Does the sound environment influence the behaviour of zoo-housed birds? A preliminary investigation of ten species across two zoos

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ABSTRACT

In the zoo, the sound environment experienced by captive wild animals will contain numerous anthropogenic features that may elicit different responses to those stimulated by naturally created, or more biologically relevant, sounds. Husbandry activities, visitor presence and neighbouring species (free-living and captive) will all influence the sounds around zoo-housed species; an animal's behavioural responses may therefore provide an insight into how its welfare state is influenced by this changing sound environment. This project aimed to investigate how animal behaviour was influenced by the sound environment at two large UK zoos; one situated in a more rural location and the other in an urban location. Species were selected based on their location in the zoo, the relevance of sound to their natural ecology (e.g., as a form of communication and/or for anti-predator responses) and their novelty as research subjects in the scientific literature. Behavioural data collection was conducted for five days per enclosure per zoo at the population and individual level for birds housed in different styles of enclosure. Instantaneous sampling at one-minute intervals was used to collect information on state behaviours, assessed using a pre-determined species-specific ethogram. Event behaviours were collected continuously for each observation period. The sound environment around or in the enclosure was recorded continuously during each behavioural recording session using a recorder mounted on a tripod. Results showed a variety of responses to the presence of visitors and potential associated changes to sound around the enclosure with some behaviours being more influenced by the presence of visitors (and increases in the volume of sound) compared to others, e.g., vigilance and vocalisations. Overall, birds showed few of the changes thought to indicate poor or impoverished welfare states linked to changes to the sound environment in their enclosure or to the presence of visitors, but we recommend that zoos consider further measurement and recording of sound on a species-by-species basis to capture individual responses and behavioural changes to variation in visitor number and the sound environment.

1. Introduction

Animal behaviour is commonly used as a means of determining zoo animal welfare states (Dawkins, 2004) and perceived coping within the individual's current environment (Wechsler, 1995). Observation of individual and group-level behaviour provides data on specific long-term states and short duration events that are commonly assessed alongside of demographic characteristics (e.g., sex, age, reproductive status), anthropogenic factors (e.g., visitor number, keeper presence), husbandry schedules (e.g., presence of enrichment, feeding schedule), conspecific influences (e.g., social networks), climate and weather

variables (e.g., temperature, wind speed) and temporal and seasonal effects (e.g., time of day, time of year) (Rose and Riley, 2021). However, the impact of different sensory environments, and particularly sound, has (until recently) been less often considered as an influence on zoo animal behaviour and welfare. The sound environment experienced by zoo animals is influenced by the human-created world of the zoo and beyond (Jakob-Hoff et al., 2019; Pelletier et al., 2020; Sulser et al., 2008), and these anthropogenic sounds mix with sounds of local wildlife and the other animal residents of the zoo (de Queiroz, 2018; Orban et al., 2017; Quadros et al., 2014). The "Listening to the Zoo" project at the University of Exeter aimed to further understand the influence of sound

on human and non-human animal behaviour; both how the zoo's animal occupants and its human visitors responded to the sound environment within the zoo (to provide further evidence for zoo education activities and how to enhance the visitor experience) (Rice et al., 2021a, 2021b), and to inform animal husbandry and welfare (Rose et al., 2021).

Assessment of an individual animal's sensory experiences can help zoos to further develop rubrics for welfare assessment and contributes to the evidence-based approach to zoo animal husbandry (Orban et al., 2017). As wildlife has been shown to adapt or change behaviour in relation to human-created "noise" or change to a natural soundscape (Barber et al., 2010; Brumm, 2004; Halfwerk et al., 2011; Nemeth and Brumm, 2009; Tennessen et al., 2014; Wood and Yezerinac, 2006), so zoo animal behaviour patterns may alter due to exposure to unfamiliar or potentially stress-inducing sounds. Past research has attempted to qualify the effect of sound on animals in the zoo to see how different auditory stimuli influence behaviour (Birke, 2002; Ogden et al., 1994). Changes to welfare state can be inferred from behavioural responses at an individual and group level. In the zoo, wild species housed in captivity are likely to be exposed to a range of unfamiliar, and non-biologically relevant natural and human-created sounds. Species held in zoos will experience a sound environment that may be far-removed from wild auditory stimuli they have evolved to respond to (Lara and Vasconcelos, 2019). Measurement of the responses of zoo animals to these different sounds may provide useful information on welfare states and quality of life in captivity (Rose et al., 2021).

The scientific field of evidence-based zoo husbandry (Melfi, 2009) encourages further investigation into areas of zoo management regimes that may be lacking in empirical evidence or scientific reason. The evolutionary adaptations to their specific habitat that wild animals possess may predispose managed populations in certain taxa to being more responsive to zoo-specific, anthropogenic stimuli. These might include, at a minimum, species that use auditory signals to organise movement patterns, manage social situations, recognise youngsters, or cement pair bonds (Black, 1988; Geissmann and Orgeldinger, 2000; Mathevon, 1996, 1997; Wittig and Boesch, 2005). However, there is little published work that examines how such species respond to soundscapes in the zoo. Research into how animal behaviour may be impacted by the sounds caused by husbandry and management, for instance, is very limited. Research on fennec foxes *(Fennecus zerda)* suggests that animals can become acutely sensitive to the noise made by keepers outside of their enclosure and commence stereotypic pacing behaviour in response to it (Carlstead, 1991). This work indicates that day-to-day routines used by caregivers in zoos may cause specific, unnatural behavioural responses in the animal population. However, care is needed with such generalisations; the startle responses of eight species of North Sea fish housed in the Rotterdam Zoo's aquarium were shown to be very species and context (e.g., group size, fish age) dependent when tested against sounds in a range of 0.1–64 kHz (Kastelein et al., 2008).

A key potential source of sound experienced by captive wild animals is zoo visitors. Work on the Visitor Effect (VE) is common (Chamove et al., 1988; Hosey, 2000; Quadros et al., 2014; Sherwen et al., 2014; Suárez et al., 2017), with different authors noting positive, negative and neutral responses to the presence of the viewing public from a variety of species, although research also suggests that any VE analysis needs to consider impacts of environmental conditions if it is to provide a thorough and meaningful evaluation of how zoo animals respond to the presence of humans (Goodenough et al., 2019). Noise - i.e., an unwanted sound with connotations of disturbance (Hatko, 2022) - has featured in work on the VE (Sherwen et al., 2014) and may be elevated where higher numbers of people view animals (Quadros et al., 2014). Popular species experienced more noise and greater audience size, though interestingly, Quadros et al. (2014) found overall behavioural responses to elevated noise was minimal. These authors state that individual variation in behavioural responses to noise as a VE was apparent, however, and is worthy of further investigation.

