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RESEARCH ARTICLE

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# Visitor presence and a changing soundscape, alongside environmental parameters, can predict enclosure usage in captive flamingos

Paul Rose[1,2] | Alexander Badman-King[3] | Samantha Hurn[3] | Tom Rice[2]

[1]Centre for Research in Animal Behaviour, College of Life and Environmental Science, University of Exeter, Exeter, UK

[2]Department of Sociology Philosophy and Anthropology, University of Exeter, Exeter, UK

[3]Exeter Anthrozoology as Symbiotic Ethics, Department of Sociology, Philosophy and Anthropology, University of Exeter, Exeter, UK

**Correspondence**

Paul Rose, Centre for Research in Animal Behaviour, College of Life & Environmental Science, University of Exeter, Exeter EX4 4QG, UK.
Email: p.rose@exeter.ac.uk

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## Abstract

The sound environment of a zoo animal is a complex milieu of animal and human-generated sounds; coming from the species itself, other species, visitors, keepers and other zoo-users. Research determining how different components of the sound environment affect animal behaviour is surprisingly lacking but could have real-world impacts for animal welfare and zoo enclosure design. The current study investigated the effects of the sound environment on two flocks of flamingos housed in open-air enclosures at British zoos. Measures of how each flock used its enclosure (as a response variable) and environmental variables (Inband Power and Peak Frequency were recorded as characteristics of the sound environment, as well as temperature, humidity and cloud cover, and finally visitor presence—all as potential predictor variables) were made over a 2-month period. Assessment of space use by zoo animals is often used as a measure of the appropriateness of an exhibit and to understand welfare. Given that flamingo activity is influenced by weather and that the sound environment of the zoo is likely to be influenced by the number and the presence of visitors, it was assumed that these predictor variables would influence where the flamingos were located at different times of the day. As expected, there was a complicated relationship between enclosure use and Inband Power (average spectral density, a measure of sound energy) in both flocks; visitors generated salient sound but other visitor characteristics such as their physical presence may have impacted the movement of the birds around their enclosures. Results show a complex picture where environmental conditions influence flamingo enclosure usage as well as visitor presence and sounds around/in the enclosure. Findings are not consistent between the two flocks, with one flock demonstrating distinct temporal change to enclosure zone occupancy and the other responsive to humidity and cloud cover variation. We believe enclosure use can provide a valuable indication of how birds react to their soundscape; however, our findings suggest more work is needed to unpick the components of captive sound environments, and their relative effects on how animals use their space.

**KEYWORDS**
animal welfare, enclosure, sound, space use, visitor effect, zoo husbandry

## 1 | INTRODUCTION

Assessment of spatial usage within an enclosure is often used as a measure of how appropriate an exhibit is for a species (Hunter et al., 2014; Rose & Robert, 2013; Ross & Lukas, 2003) as well as being a means of determining the welfare experiences of the enclosure's inhabitants (Rose et al., 2018, 2014b; Ross et al., 2009). Numerous biological and anthropogenic factors can influence how zoo animals use the space they are provided with. Proximity to other enclosures, the presence of visitors, the composition of animal groups within the enclosure, husbandry routines and weather all influence the desire of a species to spend time within specific areas of the exhibit it inhabits. Less desirable areas of an enclosure will be ignored or used for proportionally less time compared to more favourable areas (Troxell-Smith et al., 2017). Uneven space use can suggest a lack of comfort within an enclosure (Sulser et al., 2008) and therefore indicate potential negative welfare states. Conversely, some species may seek out psychological or physiological challenges when living in captivity and therefore approach potentially threatening or aversive stimuli (e.g., large crowds of noisy visitors) that increases the complexity of the animal's surroundings (Moodie & Chamove, 1990).

Previous literature on the effects of sound (natural, artificial and 'enriching') on enclosure usage and spatial preferences have predominantly focused on mammals (Ogden et al., 1994), even though other taxonomic groups (e.g., birds, fish) can be more speciose in captive collections (Melfi, 2009; Rose et al., 2019). Research suggests that visitor-generated sound can influence animal welfare by affecting whether or not individuals will venture around all areas of their enclosure (Fernandez et al., 2009). At the same time, examples of sound being used as enrichment, for example, species-specific recordings, natural sounds from the animal's habitat and music, are present in the literature (Clark et al., 2012), suggesting that there is an awareness that the sound environment can influence activity and hence enclosure usage (Robbins & Margulis, 2016; Williams et al., 2017).

Based on previous papers that illustrate sound influences on zoo-housed bird activity (e.g., Robbins & Margulis, 2016), the aim of this research was to consider the effect of the sound environment on the enclosure usage of a very common zoo bird, the flamingo. Flamingos in wild flocks use sound to organise their nesting and breeding activities (Mathevon, 1997), with referential calls noted for parents to find their chicks (Mathevon, 1996). Flamingo vocalisations have also been measured during courtship displays, with birds producing specific acoustic signals as part of their display routine (Boylan, 2000; Kahl, 1975). These birds, then, show a degree of attunement to their sonic environments and can direct their own and their flock's behaviour in response to heard sounds. Given that auditory perception may influence where flamingos are likely to be within their enclosure, added to the fact that flamingos are popular and a commonly-housed exhibit (so that research findings related to this species can have wide impact), they were identified as good subjects for a study on whether sounds influence the location of a flock within its zoo environment.

### 1.1 | Auditory range of the flamingos

Flamingos can perceive and process sound that is threatening or disturbing and alter their movements and location choice accordingly. Wild flamingos can come into conflict with farmers due to the crop-damaging actions of foraging birds in rice fields (Ernoul et al., 2014), and flamingos are dissuaded from foraging in fields via the use of alarm guns and cannons, whose sound discourages the birds from landing (Ernoul et al., 2014). At the same time, flamingo social groups or nesting colonies are noisy environments (Amat & Rendon, 2017), and flamingo communication depends upon the birds' ability to distinguish the calls of mates and offspring amid that noise.

