nearby enclosures, or from other sound sources entirely. These factors could have reduced the effectiveness of both sign treatments.

There was no significant difference in visitor noise levels between the two sign treatments. The effectiveness of the signs suggests that sign presence alone could be all that is required to modulate visitor behaviour. However, where signs displaying an image of salient eyes have proved successful at inducing cooperative behaviour in people, the signs have been displayed at eye level (Bateson et al., 2006). In the present study signs could not easily be displayed at eye level due to enclosure constraints at different zoos, and so were displayed on A2 A-frame boards, meaning that the signs were at approximately at waist height of most adults. Not having these signs at eye level may have reduced the effectiveness of the watching eyes. Other features of the signs, such as size, font and colours used could also influence their effectiveness in future. For example, in a study exploring whether different messages on signs could reduce visitors’ banging on aquarium windows, signs which appealed more to people’s emotions had a better effect than signs which were neutral but polite (Kratochvil and Schwammer, 1997). The potential seen in previous studies for signs displaying salient eyes to modulate visitor noise levels, coupled with the potential seen in this study of signs whilst displayed at a sub-optimal height, warrants further research that explores the influence of these aspects. Whether signs would have to be used sparingly for sensitive species, rather than at
every enclosure, and whether they should be varied, to avoid habituation in the viewing public are questions that would be useful to investigate.

Conclusions

This study showed that visitor number and visitor noise level significantly affected zoo-housed Sulawesi crested macaque behaviour, and increased vigilance suggests a welfare concern. Active-type behaviours were seen to increase with visitor number and to some extent with visitor noise level, although it is unclear from the literature what, if any, the implications of this change are for welfare. Further research is recommended to assess if increased active and inactive behaviours are associated with stress or instead with welcome stimulation (Mason and Veasey, 2010).

Signs requesting visitors to be quiet show promise but efforts should be made to increase their efficacy. Consequently, further research is also required to test whether the use of signs with salient eyes can be effective at modulating zoo-visitor noise levels when displayed at eye level, or with an emotion-affecting message, as all options to help reduce noise levels inside enclosures should be pursued.

Acknowledgements

This work was carried out in part fulfilment of AB’s MSc in Wild Animal Biology jointly delivered by the Royal Veterinary College and the Institute of Zoology. We would like to thank the Universities Federation for Animal Welfare (UFAW) for awarding an Animal Welfare Student Scholarship for this research. Thanks also to the trust secretaries of the Whitley Wildlife Conservation Trust, the keepers from Paignton and Newquay Zoo, and the research and education officers and keepers of ZSL London, Chester and Dudley Zoos for their help and cooperation with this study.
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Captions

Table 1. Dates of study and macaque details for each of the five participating zoos.

Table 2. Ethogram of behaviours for Sulawesi crested macaques. The symbol ‘↘’ denotes behaviour predicted to decrease, ‘↗’ denotes behaviour predicted to increase with increasing visitor number or noise level and ‘?’ denotes that predicted behaviour change with increasing visitor number or noise level is not known. The ethogram is adapted from published ethograms, see Baker, 2012; Nickelson and Lockard, 1978; Thierry et al., 2000.

Table 3. Statistically significant effects of visitor numbers and noise levels on Sulawesi macaque behaviour. The behaviour category reflects suggested behavioural interpretations, although other interpretations are possible as outlined in the Introduction.

Figure 1. The two designs of sign. (a) ‘Eyes’ sign: sign with image of salient human eyes; and (b) Control sign with image of flowers.

Figure 2. Effects of visitor noise on Sulawesi macaque (a) vigilance and (b) resting behaviour, taking zoo into account. The white bars represent the absence of the behaviour and the grey bars represent its presence.

Figure 3. Effect of signage on mean noise levels. The data are logged to reflect the statistical analysis. To correct for the significant effect of visitor number on sound levels, data are presented as dB per visitor. The minimum value on the y-axis was selected as the 5th percentile value (because sound was never zero).