Specific case studies (on VE responses) have identified behavioural responses indicative of both positive and negative affective states. For example, two species of zoo-housed cockatoo showed different responses to visitor use of a nearby playground (the study included a measurement of noise levels) (Collins and Marples, 2015), with one species withdrawing when the playground was used and the other becoming more social. Location of an enclosure within a zoo's grounds, then, can also impact on animal behaviour (Davey and Henzi, 2004; Mitchell et al., 1990). The sound experienced by inhabitants due to visitor presence may be especially pronounced for exhibits on main thoroughfares, near the entrance or around areas specifically designed for zoo visitors (e.g., restaurants, gift shops etc). Animals in such locations may experience different sensory environments compared to others within the same animal collection. Potential negative impacts on welfare can arise if individuals sensitive to auditory stimuli and visitor presence are located in areas of high footfall (Davey, 2007).

At the same time, zoo animals may habituate to anthropogenic sounds in the zoo. For instance, research has documented that ungulates can be acclimatised and thus habituated to the sounds of a chute used for veterinary procedures (Grandin, 2000), with species of a particularly "flighty" nature ignoring previously stressful sounds of clanking and banging during manoeuvring into a chute. It seems reasonable to suggest that such habituation also occurs in relation to zoo visitor sound, at least to some degree in some species. Masking anthropogenic sounds by playing ecologically-relevant sound as enrichment for zoo animals has been investigated (Ogden et al., 1994). These authors found individual differences in responses to the soundscape of indoor housing, with potential negative welfare indicators (increased agitation) when ecologically relevant sounds were played to the inhabitants. Care is evidently required when using a masking approach, and the technique is by no means an unproblematic means of counteracting visitor noise.

Unpicking the VE and associations with sound is complicated (Rose et al., 2021), as multiple factors that co-vary may be causing the animals to respond in particular ways at particular times. The aim of this study was to document the time-activity budgets of a range of different zoo-housed birds from a range of different ecological niches, to determine any change in behaviour pattern with changes in the animals' immediate soundscape. Birds were chosen as subjects for data collection as they are less popular research subjects for work on visitors and impacts of sound (compared, for instance, to mammals), and are commonly housed in enclosure that actively encourage visitors into the animal's space. Sound recordings were made in enclosures at an urban and a rural zoological collection to compare the responses of representative species to different zoo settings. The project aimed to quantify any potential effect of the zoo's visitors on bird behaviour, examining if a commonly performed event behaviour (vigilance - where causation is often an aversive stimulus) showed any relationship with sound and visitor variables.

2. Methods

Behavioural data were collected at two exhibits in Bristol Zoo Gardens (BZ) and two exhibits at Paignton Zoo Environmental Park (PZ) from April through to September 2019. BZ is an urban zoo, located close to Bristol city centre (population of 536,000) with an overall size of 5 ha. It housed around 420 species of animal and received approximately 524,000 visitors annually. PZ is located on the outskirts of the small seaside town of Paignton (population size 49,000 people) and is 33 ha in size, housing approximately 300 species with an annual visitation of approximately 530,000 people. Five days of observations were conducted at each exhibit. Data were collected for 20-minute periods at 10:00, 11:00, 12:00, 14:00 and 15:00 to coincide with regular zoo opening hours.

2.1. Sample populations and enclosures

Greater flamingos, *Phoenicopterus roseus* (N = 56) at BZ and Chilean flamingos, *P. chilensis* (N = 53) at PZ were chosen for the study as representatives of popular zoo animals commonly housed in a prominent location within a zoo's grounds. Flamingos were housed as the very first exhibit that visitors to each zoo experienced. At both zoos, the flamingo enclosure also contained a range of other wildfowl (Anseriformes) and/ or other waterbirds (e.g., wading birds and shorebirds). Data on BZ flamingos were collected on 30th April 2019 and 4–7 th May 2019; data on PZ flamingos on 15th, 26th and 29th April 2019, and 3rd and 16th May 2019. The flamingo's breeding season, in a temperate climate would be late spring and early summer (greater flamingo) and mid to late summer (Chilean flamingo). The greater flamingos were nesting during the data collection period.

Walk-through, indoor enclosures were chosen as a comparison with the outdoor flamingo flocks. At BZ, two Victoria crowned pigeons *(Goura victoria)*, two pied imperial pigeons *(Ducula bicolor)*, two Luzon bleeding-heart doves *(Gallicolumba luzonica)* and one white-rumped shama *(Copsychus malabaricus)* were observed in the "Forest of Birds" (FOB) house. At PZ, two bush stone-curlews *(Burhinus grallarius)*, four crested pigeons *(Ocyphaps lophotes)*, one wonga pigeon *(Leucosarcia melanoleuca)* and two elegant-crested tinamous *(Eudromia elegans)* were observed in the "Desert House" (DH). Data in the BZ FOB were collected on 10th, 11th, 15th, 17th and 19th June 2019. Data in the PZ DH were collected on 26th June, 13th July, 19th August, 20th August and 10th September 2019. Breeding in the DH would occur during spring and summer, and in FOB managed to coincide with spring and summer (even though the environment was climate controlled). The Victoria crowned pigeons commenced nesting during the data collection period.

A total of 12 species of bird were housed in the FOB and 15 species of bird in the DH during the period of study. FOB (c223m^2) is climate controlled and heavily planted with dense cover, recreating a range of habitat areas. Visitors walk through a single path from an entry to an exit point crossing a "rainforest stream" from its waterfall "origin". The sound of the waterfall was audible throughout FOB and would have been recorded during the acoustic measurements described below. Two separate aviaries were inside the FOB containing taritic hornbills *(Penelopides panini)*, and yellow cardinals *(Gubernatrix cristata)* and Mindanao bleeding heart doves *(Gallicolumba crinigera)* respectively that were not accessible to the birds in the main walk-through section of the exhibit. The DH (c670m^2) was not climate controlled but was mechanically ventilated; modelled to resemble an arid environment, the enclosure was open with perching and furnishing provided in discrete areas of the exhibit. Visitors walk through a single path from an entry to an exit point. In both enclosures, birds were freely able to access off-show areas away from public viewing. Further details of the BZ (c330m^2) and PZ (c895m^2) flamingo enclosures and population of these birds can be found in Rose et al. (2021). Example illustrations of the enclosure layout in FOB and DH are provided in Fig. 1.

The flamingos at both BZ and PZ were located at the front of the zoo, being one of the first enclosures that visitors would experience upon commencing their journey around each animal collection. BZ flamingos were located next to an enclosure for drills *(Mandrillus leucophaeus)* whereas PZ flamingos were adjacent to the "Reptile Tropics" (RT), the zoo's walk-through reptile house. FOB at BZ was adjacent to zoo offices and near a small children's playground, and the DH at PZ was attached to the aforementioned RT exhibit, with visitors walking through from RT into the DH, following a one-way system.