Information on the auditory range of flamingos and their auditory sensitivity is limited. However, some work, for example (Mathevon, 1996, 1997), is available to guide understanding of what flamingos may be able to hear. Mathevon (1997) provides some useful information on contact calls in greater flamingos *(Phoenicopterus roseus)*, which is applicable to both flocks in this study. One flock consists of greater flamingos and the other flock is of Chilean flamingos, *P. chilensis*, a species in the same genus. Selected parameters for contact calls in greater flamingos vary between individuals but for Mathevon (1997), in his study of five of these birds the frequency at which calls had the greatest energy was c2580 Hz (for two birds), 1538 Hz (for one bird) and c880-c960Hz (for two birds) (Mathevon, 1997). Mathevon (1997) presents a spectrogram for these contact calls that ranges in frequency from below 1.5 kHz to above 4.5 kHz. As reviewed in Beason (2004), the social vocalisations (contact, display and aggressive calls) of the African penguin, *(Spheniscus demersus*), another colonial, 'noisy' waterbird (Favaro et al., 2014), have a lower limit of 100 Hz and an upper limit of 15 kHz (and the penguins are most sensitive to hearing sounds in the range of 0.6–4 kHz). Close relatives of the flamingos, the pigeons, Columbidae (Zhang et al., 2014), have a lower limit of 50 Hz to an upper limit to their auditory range of 11.5 kHz (most sensitive between 1.8 and 2.4 kHz). We used these environmental, ecologically and taxonomically similar sonic and auditory ranges to assess the impact of the sound environment that we recorded at these two zoological collections on the flamingos housed there. Flamingos are likely to have a fairly wide range of acoustic sensitivity, with an area of peak sensitivity in their auditory range of between 1 and 5 kHz, extrapolating from Mathevon (1997). As such flamingos are likely aware of visitor and other anthropogenic noise within the zoo environment.

The aim and objectives of this study were to determine whether flamingos respond to change to the sound environment by changing their usage of their zoo enclosure. This aim was accomplished by recording the enclosure usage of two flocks of flamingos at two different zoos by zoning each enclosure into zones of biological relevance (i.e., resources available to the birds such as nesting area or feeding area) and determining how many flamingos occupied these zones at different times of the day. Whilst recording where birds were within their enclosure, we continuously recorded the sound environment and visitation to the enclosure to analyse the potential impacts of these variables on enclosure use.

## 2 | METHODS

Two species of flamingo, greater and Chilean, were studied at Bristol Zoo Gardens (hereafter BZ) and Paignton Zoo Environmental Park (hereafter PZ) respectively. Greater flamingos ($N = 56$) at BZ were housed in an open-air, walk-in aviary containing several other species of wildfowl (white-faced whistling duck, *Dendrocygna viduata*, and Meller's duck, *Anas melleri*) and wading birds (Eurasian avocet, *Recurvirostra avosetta*). Chilean flamingos ($N = 53$) at PZ were housed in an open-topped walk-past exhibit that included several species of captive wildfowl (e.g., mandarin, *Aix galericulata*, and North American wood duck, *A. sponsa*) plus native birds that were free to enter the enclosure (e.g., mallards, *Anas platyrhynchos*; herring gulls, *Larus argentatus*; and moorhens, *Gallinula chloropus*). Flamingos were fed on bespoke flamingo pellet provided in bowls (at PZ) and in a separate feeding pool (BZ) in the morning and late afternoon depending on keeper routine. Flock husbandry during the study period was minimal. Keepers were seen to observe and make notes on nesting activity at BZ using binoculars.

Enclosure zones were defined based on their biological relevance to the flamingos (i.e., feature provided within the exhibit that the flamingos could access and use for specific activities) and measured as discrete sections of overall enclosure area (Figure 1). The total areas of each enclosure have been taken from Google Earth Pro v. 7.3.2.5776 using the 'draw polygon' function (Google, 2019).

Pools were split into the areas defined in Figure 1 based on their proximity to visitors and links to other resources in the enclosure that could influence their attractiveness to the birds (e.g., at BZ, the pool around the waterfall being deeper and the channel to the flamingo house being shallower than other pool areas). Photographs of each enclosure are provided in the supplementary information (Figure S1).

Each flock of flamingos was observed for five days. PZ on 15th, 26th, 29th April and the 3rd and 16th May 2019; BZ on 30th April and from the 4–7th May 2019. Observations were 20 min long and took place at 10:00, 11:00, 12:00, 14:00 and 15:00 for each day, except for 15th April at PZ when no 15:00 observation took place due to unforeseen circumstances. These observation times were chosen to account for the natural change in flamingo activity over time, with birds being more active in the morning and later afternoon and less active midday (Rose et al., 2018) whilst remaining within the public opening times of each zoo. For both flamingo flocks, instantaneous scan sampling with 1-min sample intervals (Martin & Bateson, 2007) was utilised to count the number of birds within each of the enclosure zones listed in Figure 1. Continuous video recording of the flock for each 20-min period, using an HD Panasonic Lumix digital camera, enabled individuals within each enclosure zone to be counted accurately. Still photos, using an Honor 10 Lite smartphone were taken of birds out of sight of the video recorder to capture all individuals for each sampling point. Sound at the enclosure was recorded from public viewing areas using a Zoom H4nPro. The sound recorder was fixed to the top of a tripod (1.65 m high) with an omnidirectional XY microphone configuration and a fixed recording level of 70 and no limiter or compressor. A microphone windshield was used in all conditions. Recordings were 16 bit, made in WAV format

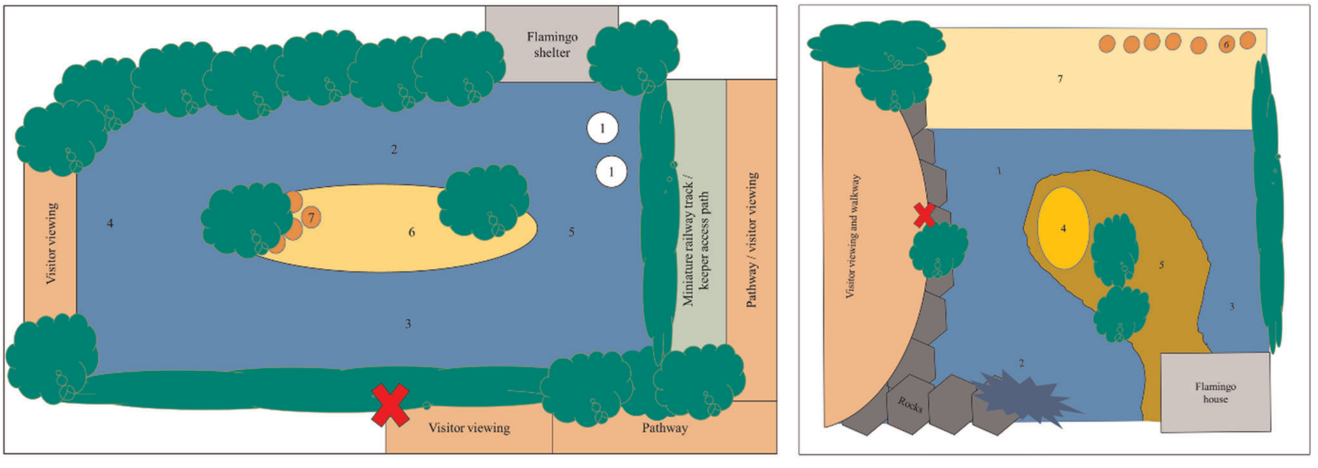


**FIGURE 1** Enclosure zones, area and percentage of whole exhibit for Chilean flamingos (Paignton Zoo, left) and greater flamingos (Bristol Zoo, right). Map of each enclosure (not to scale) corresponds to zones in the table. Red cross in each diagram indicates the location of the observer [Color figure can be viewed at wileyonlinelibrary.com]

with a mono mix and had a sample rate of 44.1 kHz. As indicated in Miyara et al. (2010) the Zoom H4 recorder is suitable for acoustical measurements. The recorder microphones were not calibrated, meaning that the sound measurements we produced were not absolute. Whilst we are able to make relative comparisons, we recognise this limitation and a lack of calibration could potentially account for some of the variation in the sound measurements between the two enclosures.

The sound recorder was positioned in the same location at the edge of each exhibit for all bouts of space use data collection. At PZ, the sound recorder was usually 10 m away from the main flock (on the island within their exhibit) but flamingos could be 40 m away the widest point and 2 m away at the nearest point. At BZ, the flamingos were usually 15 m from the observer, but they could be 20 m away at the furthest point and as close as 2 m. Distances were estimated via enclosure dimensions and 'draw path' in Google Earth Pro. Ideally the microphones would have been placed in the enclosure to reproduce the acoustic position of the birds, but this could not be done without causing disruption to the birds' activities during nesting and potentially creating some risk of harm to them and the equipment. We were in any case interested in whether we could associate the relative noise levels issuing from the visitor areas with patterns of enclosure use by the birds.

## 2.1 | Sound measurement

Measurement of the sound environment was conducted by recording sound continuously during observation periods from where the observer was located at the edge of the enclosure, and then analysing specific sound characteristics at the point when birds were observed. Analysis of the sound environment was undertaken in Raven Pro v.1.6 (Center for Conservation Bioacoustics, 2019). Each 20-min sound recording (as a WAV file) was uploaded into Raven Pro and the spectrogram and waveform (Figure S2) of the recording was evaluated using measurement tools within Raven Pro. The spectrogram represented the signal strength present in the waveform. Measurements of Peak Frequency (Hz) and Inband Power (dBFS, decibels relative to Full Scale) were selected from the spectrogram. Inband Power measurements included all frequencies present in the waveform. Inband power (IP) is defined as the average power spectral density (energy per unit frequency per unit time) over the band of interest with respect to time (in this case IP was recorded at 1 min interval for every 20 min observation). As dBFS can never be higher than 0, all values are negative (Price, 2007) and negative numbers closer to 0 indicate more energy and therefore more power (Scott, 2012). Peak frequency (PF) is defined as the frequency of maximum power at a specific time point (Center for Conservation Bioacoustics, 2019). In our analysis that specific time point was the one at which the observations of the birds were made. These sound metrics were chosen to characterise the 'noise' around the enclosure as well as describe the variation in sound between each sample point. IP provides a measure of the sound's power through time and has been useful in understanding behaviour and habitat preferences relative to background noise and environmental features in other non-domestic species (Hedwig et al., 2018; MacLeod et al., 2019). Other research performed on birds, and their responses to a 'noisy environment', used measurement of PF as the preferential measure of acoustic variation (Halfwerk & Slabbekoorn, 2009; Zollinger et al., 2012), hence the decision to extract this additional metric from the recordings taken at each zoo.

Selections from the spectrogram were taken at the corresponding sample point for recording flamingo location (i.e., at the minute 1, minute 2, minute 3 points and so on for each recording period). The selection tool was moved along the waveform until the corresponding time of the space use data recording was identified and then that minute (noted in seconds on Raven Pro) was selected. The spectrogram was then used to determine the measurements noted above. When each minute had been measured, the sound measurements from the table under the waveform and spectrogram were copied directly into Microsoft Office Excel for statistical analysis and comparison with space use data. An example of the selection process is shown in the supplementary information (Figure S2), which illustrates both the waveform and the spectrogram, and the selection points used for that recording.

## 2.2 | Visitors and weather

The total number of zoo visitors who stopped/observed/entered/experienced each enclosure was recorded for each observation period (visitor total), as well as the maximum number of visitors at or in the exhibit at each specific observation time (visitor max). Visitor number was tallied as people walked past the observer to reduce the likelihood of counting the same people more than once. These two measures were taken to categorise how busy (with visitors) each enclosure was; for example, there may have been a large total number of visitors per observation period, but each discrete group was small, or there may have been a lower number of people overall as they all arrived together (giving a low total visitor number but a high maximum group size). Flamingo behaviour can be influenced by weather and sunshine, and both greater and Chilean flamingos can show wider enclosure usage with increasing environmental temperature (Rose et al., 2018). The 'visitor effect', that is, the behavioural response of zoo animals to the presence of visitors (Hosey, 2000), and visitor presence at the zoo is influenced by the weather (Goodenough et al., 2019; Rose et al., 2020). As a result, temperature (°C), humidity (%) and cloud cover (%) were also recorded for each observation session using Google Weather on a smartphone. In the same manner as Rose et al. (2018), cloud cover estimations from Google Weather were checked against actual visual observations by the researcher of the degree of open sky/cloud at the time of the recording. Flamingo flock activity may be influenced by exposure to direct sun (King, 2008) hence our attempt at estimating weather variables. Flamingo observations took place in April and May (random dates) for each zoo to limit any climate or weather effect on flamingo activity. Observations were conducted during the week and over a weekend, to provide variation in visitation across different days and times.

## 2.3 | Data analyses

The flock's occupancy of the enclosure zones was assessed using the modified Spread of Participation Index (SPI) (Plowman, 2003). SPI provides a value between 0 (maximum occupancy of all enclosure zones) and 1 (biased usage of one specific zone) and compared an expected frequency of enclosure zone occupancy with that directly observed. The formula for the modified SPI = $\sum | fo - fe | /2(N - fe_{min})$. Where $N$ is the number of all observations in all zones; $fo$ is the observed frequency of zone occupancy; $fe$ is the expected frequency of zone occupancy; $fe_{min}$ is the expected frequency of occupation in the smallest zone. $fe$ was calculated by dividing the percentage area of each enclosure zone by 100 and then multiplying by the total number of birds.