2.2. Behavioural recording

The ethogram of state (long duration) behaviours (Bateson and Martin, 2021) included preening (cleaning of feathers with bill); bathing (washing of feathers with water); foraging and feeding (searching for and ingestion of food); alert (prolonged vigilance in an aroused posture); locomotion (walking, running, climbing, swimming); flying; courtship (reproductive display specific for that species) and nesting (building of a nest and incubation of eggs/chicks); social (interaction lasting for the minute sample period, both between and within species including aggression); vocalisation (long-duration calling that occurred for the minute sample interval); perching (on feature around the enclosure in a relaxed state); perching high (at the top of trees or infrastructure of the aviary well above head height of visitors, again in a relaxed state); sitting or loafing (resting on a perch or the ground, or standing without movement in a relaxed manner); perching in cover (the bird was not

Fig. 1. Top photos show the furnishing and layout of the FOB at BZ. Top left: location of tripod and observer in front of the rock the sound recorder is placed on. Top middle: taller trees and higher perching. Top right: lower planting an internal aviary. Bottom photos show the furnishing and layout of the DH at PZ. Bottom left: path through exhibit. Bottom middle: location of tripod and observer in front of the rock the headphones are placed on. Bottom right: planting and substrates provided in the enclosure with off-show areas at the far back of the picture.

immediately visible to visitors); roosting (the bird was perching or sitting but asleep); dustbathing (the bird used dirt and sand to clean its feathers); stereotypic pacing (repeated walking up and down a fence line or barrier).

For the purposes of analysis of the flamingo data, preening and bathing ("preening"), and sitting and loafing ("inactive"), locomotion and flight ("movement") were combined. For analysis of the indoor bird data perching, perching high, perching in cover, sitting, inactive and roosting ("perching"), and vocal, social, courtship and nesting behaviours ("social"), and preening and dustbathing ("preening") were combined.

Vigilance, as a welfare-specific event - short duration (Bateson and Martin, 2021) - behaviour was counted continuously (using all-occurrence sampling (Bateson and Martin, 2021)) as and when it occurred during each full 20-minute observation period. Vigilance was the raising of the bird's head to look at a potential disturbance momentarily before resuming the original activity. Vigilance events were counted for all individuals in each flamingo flock and for specific species in the FOB/DH. Vigilance was decided upon as a potential welfare indicator as previous research has shown that birds will disrupt ongoing maintenance or homeostatic-driven behaviours to perform an alarm or vigilance response (Dutour and Danel, 2021).

2.2.1. Behavioural recording for flamingos and for birds in indoor enclosures

Instantaneous scan sampling of the whole flamingo flock was used to collect behavioural data for each zoo. One-minute sample intervals were used when counting the number of individuals performing state behaviours outlined in the pre-defined ethogram. For both flamingo flocks, video recording (with a Panasonic Lumix digital camera) of behaviour was used with individuals being counted after each video was watched post-observation. Still photos, using a Honor 10 Lite smartphone camera were taken of birds out of sight of the video recorder to capture as many individuals as possible at each sampling period. Direct recording of event behaviours and visitor number occurred during the observation.

For FOB and DH birds, focal follows were conducted on all individuals present for the Victoria crowned pigeon, wonga pigeon, shama, stone-curlew and for two of the three elegant-crested tinamous. Due to the lack of individual recognition, random individuals of pied imperial pigeon, crested pigeon and bleeding-heart dove were used for data collection. For these species, if that sample bird went out of sight, a new individual was not followed, and the behaviour was recorded as out of sight. The same recording interval (1 min) was used for state behaviours for FOB and DH data collection.

To compare vigilance levels for large, obvious (to visitors) ground-dwelling species in the walk-through exhibits, all occurrence sampling for both individuals continuously per observation period was conducted on Victoria crowned pigeon (FOB) and elegant crested tinamou (DH). For the birds in FOB and DH, both state and event behaviours and visitor number were recorded during the observation itself. Still photos were taken to determine any behaviours of animals that were hard to identify during the actual observation itself. For each observation, data collection was undertaken from normal public areas of each enclosure and animals were free to move normally around their exhibit.

2.3. Sound recording and visitor presence

Sound was recorded from normal public viewing areas for both indoor and outdoor enclosures for each of the sample species. The tripod was always set up in the same location for each exhibit for each bout of recording. Sound was recorded using a Zoom H4nPro that 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. The tripod was positioned at the edge of the enclosure (for the flamingos) or at the edge of public path for the FOB and DH enclosures and faced into the middle of the exhibit for each enclosure. The

tripod was used to ensure that there was no interference around the sound recorder, e.g., from enclosure furnishings or from the ground, when recording sound waves). Ideally, the microphone would have been placed within the enclosure for all species, but this was not feasible at all sites, would have potentially caused additional stress to the birds and made access by the observer difficult. However, this would be the ideal for future zoo-based bioacoustics research. The sound recorder and digital camera were both started at the same time to ensure synchronicity between the sound being captured and the animal's behaviour. The sound on the camera's video recording was also cross-checked against that from the actual sound recorder when evaluating potential sound influences over behavioural change in the animals.

A microphone wind shield was used in all conditions. Recordings were 16 bit, made in WAV format with a mono mix and had a sample rate of 44.1 kHz. As indicated in Miyara et al. (2010) the Zoom H4nPro recorder was suitable for acoustical measurements. The recorder microphones were not calibrated, meaning that the sound measurements we produced were not absolute. Therefore, whilst we can make relative comparisons, we recognise this limitation, and that lack of calibration could potentially account for some of the variation in the sound measurements between the four specified enclosures.

Sound was recorded continuously during all observations from the observer's location. Specific sound characteristics were analysed at the point when bird behaviour was recorded. Analysis of all sound recordings was undertaken in Raven Pro v.1.6 (Center for Conservation Bioacoustics, 2019). Each 20-minute sound recording WAV file was uploaded into Raven Pro and the spectrogram and waveform of the recording evaluated using the software's measurement tools. Measurements of Peak Frequency (Hz), Inband Power (dBFS, decibels relative to Full Scale) and (equivalent to) Continuous Sound Level (LEQ, a single decibel reading) 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-minute intervals for every 20-minute 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). IP and PF measurements were used in an analysis of the enclosure usage of several of the same animals at these same zoos in an earlier paper (Rose et al., 2021), and for consistency and to aid comparison, these measurements were carried over into the analysis of animal behaviour data. We suggested that birds may vocalise more or move away from higher frequency sounds that could be unsettling and therefore a behaviour change with PF may be apparent. LEQ is a useful method to describe varying sound levels over time (Center for Conservation Bioacoustics, 2019) and provides a single decibel value of the total sound energy over the period of time recorded (Center for Conservation Bioacoustics, 2019). The reference sound pressure for LEQ in RavenPro was 20 microPa. 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 to describe the variation in sound between each sample point.