### 2.3.1 | Modelling sound and other potential predictors of enclosure usage

Data were analysed in RStudio v. 1.2.1335 (RStudio Team, 2018) using R v. 3.6.1 (R Core Team, 2019), with SPI value as the outcome variable and time of day, visitor number, Inband Power, Peak Frequency and weather information as predictors of enclosure usage. To determine which was the most appropriate measure of flamingo enclosure zone occupancy, mixed-effects models were run using the 'lmerTest' package (Kuznetsova et al., 2016) with either the average SPI measurement OR the maximum SPI measurement for that observation session as the dependent variable. Models were also run with either Vistor total and Visitor max OR Visitor total only OR Visitor max only. Using the 'car' package (Fox & Weisberg, 2011) to calculate the variance inflation factor for the model, Visitor max and Visitor total were correlated and therefore Visitor total was included in the final model. Running the model with Visitor total or Visitor max and calculating the $r^2$ value showed a higher $r^2$ for Visitor total (.6) compared to Visitor max (.3). Other predictors were maximum Inband Power, maximum Peak Frequency, time of day, temperature, humidity, cloud cover (as a measure of sunshine exposure) and the interaction for total visitor × temperature, total visitors × humidity and total visitors × cloud cover. The interaction for total visitors × Inband Power and total visitors × Peak Frequency was also included in models and $r^2$ values assessed. Date were also included as a random factor as the same measurements were repeated each day in the same population, therefore 'date' is the factor that changes. $r^2$ values were calculated using the 'MuMIn' package (Bartoń, 2013) in RStudio and compared between models to determine the model with the best fit. Replicate analyses were run on each flamingo flock.

Correlations of visitor number against environmental parameters (temperature, humidity and cloud cover) and sound measurements (Inband Power and Peak Frequency) were run to determine any significant interactions to include in the mixed-effects models run on SPI output. At both zoos, visitor number per observation period correlated with temperature (PZ $r = -.73$; $N = 24$; $p < .001$; BZ $r = -.46$; $N = 25$; $p = .02$) with fewer people being present around or in the enclosure on hotter days. Visitor number also correlated with Inband Power at BZ ($r = .46$; $N = 25$; $p = .02$); higher number of visitors create more sound energy. For each model, significance of fixed effects was determined using $F$ tests with Satterthwaite's method for corrected degrees of freedom.

The final model run (for each zoo) was SPI approximately (1 | Date) + Time + Visitor total + Temperature + Humidity + Cloud cover + Inband Power (max) + Peak Frequency (max) + Inband Power × Visitor total + Temperature × Visitor total. This model provided the highest conditional $r^2$ value per Zoo. Across model output, where multiple $p$ values are presented and compared, a Benjamini and Hochberg (1995) corrected alpha level was applied to reduce the chance of false discovery rates.

We did not expect to find a clear relationship between PF and the flamingos' enclosure usage as we expected high variability in our PF measurements due to the dynamic nature of the zoo sound environment. We did, however, wish to explore the extent to which PF fell within what we estimated to be the flamingos' range of maximum sensitivity of 1–5 kHz (as per Mathevon, 1997), although as mentioned above (with reference to Favaro et al., 2014 and Zhang et al., 2014) the range of frequencies audible to flamingos is potentially much wider. We present descriptive statistics on the variation in the PF at the start of the relevant section in the Results.

### 2.3.2 | Unpicking the 'visitor effect'

To understand how visitor grouping may influence enclosure usage, a scatterplot with liner regression was draw to illustrate any relationship between visitor group size at enclosure (the maximum number of visitors counted at any one time during each observation period) and the mean SPI for that observation period. To unpick any influence of time of day on the maximum visitor number (at any one time at/in the enclosure per observation session) for both zoos, and of time of day on enclosure usage for the flamingos at BZ, these relevant data (that were normally distributed) were entered into a one-way ANOVA, again in RStudio. Categories of time (morning, late morning, midday, early and later afternoon) were included as the predictor in the ANOVA. Finally, to understand the effects of weather on the total number of flamingos in key zones (nesting areas, loafing areas and pools) a linear model was run for each zone (nests, island, pool) at each zoo against the degree of direct sunshine over the enclosure (100% cloud cover). Again, these data for this linear model were tested for normality. Graphs to show any relationship between SPI, humidity and cloud cover have converted percentage humidity and cloud cover to a proportion to enable scaling of axes.

### 2.3.3 | Assessing any measurement effect on enclosure use assessment

Based on previous work (Rose et al., 2018), the degree of enclosure zoning (in large exhibits) can influence the reliability of SPI in determining overall flamingo enclosure usage. Therefore, for the large enclosure at PZ, all analyses were run on the original zoning of the enclosure (Figure 1) and again with all sections of the island and all sections of the pool (except the feeding area) merged, giving an enclosure with only three zones.

## 3 | RESULTS

### 3.1 | Modelling sound and other potential predictors of enclosure usage

Flamingo enclosure usage at PZ showed occupancy of more zones at IP values closer to 0 (i.e., sounds with more power), with lower SPI values indicative of a wider enclosure zone occupancy (Figure 2). To further illustrate the variation of the sound environment, the range of PF recorded is illustrated in Figure 2 but shows no relationship to the flamingo's enclosure usage at either Zoo. Only one PF measurement was recorded as higher than the estimated peak range of flamingo's auditory sensitivity, 5 kHz, at PZ. The maximum PF at BZ was 3.18 kHz. The modal PF at both Zoos was 0.188 kHz but the range in PF was greater at PZ (interquartile range 187.5– 9375) than BZ (187.5–750.0). The significance of multiple *p* values from the model output was compared to a corrected alpha level of .017 to reduce false discovery (Benjamini & Hochberg, 1995) and the conditional $r^2$ for the PZ model was $r^2 = .6$. Predictors of change in enclosure zone occupancy for PZ flamingos are described in Table 1. Flamingos at PZ reduced enclosure use at higher temperature (estimate 0.002 ± 0.004) and widened enclosure use with more cloud cover (estimate −0.004 ± 0.002). At IP closer to 0, the flamingo's enclosure usage was wider (estimate −0.118 ± 0.054) but the estimate for Visitor total (0.016 ± 0.0047) suggested that increasing total numbers of visitors corresponded with more restricted enclosure usage. A relationship between the flamingo's enclosure usage

**TABLE 1** Predictors of flamingo enclosure usage (change in SPI value) at PZ

| Predictor | F | Df | p | Q |
|---|---|---|---|---|
| Cloud cover | 11.36 | 1, 10.16 | .007 | .0111[a] |
| Visitor total | 11.16 | 1, 10.13 | .0073 | .0167[a] |
| Visitor total × Inband Power | 11.86 | 1, 10.87 | .0056 | .0056[b] |
| Inband Power | 4.87 | 1, 11 | .049 | .028 |
| Temperature | 5.43 | 1, 10.99 | .04 | .02 |
| Visitor total × temperature | 4.38 | 1, 11 | .06 | .03 |
| Time of day | 1.95 | 4, 9.91 | .180 | .04 |
| Humidity | 0.29 | 1, 6.28 | .6086 | .04 |
| Peak Frequency | 0.04 | 1, 9.96 | .8379 | .05 |

[a]Significant predictors (*Q* values from Benjamini and Hochberg (1995) corrected alpha level of .017).
[b]Borderline significant predictors.

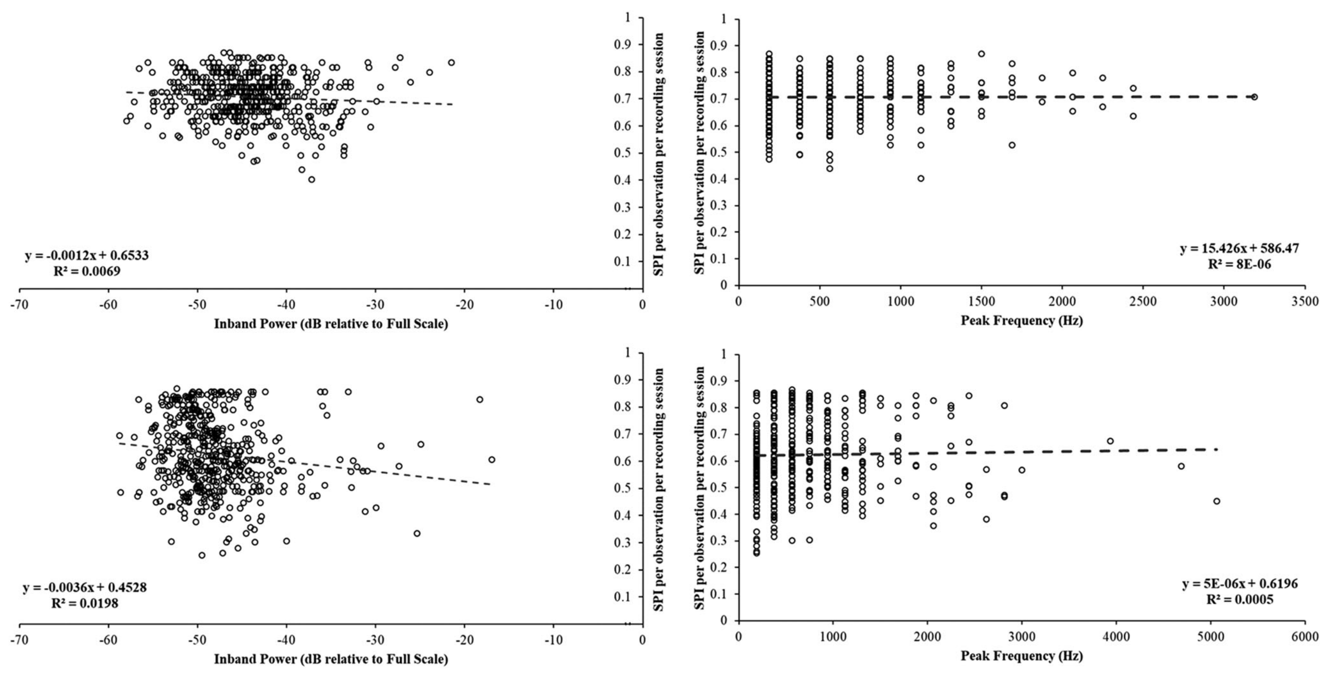


**FIGURE 2** Left- plots of Inband Power for BZ (top) and PZ (bottom) against SPI. Right: plots of Peak Frequency for BZ (top) and PZ (bottom) against SPI (right)

and the interaction between the total visitor number and IP may be present (restricted enclosure usage with increasing visitors and IP, estimate = 0.0005 ± 0.0001).

Figure 2 shows that for flamingos at BZ, there is no relationship between SPI value and calculated measures of the sound environment. When modelling the effects of key predictors (conditional $r^2$ value = .65) no corrected alpha level was required as change in enclosure usage was not significantly predicted by any factor. Time of day approaches significance ($F = 3.22$; $df = 4, 12$; $p = .052$)—model estimates showed widest enclosure usage in the morning (estimate = 0.078 ± 0.032) and in the late afternoon (estimate = 0.1 ± 0.03). Visitor number, weather, sound measures or interactions between the sound and visitor number and sound and temperature predicted enclosure usage.

## 3.2 | Unpicking the 'visitor effect'

Figure 3a illustrates that BZ enclosure usage (mean SPI for that observation session) increased when the maximum number of visitors (as a discrete count) increased at the enclosure, but this was nonsignificant trend (estimate = −0.0072 ± 0.07; $p = .27$). Figure 3b shows a similar pattern at PZ but again the trend is nonsignificant (estimate = −0.002 ± 0.004; $p = .63$); however, any relationship with maximum visitor number at PZ may be complicated by outliers. Two outliers of 25 and 33 visitors were identified and these two outliers had suggested wider enclosure use with increasing visitor numbers, Figure 3b. Removing them, Figure 3c, alters the trend shown on the graph (estimate = 0.0043 ± 0.014) but does not reveal a significant relationship ($p = .756$).

When assessing the time of day at which highest numbers of visitors (as a discrete count) were seen at the enclosure, there is no temporal effect on the maximum visitor group at the PZ flamingo enclosure ($F = 1.69$; $df = 4, 19$; $p = .193$). However, for BZ significantly larger groups of visitors watched the flamingos in the morning compared to at other times of the day ($F = 2.87$; $df = 4, 20$; $p = .05$), mean maximum group size for mornings = 27.2; mean maximum group size for later afternoon = 9.4. Flamingos had a wider zone occupancy (lower overall SPI) in the morning compared to in the later afternoon ($F = 3.54$; $df = 4, 20$; $p = .024$); the mean SPI in the morning = 0.632 (±0.06) and the mean SPI for the afternoon = 0.740 (±0.04). The relationship between flamingo enclosure use and visitor number is even less clear at PZ, where there is no time of day effect on the flamingos (Figure 4).

Environmental conditions can influence the enclosure usage of captive flamingos differently (Figure 4). There is an apparent relationship between visitors and SPI for the BZ flamingos, but environmental factors show no consistent effect. However for PZ, cloud cover/degree of sunshine significantly affects the pool and island usage of the Chilean flamingos with birds using the island more when it was sunny (estimate = 6.83 ± 1.55; $df = 22$; $t$ value = 4.41; $r^2 = .45$; $p < .001$) and their pool when it is more cloudy (estimate = −5.27 ± 1.43; $df = 22$; $t = −3.7$; $r^2 = .36$; $p = .001$). There is no cloud/sunshine effect on usage of the flamingo's nesting area. For greater flamingos at Bristol Zoo, there is no cloud/sunshine effect on where the birds are likely to be.