Selections from the spectrogram (for PF and IP) or waveform (for LEQ) were taken at the corresponding sample point for behavioural recording (i.e., at the minute 1, minute 2, minute 3, etc, specific time point and not for the full 60-seconds for each full minute between behavioural recording). The selection tool was moved along the waveform until the corresponding time of the behavioural observation was identified and then that specific recording point (noted in seconds on Raven Pro) was selected. The spectrogram/waveform was then used to determine the measurements noted above. When each minute point had been measured, the sound measurements from the table under the waveform/spectrogram were copied directly into Microsoft Office Excel

for statistical analysis and comparison with behavioural data. An example of how data were collected from the spectrogram/waveform views in Raven Pro can be found in Rose et al. (2021). We do not review audiogram data for each species (due to a lack of audiogram information available for all bird species observed), and hence we recognise our ultimately anthropocentric interpretation of sound. However, we are seeking to examine general relationships between sound energy in the enclosure environments and bird behaviours in this paper, rather than making detailed or fine-grained inferences about how particular bird species perceive and experience sound.

2.3.1. Recording visitor number and weather variables

Visitor presence was recorded continuously during each 20-minute observation period. The overall number of people at/within each enclosure was recorded as an overall total for the observation period ("Visitor total") as well as the discrete maximum number of visitors at or in the exhibit seen during that 20-minute period ("Visitor max"). Visitor number was tallied as people walked past the observer (moving from entry to exit of the exhibit) to reduce the likelihood of counting the same people more than once. As any "visitor effect" - impacts on animal behaviour due to the presence of the zoo's visitors (Hosey, 2000) - correlates with environmental variables (Goodenough et al., 2019; Rose et al., 2020), for flamingo enclosures, external temperature (°C), humidity (%) and cloud cover/sunshine (%) were also recorded for each observation period using Google Weather on a smartphone during the observation period. 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. The external temperature was taken from Google Weather after the sampling days were finished for FOB and DH was recorded (again to check for any influence on visitor number).

2.4. Data analysis

Data analysis was conducted in R 4.1.2 (R Core Team, 2021) using RStudio v. 1.2.1 (RStudio Team, 2021).

2.4.1. Predictors of flamingo state behaviours

To analyse any influence of visitation (total number of visitors), sound metrics (maximum IP, maximum LEQ and maximum PF) and weather (temperature, humidity, sunshine) for each time period on the state behaviours of the flamingos (proportion of individuals performing each behaviour for that observation period), a linear mixed effects model was run in RStudio using the lmertest package (Kuznetsova et al., 2017). Model fit was assessed using the "plot (insert model name)" function for standardised residuals, as well as the r^2 value- calculated using the MuMIn package (Bartoń, 2013). To remove predictors that were highly colinear, Variance Inflation Factors (VIFs) were calculated using the car package (Fox and Weisberg, 2019) and any VIFs above 2.5 were immediately excluded from the model. Any impact on model fit and r^2 values of predictors with VIFs between 2 and 2.5 was investigated further before deciding to retain the predictor in the model.

The total number of visitors and maximum discrete group size (Visitor max) were correlated for both flamingo enclosures and were not included in the model. The final model run flamingo state behaviours as outcome variables was Behaviour ~ Zoo + maximum IP + maximum PF + maximum LEQ + total number of Visitors + Temperature + Humidity + Sunshine + Time (of observation) + Date (included as a random factor). The "anova(model name)" function was used to identify significant predictors using Satterthwaite's method. To remove any chances of Type I error, a new corrected significance value (Q value) was calculated using Benjamini and Hochberg (1995) correction factor. Flamingo were only observed pacing at BZ and therefore this behaviour was analysed for this flock only without zoo as a potential predictor.

2.4.2. Predictors of indoor bird behaviours

The same repeated measures modelling was used for indoor bird behaviour (proportion of time spent on behaviour for that observation period). The same calculation of r^2 values and VIF and checking of model fit. It was first attempted to include both zoo's data into the same dataframe, but zoo was highly colinear and was therefore removed. Individual model fits were markedly improved when each zoo's data were analysed independently. External temperature was at first included in the model for DH (as this house had open windows and was not internally heated). Unlike in the outdoor enclosures, total visitors and maximum number of visitors seen in a discrete group within the sampling period did not correlate and therefore both factors were included in the model. Temperature was removed due to a high VIF and there was a better model fit after temperature was removed. Model fit was unchanged when LEQ was removed.

The final model run was: Behaviour ~ Time + Species + maximum PF + maximum IP + maximum LEQ + total number of Visitors + maximum Visitors (as a discrete group) + Date (as a random factor) + Individual (as a random factor).

2.4.3. Influences on vigilance behaviour

Predictors of flock-wide vigilance rate in the flamingo and total vigilance rate for the two Victoria crowned pigeons and two elegant-crested tinamous were analysed using repeated measures models and Poisson regression. For BZ flamingos, there was strong collinearity between humidity and temperature and visitors, therefore temperature (as a non-significant predictor in the first model run) was removed from the final model. The final model was: Vigilance rate ~ Time + maximum IP + maximum PF + maximum LEQ + total number of Visitors + Humidity + Sunshine. This model had an r^2 value of 70% and all VIF values were < 1.8.

For PZ, LEQ was highly colinear, as was Visitor (maximum group) and these were removed. The final model run was: Vigilance rate ~ Time + maximum IP max + maximum PF + total number of Visitors + Temperature + Humidity + Sunshine. This model had an r^2 value of 22% and all VIF values were < 2.0.

Total count of vigilance events for the Victoria crowned pigeons and for the elegant-crested tinamous were inputted into a Poisson regression. For Victoria crowned pigeons, date, visitor max, and temperature were highly correlated, and these were removed from the model. The final model run was: Vigilance total ~ Time + Visitor total + maximum IP + maximum PF + maximum LEQ. The r^2 for this model was 45% and all VIF values were below 1.7. For elegant-crested tinamou, LEQ was highly colinear and was removed from the model. The r^2 for this model was 45% and all VIF values were below 1.4. The final model run was: Vigilance ~ Date + Time + Visitor total + maximum PF + maximum IP.

2.4.4. Analysing correlations between total visitor number, environmental conditions, and sound measures

For each enclosure, the total number of visitors and corresponding sound measures and environmental measures were included in a Spearman's rank correlation to understand any outside influences on the sound environment of the enclosure which would enable further analyses of any significant results.

3. Results

To provide overall illustration of the characteristics of the sound environment at each zoo, descriptive statistics were calculated for each day of study and for the overall five days of observation at that enclosure (Table 1). IP values closes to 0 show more power in the sound environment. LEQ values show the change in continuous sound level compared to the reference value; lower values show more variation in sound power.

Table 1 shows that overall sound power at BZ in both the outdoor flamingo and indoor FOB exhibits was higher than that of PZ's flamingos

Table 1
Median sound values + /- standard deviation for each enclosure for each day of study and overall.