## 3.3 | What about a measurement effect?

The original zone categorisation at PZ was compared to a simplified enclosure zoning for these Chilean flamingos in Figure 5 (mean SPI for each method of zoning including the mean IP measure for each observation session). Running the same modelling on the PZ flamingos but with this simplified enclosure zoning showed that only cloud cover ($F = 13.24$; $df = 1, 10.74$; $r^2 = .72$; $p = .004$; $Q = .0056$) significantly predicted enclosure usage. A corrected alpha level of .006 was calculated (Benjamini & Hochberg, 1995) to avoid false discovery of significance. The previous significant influences of visitor total ($Q = .0167$) and Visitor total × IP ($Q = .01$) disappear. Therefore, careful consideration of how an enclosure is zoned when assessing influences of the sound environment, of climate and of the visiting public is required. Combining all pool areas together at BZ

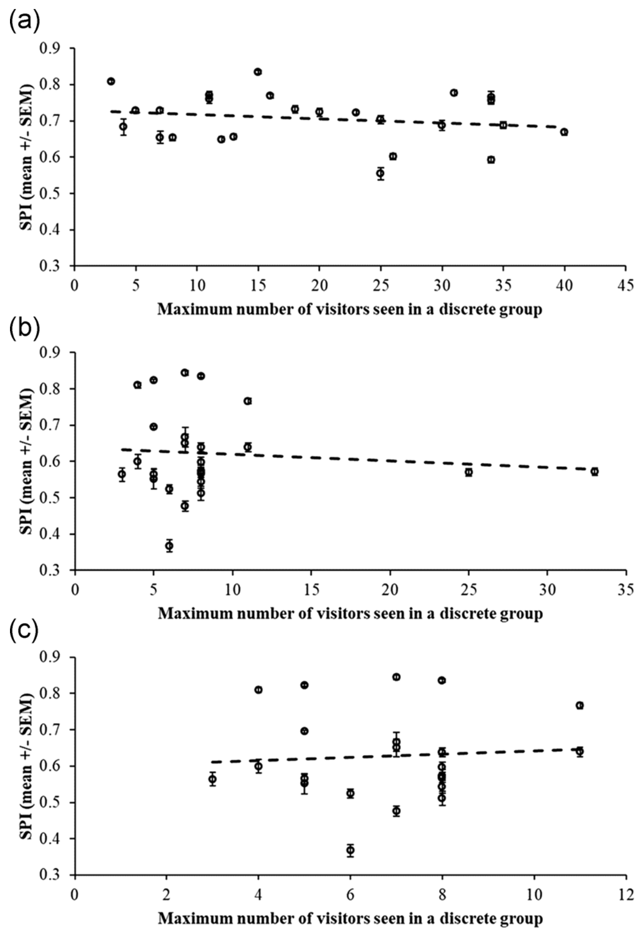


**FIGURE 3** Scatterplots with fitted linear regression lines to show the maximum number of visitors seen at each enclosure, at any one time, compared to the mean SPI value for that observation session. BZ greater flamingos (a), PZ Chilean flamingos with outliers (b) and without outliers (c)

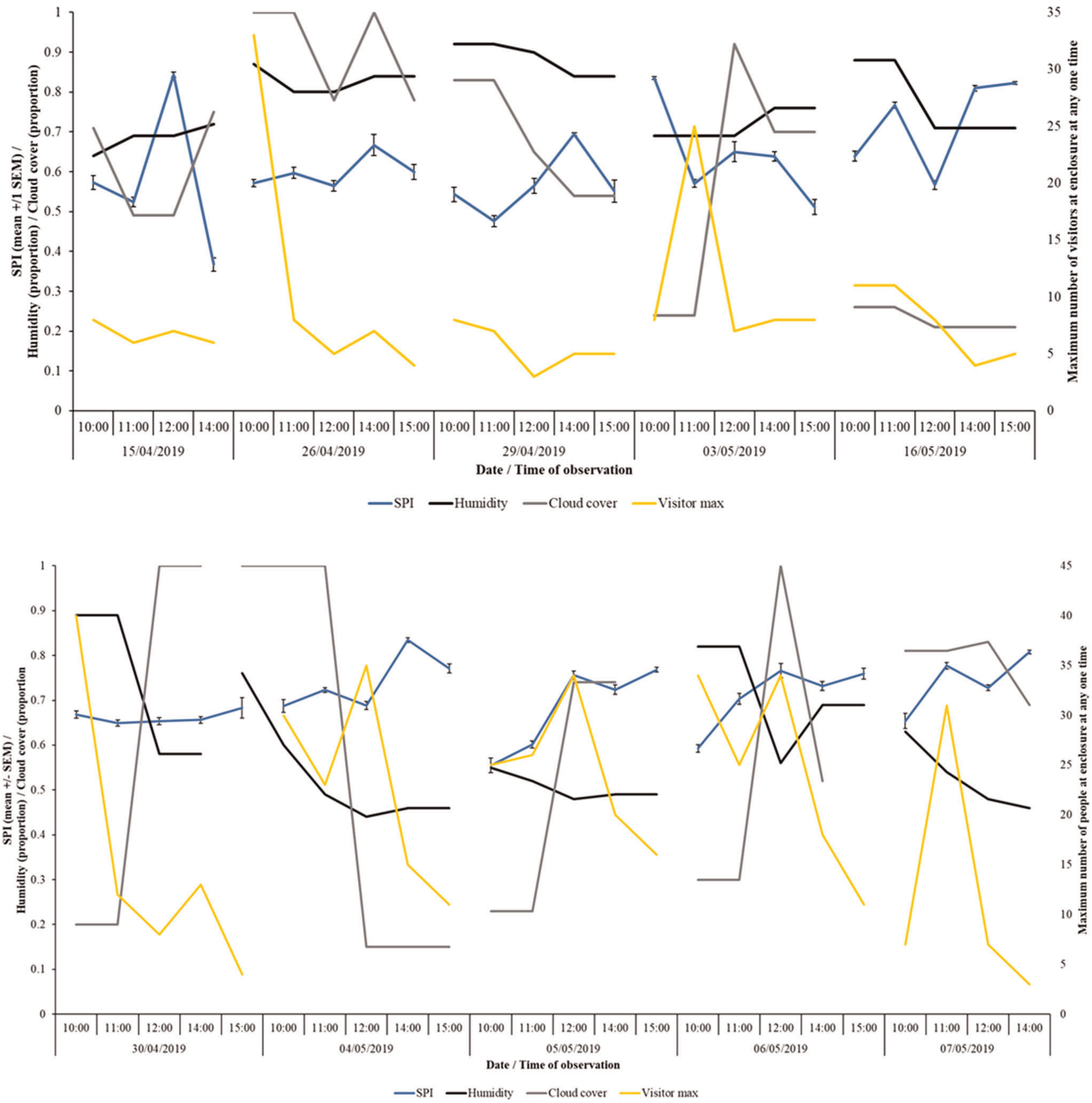


**FIGURE 4** Enclosure use (mean SPI) by captive flamingos plotted against humidity, cloud cover and maximum numbers of visitors (per observation session). Top: PZ flock. Bottom: BZ flock [Color figure can be viewed at wileyonlinelibrary.com]

and keeping the nest site, sanded beach, island and feeding area separate does not affect SPI calculation for each day of the study and no further analysis was conducted.