Enclosure	Day of study	Median IP (dBFS)	Median PF (Hz)	Median LEQ (dB)
PZ flamingo	1	-44.9 (6.3)	187.5 (569.6)	-44.7 (13.5)
	2	-46.2 (5.1)	187.5 (261.6)	-48.71 (11.34)
	3	-49.1 (2.3)	562.5 (839.0)	-51.6 (9.0)
	4	-51.0 (4.1)	750.0 (615.8)	-50.3 (8.6)
	5	-51.4 (2.7)	656.3 (565.4)	-53.4 (9.7)
	Overall	-48.9 (5.3)	562.5 (641)	-48.9 (10.9)
BZ flamingo	1	-45.5 (4.5)	750.0 (444.3)	-46.5 (9.7)
	2	-43.3 (5.5)	562.5 (495.7)	-42.3 (10.3)
	3	-45.0 (4.9)	375.0 (361.0)	-43.1 (10.0)
	4	-41.6 (5.1)	187.5 (405.3)	-43.7 (12.9)
	5	-47.8 (6.1)	187.5 (384.7)	-50.2 (12.1)
	Overall	-44.4 (5.6)	562.5 (440.1)	-45.2 (11.4)
PZ DH	1	-45.6 (7.8)	517 (1374)	-49.4 (13.3)
	2	-45.7 (6.6)	904 (1550)	-47.7 (9.8)
	3	-39.3 (5.6)	517 (1159)	-41.7 (12.5)
	4	-42.2 (6.3)	603 (1408)	-46.1 (11.0)
	5	-44.5 (5.2)	2885 (1413)	-49.1 (12.3)
	Overall	-43.3 (6.8)	689.1 (1465.2)	-46.7 (12.0)
BZ FOB	1	-36.8 (3.4)	187.5 (198.1)	-38.9 (10.9)
	2	-36.0 (3.3)	187.5 (696.5)	-37.6 (10.7)
	3	-34.6 (2.8)	86.1 (467.7)	-36.4 (9.4)
	4	-35.1 (3.1)	86.1 (404.0)	-39.0 (10.1)
	5	-34.7 (2.6)	86.1 (334.8)	-36.2 (9.5)
	Overall	-35.3 (3.2)	86.1 (452.0)	-37.7 (10.2)

and DH (both for IP and LEQ). PF shows a wide range of variation around the median for each enclosure and more variation between days too, except for BZ FOB. Overall change in LEQ by time of day (observation period) is limited and therefore the average power of the sound environment at these enclosures may be constant, however wider ranges were noted, e.g., for morning PZ outdoor enclosure and morning and afternoon PZ indoor enclosure.

3.1. Flamingo behaviour

The commonest behaviours performed by the PZ flamingos were preening (mean 29% ± 0.01 SE), inactive (23% ± 0.012 SE) and movement (14% ± 0.007 SE). For BZ flamingos the commonest behaviours were nesting (56% ± 0.006 SE), inactive (19% ± 0.005 SE) and preening (10% ± 0.004 SE). An illustrative time-activity budget for each flock is provided in the supplementary material (Fig. S1) and full model output tables are also provided in the supplementary material (Table S1). A significant predictor of flamingo behaviour for both zoos combined was increased humidity that increased preening (estimate= 0.369; SE= 0.156; df= 27.67; t value= 2.36; P = 0.025). Movement around the enclosure also significantly increased later in the day, specifically later in the afternoon (estimate= 9.37; SE= 3.20; df= 35.02; t value= 3.01; P = 0.0048). Flamingos were more likely to be alert at PZ (estimate= 3.36; SE= 1.51; df= 36; t value= 2.22; P = 0.033) and also more alert later in the afternoon (estimate= 4.56; SE= 1.91; df= 36; t value= 2.39; P = 0.022).

Predictors that showed a general trend were, for preening, the zoo (more preening at PZ, estimate= 12.76; SE= 5.91; df= 9.04; t value= 2.16; P = 0.059). Similarly for movement, PZ flamingos potentially moved around more than BZ flamingos (estimate= 7.69; SE= 3.53; df= 8.74; t value= 2.18; P = 0.06). Inactivity tended towards significance with maximum LEQ, and birds were less likely to be inactive as LEQ increased (estimate= −0.857; SE= 0.441; df= 35.9; t value= −1.94; P = 0.059). Maximum Inband Power showed a general trend with foraging (estimate= −0.506; SE= 0.264; df= 36; t value= −0.354; P = 0.06) with less foraging occurring at more powerful IP. An extended period of data collection may have yielded a significant result here. Movement tended towards significance with increasing number of

visitors (estimate= 0.05; SE= 0.03; df= 35.9; t value= 1.94; P = 0.06). However, many of these potential influences, including sound measures and visitor effects, disappear when a Benjamini and Hochberg (1995) corrected level of significance is applied (see supplementary information).

To analyse time spent pacing, a separate lmer model was run for the BZ flamingos, and this model showed no significant sound, visitor or weather predictor of pacing. Temperature approached significance for pacing (estimate= 0.276; SE= 0.123; df= 7.20; t value= 2.23; P = 0.059).

3.2. Indoor bird behaviour

Time-activity budgets for the different species of bird in the two indoor enclosures show a diverse range of time spent on state behaviours (Fig. 2). The white-rumped shama in the BZ FOB exhibit spent the most time vocalising of all species and breeding activity dominated the activity pattern of the two Victoria crowned pigeons. In the PZ DH, the tinamous appeared to be the most evidently vocal to a human visitor, and the species most likely to be under cover, out of all the DH species used for data collection. The crowned pigeons were most likely to be perching in the open, and the stone-curlew and wonga pigeon were most likely to be inactive. Full model outputs from analysis of predictors of behaviours are provided in supplementary information (Table S2 and S3). Significant predictors of behaviour in FOB and DH are provided in Table 2.

Significant differences presented in Table 2 compared the behaviour performed by the bleeding-heart doves for FOB against all other species, and that performed by the crested pigeons against all other species for the DH. Differences in Time of Day are compared back to the first observation period. In FOB, all the bleeding-heart doves foraged and moved around the enclosure significantly more than all other species but were the least likely to display alert behaviours. For the FOB, species performing alert behaviour showed a general trend with the late afternoon (estimate= 4.27; SE= 2.22; df= 158.6; t value= 1.92; P = 0.057). For the crested pigeons in the DH, all other species preened significantly less, and the tinamous and bush stone-curlews were more significantly more likely to be seen alert. Both PF and visitor number influenced the time spent on alert behaviour in the FOB. Both visitors and sound influenced preening in the DH and the power of the sound environment affected social behaviour. Movement and foraging showed a relationship with PF in the DH.

3.3. Event behaviours

There is no clear relationship between a sound measure (Inband Power), the number of visitors per observation period at/in the enclosure and the vigilance performed by the birds within (Fig. 3). The flock-wide vigilance rate at BZ was significantly higher at midday (estimate= 7.468; SE= 3.21; df= 13.49; t value= 2.32; P = 0.036) and in the later afternoon (estimate= 10.95; SE= 4.15; df= 12.15; t value= 2.64; P = 0.021). There were no significant predictors of flock-wide vigilance rate for the PZ flamingo flock.

Significant predictors of vigilance in the Victoria crowned pigeons are provided in Table 3. For time of day, results are compared to the first morning (10:00) period. For the elegant-crested tinamous, IP was considered a significant influence on increased vigilance count (estimate= 0.037; SE= 0.015; z value= 2.28; P = 0.025) but this value was not significant after a Benjamini and Hochberg (1995) was applied to all model outputs.

3.4. Correlations of visitors, sound, and environmental conditions

It appears that there is a complex relationship between the number of zoo visitors that were counted at each enclosure for each observation period and prevailing environmental and sound conditions. For both PZ
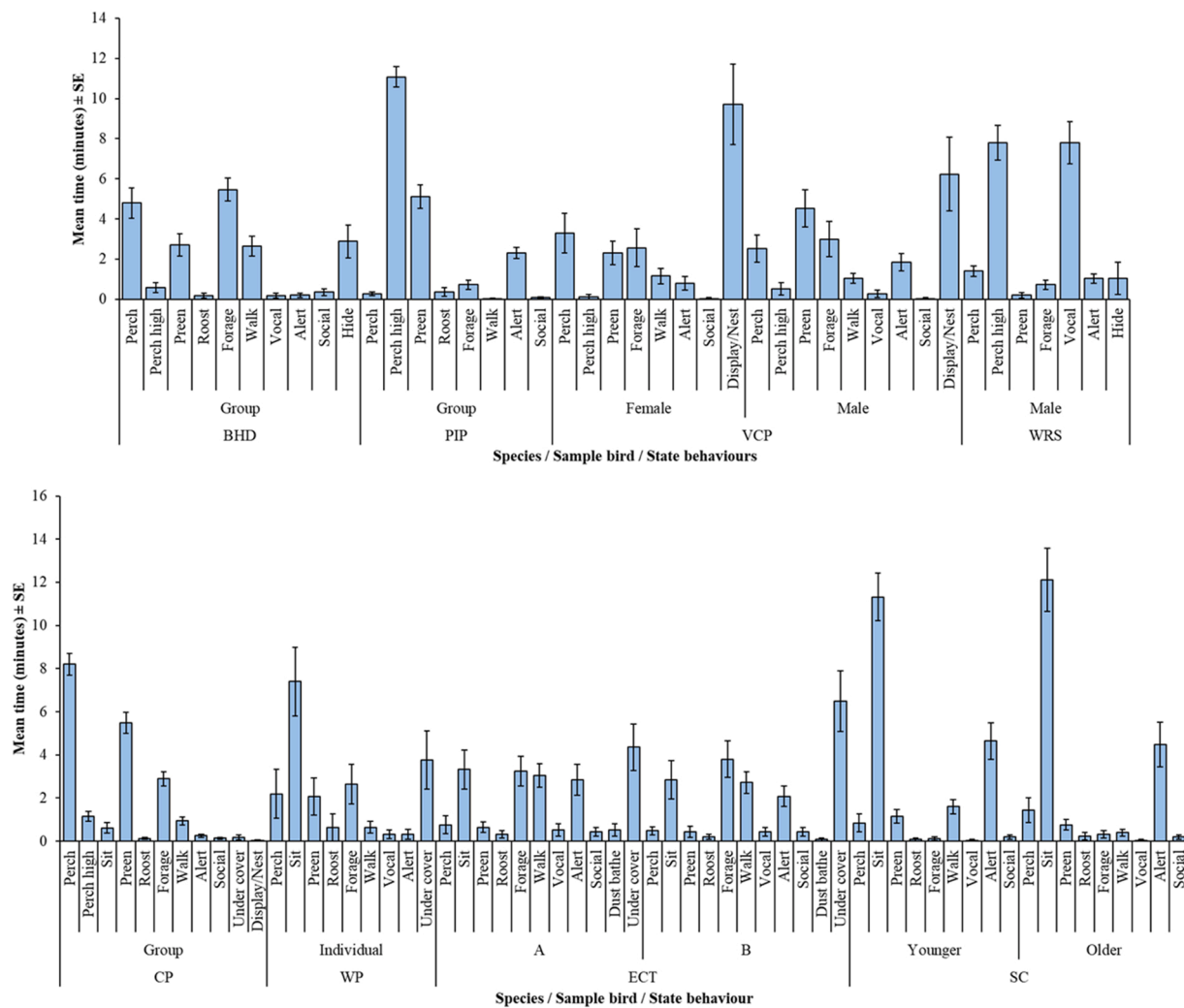
Fig. 2. Time-activity budgets for the birds in the BZ FOB enclosure (top). BHD= bleeding heart dove, PIP= pied imperial pigeon, VCP= Victoria crowned pigeon, WRS= white-rumped shama. Time-activity budgets for birds in the PZ DH (below). CP= crested pigeon, WP= wonga pigeon, ECT= elegant-crested tinamou, SC= bush stone-curlew.

and BZ flamingo flocks, higher temperatures negatively correlated with total number of visitors (PZ r = −0.458; N = 24; P = 0.024. BZ r = −0.730; N = 25; P < 0.001). For BZ flamingos, higher visitor number correlated with higher power of the sound environment, for IP (r = 0.422; N = 25; P = 0.02) and for LEQ (r = 0.427; N = 25; P = 0.03).

For indoor enclosures, total visitor number showed no significant correlation with any sound or environmental variables. In the PZ DH, the correlation between total visitor number and increasing power, IP, showed a non-significant general trend (r = 0.380; N = 25; P = 0.06).

Scatterplots with linear regression lines for each environmental (temperature, humidity, and sunshine) and sound measure (IP, LEQ and PF) against total number of visitors are provided in the supplementary information, Fig. S2.

4. Discussion

Our results showed that impacts from the sound environment on the behaviour of zoo housed birds was complex and specific to individuals and to species within an enclosure. For species in the indoor FOB exhibit, vigilance counts increased at higher sound power (higher LEQ) and vigilance count was higher when more people passed through the enclosure during observation periods. It is therefore possible that a VE may be present on some of the bird species in this walk-through

immersive exhibit. When considering a behavioural measure of welfare to generalise across species, there was limited impact on vigilance from the presence of visitors or increased sound levels in the enclosure for flamingos (with low vigilance rates noted overall), and an influence of sound caused an increase in vigilance that approached significance for the tinamous. Only for the Victoria crowned pigeons did vigilance rates increase significantly when more visitors were present. Descriptive statistics revealed that the sound environment at BZ (the urban zoo) was likely to be more powerful ("noisier") than the suburban setting of PZ; however, median IP and LEQ from each site were similar and therefore differences in the season of data collection may account for this. Birds may also be responding to the behaviour of conspecifics and of other avian species around them; therefore, intra- and inter-specific interactions and their associated effects on behaviour patterns should also be measured to ensure that any behaviour change attributed to visitors, or a change in the sound environment from visitors, has not been initiated by another animal in the enclosure.