## 4 | DISCUSSION

This research aimed to investigate how change to the sound environment in and around a flamingo's enclosure at the zoo affected the location of the birds within their exhibit. These results suggest that enclosure usage in zoo-housed birds can be influenced by auditory stimuli, but climatic factors and human presence play a role too. This is a complicated relationship between many covariates, and it is hard to gauge precisely the overall effect of each. A summary of the key findings from both flocks is provided in Table 2. Flamingos at each zoo showed different results in relation to all of the measurements taken but for both flocks, maximum number of visitors at/in the enclosure at any one time showed a relationship with a wider enclosure usage. The relationship between wide enclosure use in the flamingos

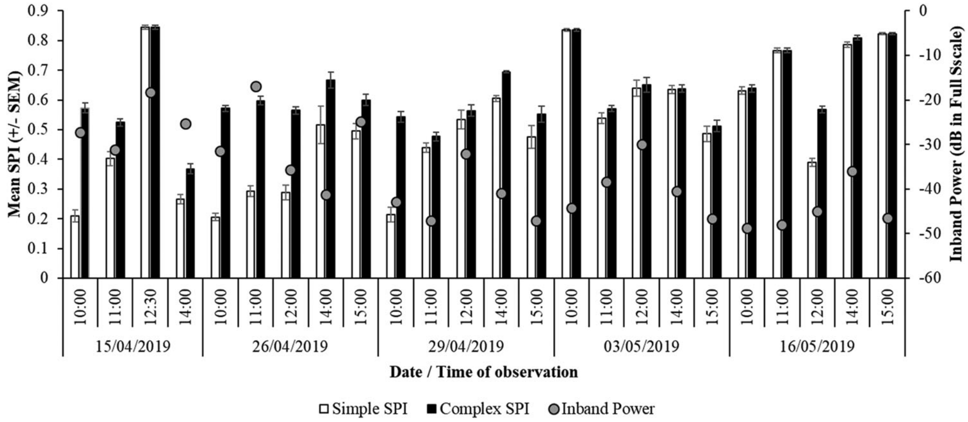


**FIGURE 5** Comparison of complex zone allocation (black bar) compared to simple zone allocation (white bar) for the Chilean flamingo flock, overlaid with mean Inband Power for that observation period to show how the method of determining enclosure use may influence interpretation of the influence of other variables (i.e., features of the sound environment) on flamingo space use

and the influence of visitors may be an effect of the time that the birds are active, their activity subsequently drawing people in to see them. Sound may have an impact on flamingo enclosure use at PZ where the occupancy of more enclosure zones was influenced by the total number of visitors and the related higher Inband Power measurements. This may indicate that the flamingos move around when sound levels are higher, because they are avoiding noisy crowds of visitors. Consideration of resource allocation and enclosure zoning is needed in such research; under the simpler enclosure zoning for the PZ flamingos, for some days of observation, enclosure use becomes wider and flamingos are deemed to be inhabiting 'more' of their enclosure. Published work on sound, the visitor effect and species' responses indicates that with increasing visitor number come increasing sound energy levels (noise) with a potentially pronounced change in animal behaviour (at the levels of both individual animal and species) involving increases in vigilance and movement (Quadros et al., 2014).

Species and husbandry differences may account for some of the results seen. Chilean flamingos occur at higher altitudes than greater flamingos (del Hoyo, 1992; Valqui et al., 2000) and therefore sunshine may play more of role in directing and influencing flock activity. This may be especially true around breeding time. In this study, birds were performing their courtship display and investigating nesting sites during the course of data collection. As noted in other research on Chilean flamingos, a flock's enclosure usage becomes more restricted as weather conditions become sunnier and their general activity is less affected by time of day compared to other flamingo species (Rose et al., 2018). These flamingos at PZ may be following a similar pattern of enclosure usage to that seen in other captive flocks. As birds in this group moved on to the island during sunnier weather, birds may be congregating in 'safe' spaces of the enclosure (i.e., the island surrounded by water for preening, loafing for nest site inspection). A lack of any relationship between increasing sunlight and wider enclosure usage is noted in other captive greater flamingos (Rose et al., 2018) Greater flamingos are a widespread species, occurring across many countries and climatic regions (Bird Life International, 2018; del Hoyo, 1992), able to cope with a range of habitats and conditions; therefore, climate-related activity changes may be limited in captivity when compared to flamingos from a more restricted, more specialised range. Wild flamingo flocks are known to be disturbed by human presence (Brown et al., 1973; Espino-Barros & Baldassarre, 1989; Frid & Dill, 2002; Yosef, 1997, 2000) and will increase in vigilance behaviours when humans are near or move away from areas frequented by people. Flamingos live for a long time (Rose et al., 2014a; Wasser & Sherman, 2010) and many birds in zoos are wild founders; such individuals may be more wary of human presence than captively bred birds. Consequently, it is not unreasonable to speculate that zoo-housed flamingos may move away from large crowds around their enclosure to quieter parts of their exhibit, consistent with findings on the movements of wild birds (Ernoul et al., 2014).