4.1. Flamingo time-activity budgets

Flamingo behaviour at both zoos was similar, even though BZ flamingos were in their nesting cycle and PZ flamingos were starting their courtship displays. Both flocks spent a large proportion of time preening and inactive, as has been shown in other flamingo research

Table 2
Significant model estimates for predictors of bird behaviour in the two indoor enclosures.

Forest of Birds behaviours	Predictor	Estimate	SE	df	t value	P value
Perch	Time (later AM)	-12.96	6.48	160.9	-1.99	0.047
	Species (pied	16.40	4.69	156.9	3.49	< 0.001
	imperial pigeon)	-26.10	4.69	156.9	-5.56	< 0.001
	Species (Victoria	11.87	4.69	149.1	1.98	0.049
	crowned)					
	Species (shama)					
Preen	Time (later AM)	11.56	4.83	157.0	2.39	0.018
	Species (pied	12.00	3.58	158.4	3.35	0.001
	imperial pigeon)	-16.48	5.59	158.8	-3.58	< 0.001
	Species (shama)	-1.23	0.59	26.9	-2.06	0.049
	Visitor max					
Forage	Species (pied	-23.70	3.41	162.0	-6.94	< 0.001
	imperial pigeon)	-13.40	3.41	162.0	-3.93	< 0.001
	Species (Victoria	-23.70	4.18	162.0	-5.67	< 0.001
	crowned)					
	Species (shama)					
Move	Species (pied	-13.00	2.00	158.6	-6.49	< 0.001
	imperial pigeon)	-7.70	2.00	158.6	-3.84	< 0.001
	Species (Victoria	-13.2	2.45	158.6	-5.38	< 0.001
	crowned)					
	Species (shama)					
Alert	Species (pied	10.6	1.46	156.7	7.23	< 0.001
	imperial pigeon)	5.60	1.46	156.7	3.82	< 0.001
	Species (Victoria	3.96	1.83	94.4	2.16	< 0.033
	crowned)	0.002	0.001	158.9	3.13	0.002
	Species (shama)	0.382	0.142	111.1	2.70	0.008
	PF	-0.693	0.299	136.1	-2.32	0.021
	Visitor total					
	Visitor max					
Social	Species (Victoria	38.10	5.55	157.5	6.86	< 0.001
	crowned)	36.49	5.55	65.2	5.34	< 0.001
	Species (shama)					
Desert House behaviours	**Predictor**	**Estimate**	**SE**	**df**	**t value**	**P value**
Perch	Species (stone	13.76	4.71	81.2	2.92	0.004
	curlew)	18.69	6.08	33.1	3.07	0.004
	Species (wonga	15.51	6.35	192.3	2.44	0.015
	pigeon)					
	Time (later PM)					
Preen	Time (later AM)	12.37	4.13	211.6	3.00	0.003
	Time (PM)	16.70	4.74	206.9	3.52	< 0.001
	Species (tinamou)	-23.20	2.84	207.9	-8.18	< 0.001
	Species (stone	-22.60	2.84	207.9	-7.96	< 0.001
	curlew)	-17.00	3.66	207.9	-4.64	< 0.001
	Species (wonga	0.004	0.001	208.0	2.70	0.008
	pigeon)	0.677	0.277	164.8	2.45	0.015
	PF					
	Visitor max					
Forage	Time (midday)	-9.01	3.80	210.1	-2.37	0.019
	Time (PM)	-15.23	4.31	163.4	-3.54	< 0.001
	Time (later PM)	-8.12	3.58	194.2	-2.27	0.024
	Species (stone	-13.35	2.67	209.3	-5.00	< 0.001
	curlew)	-0.002	0.001	167.9	-2.08	0.039
	PF					
Move	Species (tinamou)	9.70	1.63	100.6	5.93	< 0.001
	PF	0.002	0.001	127.2	2.88	0.005
Alert	Species (tinamou)	11.05	2.28	208.9	4.85	< 0.001
	Species (stone	21.55	2.28	208.9	9.47	< 0.001
	curlew)					
Social	Species (tinamou)	3.90	0.733	209.5	5.31	< 0.001
	LEQ	0.291	0.109	155.5	2.66	0.008

(Rose et al., 2018), as well as reproductive activity (nesting and movement patterns for courtship). Measurement of the responses of PZ flamingos if any nesting occurred would further strengthen the evaluation of impacts of sounds and visitors on their behaviour. Likewise, for BZ flamingos, it may be that birds were so preoccupied with nesting and chick rearing duties that other stimuli were given lesser importance. As the BZ birds were nesting adjacent to a visitor path that ran around the side of the exhibit (birds were screened by tall reed matting against the aviary mesh), there may be evidence that sounds, and visitors are not a threat to nesting flamingos if the birds are settled in their colony. The layout of the enclosure may have minimised external disturbance and zoo staff have managed visitor presence using screening and siting of the nesting area. This may be supported by Blanchett et al. (2020) who showed that whilst some birds moved away from noisy visitors, little overall changes to behaviour that indicated poor welfare were noted. Further research on the behaviour of the birds in the build-up to nesting and individual behaviour changes in this nesting zone with different numbers of visitors would be helpful.

Research into the enclosure usage of these flamingos at these two zoos has identified some potential links between space occupancy, visitor presence and sound (Rose et al., 2021). Change in movement patterns within an enclosure (moving away from areas of high sound power) has been identified in captive birds housed in a walk-through enclosure (Blanchett et al., 2020), potentially indicative of control over where to be when sound levels are higher and therefore reducing negative welfare impacts. Measuring the sound directly within the enclosure would provide information on what the flamingos are actually listening to or hearing, and therefore would enable more precise evaluation of behaviour patterns to determine if individuals are moving away from sounds that they find disturbing.

The distance of the observer and sound measurement equipment from the centre of the enclosure was different for each flamingo exhibit. This would have impacted on what sound was recorded compared to what was audible to the birds. As noise pollution can be higher around and within an animal enclosure with more visitors present (Quadros et al., 2014), further study should consider standardising the distance from the recording equipment to the animals and placing recording equipment within the enclosure to correlate with measures taken from publicly accessible areas.

4.2. Indoor bird time-activity budgets

For the time budgets of indoor-housed birds, a wider range of behavioural profiles were noted, however, these did align with the ecology of each species. For example the white-rumped shama spent the majority of his time singing and perching in vegetation, similar to behavioural budgets described by Roberts et al. (2020); the bush stone-curlews were inactive during the day as befitting a cryptic, nocturnal species (Andrews, 2000); and the elegant-crested tinamous displayed a mixture of active, foraging behaviours, and resting and preening under vegetation, and calling when alarmed as described in wild birds (Gomes, 2020). The diversity of time budgets suggested that these enclosures provided some species of bird with a stimulating and engaging, ecologically relevant environment to perform naturalistic time-activity budgets based on their individual form and function. The importance of the suitability of the captive environment is noted in other research that has assessed impacts of visitor presence and noise on bird activity in walk-through enclosures, showing that the enclosure and how it is used by the birds can reduce or mitigate any negative effects from visitor presence (Blanchett et al., 2020).