The sound produced by each flamingo flock contributed to the soundscape of the enclosure at each zoo and whilst this was recorded, it could not be isolated from the recording. Whilst not measured specifically and based on observation, the Chilean flamingo flock was much quieter than the greater flamingo flock during this data collection period, only becoming louder and more vocal during courtship display or when birds argued over resources. By contrast, the greater flamingos were much more vocal during a wider range of activities throughout observation days. Chilean flamingos could be a more sound-sensitive species, coming from a quieter social environment, and this is worthy of further investigation, given the existing literature that states individual species' sound tolerances and sensitivities can affect how they cope with the sonic environment of the zoo (Dancer & Burn, 2019; Harley, 2019). Closer study of the auditory range of the flamingo would be a useful and relevant extension to this research, as would calibration of the recording equipment to maximise the accuracy of the sound measurements and strengthen measurement comparisons. We state calibration

**TABLE 2** Summary of the impact or influence of auditory, anthropogenic, environmental, temporal and methodological variables on enclosure usage data from these two flamingo flocks

| Species | Impact of sound? | Impact of visitors? | Impact of weather? | What influences visitor number? | Impact of time of day? | Consider enclosure zone number? |
|---|---|---|---|---|---|---|
| Chilean | Inband Power closer to 0 may correspond to increased occupancy of more enclosure zones | Potential reduced enclosure usage seen when more visitors are present. Complex relationship with IP (and hence enclosure use) may be apparent | Zone occupancy is sensitive to cloud cover and may be affected by increasing temperature | No time-of-day effect on maximum number of visitors at the flamingo enclosure | No effect on enclosure usage | Yes. Combining all areas of a larger pool widens enclosure usage estimates. And negates a sound or visitor effect |
| Greater | No effect of sound environment on enclosure usage | Non-significant but wider enclosure usage may correspond to bigger crowds at the enclosure | No environmental predictors of zone occupancy | Significantly more people present at the enclosure in the morning | Wider enclosure use in the morning and late afternoon | Not for this exhibit. Five combined zones give the same results as seven distinct zones |

*Note*: Impact of sound refers to change in enclosure use associated with a higher Inband power (IP closer to 0); impact of visitors refers to change in enclosure usage when visitor number increases. Impact of weather describes any relationship between changes to SPI and temperature, humidity or sunlight fluctuations; influences on visitor number refers to the time of day when higher number of visitors were seen at the enclosure; impact of time of day refers to when the bird's use of space was widest; consider enclosure zone number refers to whether the number of zones defined within the enclosure had an influence on calculated SPI values.

information as an example of open science, fully explaining our methods for sound recording in line with best practice (de Queiroz, 2018).

Enclosure usage could also be influenced by the physiological state of the birds. The BZ greater flamingos were nesting (on eggs and chicks) whilst the observations took place and so breeding pairs split their time between the feeding area and nesting area. Changes to enclosure usage (Figure 4) with time of day could be explained by (i) birds feeding in the morning and returning to the nesting area for the remainder of the day and (ii) the time when keepers are likely to be servicing the exhibit, checking on eggs and nests, and providing flamingo pellet in the feeding area.

Any potential interaction between increasing number of visitors and the flamingo's enclosure usage also needs to be examined from husbandry, management and visitor interest angle. Flamingos respond to changes in husbandry and are more spread around their enclosure when they are being fed or when the exhibit is being managed directly by keepers. The zoo's visitors are drawn to the enclosure by the bird's (and potentially the keeper's) activities. More people talking to each other may increase the loudness of the sound environment. Consequently, a multifactorial explanation of where the animals are and why they are there is presented. Interaction between environmental parameters, keeper presence and visitor number is noted in a case study on captive hornbill (Bucerotidae) behaviour (Rose et al., 2020), with visitor presence affecting how the birds interact with their keeper. The presence of a keeper is likely to draw public to the enclosure, as this can be seen as unusual and 'exciting' by the zoo's visitors, consequently adding further confounding factors to an assessment of why animals are located in specific enclosure zones. An extension of this study should be to assess the latency of any change to space use by recording what happens to individual animals when the crowds disappear and keepers leave the enclosure. Consistency in patterns of enclosure usage over time would provide a benchmark of normal enclosure occupancy that could be used to quantify the effects of disturbance (e.g., large crowds or husbandry interventions) on how zoo animals use their space. A relevant future extension to this study would be to count the number of visitors within the enclosure at each specific observation point and directly compare this value with the zone occupancy of the birds at each corresponding sample point.

The effects of visitors and sound may be difficult to quantify as animals in the zoo may habituate to the 'general' background noise of visitors over time, and specific responses that instigate sudden changes in location or activity may not be adequately captured by a scan sampling method or one that seeks to gauge average sound levels. Previous work on sudden, intense changes to the sound environment (specifically a sonic boom) showed that zoo animals would raise their heads and be alert to the change but otherwise show subtle change to behaviour (Bell, 1972). The same work also states that wild birds can show alarm responses such as crowding together or taking flight. Consequently, a flamingo flock may spook at a sudden sound and move to a new area momentarily (e.g., when a motorcycle is heard on the road outside the zoo, personal observation), but this change in location does not persist, with birds moving back to their original position; therefore, enclosure usage does not appear to be drastically altered. As noted in a case study on a mixed species aviary (also at PZ), whilst some bird species did seem to show a visitor effect, changing location within the enclosure when visitor number increased, the overall influence of visitors on bird behaviour is hard to judge (Downes, 2012). At the same time, flamingos display individual personalities that influence their behavioural choices (McCully et al., 2014), further complicating the relationships explored in this study.

## 5 | CONCLUSIONS

Measurement of enclosure usage by two flamingo flocks has highlighted more differences than similarities in each flock's reactions to changes in the immediate environment. Whilst the number of visitors at the flamingo's enclosure appears to influence enclosure usage, any relationship weakens when other considerations (such as the influence of outliers as well as bird husbandry effects and feeding schedules) are taken into account. Likewise, effects of sound as measured by Inband Power are present for the Chilean flamingos, but their influence could also be related to climatic conditions and the birds' preference for using specific locations according to the amount of direct sunshine they receive. Our paper demonstrates the complexities of understanding how zoo-housed individuals respond to sound and illustrates the challenges associated with isolating sound as a specific factor that influences enclosure usage in zoo-housed birds. In the case of the study flocks, the zoo's sound environment does not appear to be implicated in any major welfare or quality of life impairments. The visitor effect on captive bird enclosure usage is clearly a complex one and change in the sound environment is part of that effect; however, continued research into individual animal responses, measured over both longer and shorter timeframes, is needed to fully understand how the auditory environment in interplay with other sensory factors manifests changes in space use and choice of location within an exhibit.

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### CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request. Raw data from this project are available upon reasonable request from the corresponding author.

### ETHICS STATEMENT

Methods were scrutinised by members of the EASE group at the University of Exeter in October 2018. Finalised data collection methods were submitted to and reviewed by the research teams and ethics committees of the two zoos involved on 5th November 2018 and 22nd November 2018, respectively. Feedback was provided before data collection commencing in April 2019.

### ORCID

*Paul Rose* http://orcid.org/0000-0002-5375-8267
*Alexander Badman-King* https://orcid.org/0000-0003-1049-3446
*Samantha Hurn* https://orcid.org/0000-0003-4876-458X
*Tom Rice* https://orcid.org/0000-0002-7674-030X

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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