Environmental effects are highlighted by the responses of the bush stone-curlews. This species spent significantly less time foraging compared to other species and higher proportion of time alert. Limited foraging is likely explained by the nocturnal nature of the stone-curlews, with feeding behaviours occurring after dark in a diverse array of habitats (Murialdo et al., 2015). The time spent alert by the bush stone-curlews may also be explained by ecology, relying on crypsis and vigilance to avoid threats. The uniform substrate of the DH may have played a role in the reduced foraging activity and increased vigilance of this species. Wild bush stone-curlew prefer mixed substrates of leaf litter, fallen branches and grass ground cover, all of which increase foraging opportunities and provide a better background colour palette for them to camouflage against.
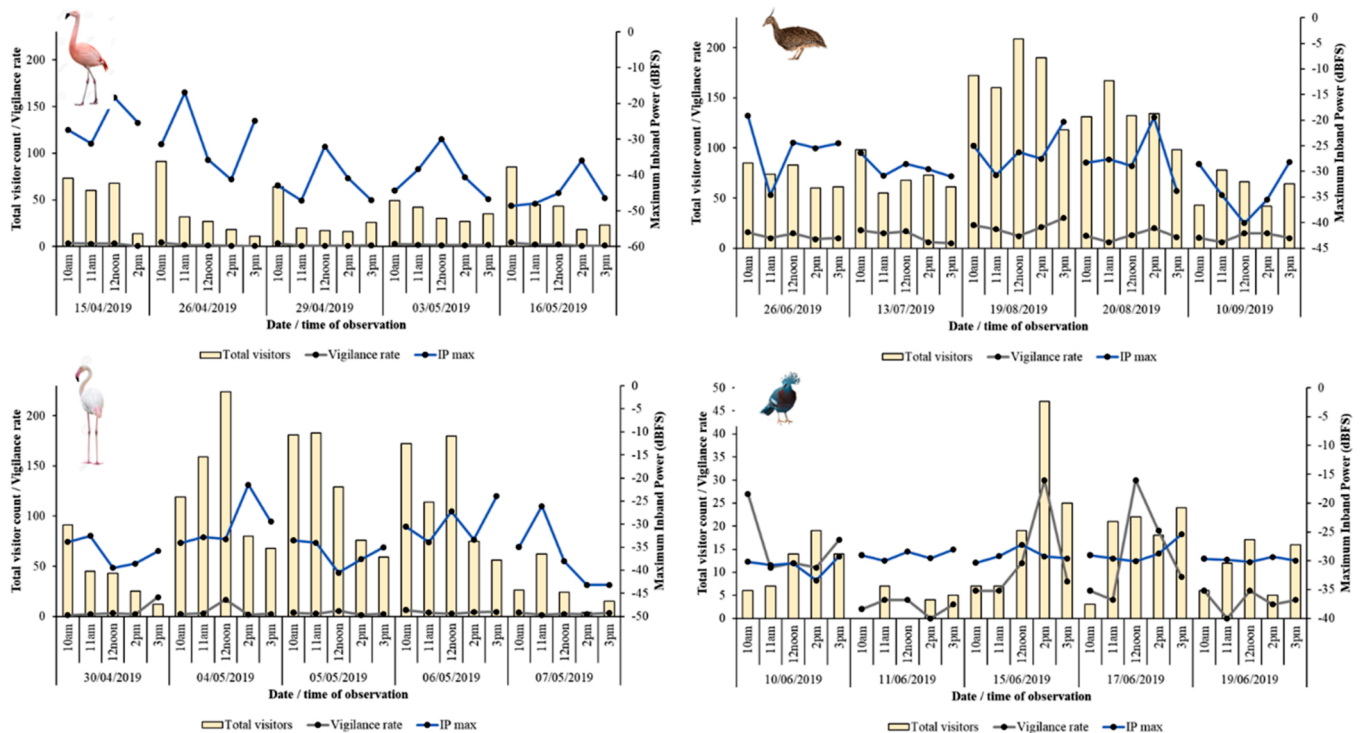
Fig. 3. Vigilance rates for PZ flamingo (top left) and BZ flamingos (bottom left), vigilance count for tinamous in the PZ DH (top right) and Victoria crowned pigeons in the BZ FOB (bottom right). Total number of visitors per observation per day are plotted alongside of maximum Inband Power for that observation period. Different scales are shown on the Y axes dependent on species' response and on the enclosure.

Table 3
Significant predictors of vigilance for Victoria crowned pigeons. A corrected significance level of 0.03125 was applied and Q values of significance provided.

Victoria crowned pigeon (BZ)					
Predictor	Estimate	SE	Z value	P value	Q value
Time	-0.877	0.258	-3.40	< 0.001 *	0.0063
Later AM	-0.769	0.321	-2.39	0.017 *	0.031
PM	-0.873	0.253	-3.45	< 0.001 *	0.013
Later PM					
Visitor total	0.05	0.008	5.98	< 0.001 *	0.019
LEQ	-0.121	0.038	-3.16	0.002 *	0.025

4.2.1. Effects of sound and visitors on indoor bird behaviour

Previous research on zoo-housed birds and influences on their behaviour from visitor-associated changes to the sound environment has noted the challenge of isolating the specific responses to sound (Blanchett et al., 2020). Similarly, for wild birds, habitat occupancy can remain unchanged even when the environment becomes "noisier" (Francis et al., 2011) when it may be assumed that they would move away. Indoor zoo enclosures are also more likely to be hotspots of heightened visitor noise and variability in the sound environment (Pelletier et al., 2020) and even if the zoo soundscape overall is not detrimental to welfare, such indoor hotspots may be a wellbeing challenge. Behavioural flexibility and alterations to behaviour patterns may be used to cope with variation in the characteristics of the sound environment that a bird is experiencing. For example, in the DH, more time was spent preening at higher PF and when discrete groups of visitors in the enclosure were higher. Preening may be a comfort behaviour, performed by the birds in response to external stressors. As PF describes the most prominent or maximum point of energy in the sound wave it may be that birds were performing comfort behaviour when the frequency of sound environment suddenly became overly stimulating or uncomfortable. Further observation and recording of preening rates as a welfare indicator may be more useful to the evaluation of VE on zoo-housed

birds alongside of vigilance rates. In domestic fowl (Gallus gallus domesticus), mild, short-term stressors initiated displacement preening actions, as reviewed in Duncan (1998), and similar responses may be present in birds in the DH when presented with sudden, large groups, of visitors that created unusual variation in the sound environment.

The species in the FOB, birds of covered habitats, may display increased vigilance when alarmed to identify the source of the stressor, and this has manifested as the relationship between increased sound levels and increased (overall) visitor number that increased alert behavioural responses. Cumulative effects of a larger number of visitors passing through FOB may have increased bird vigilance rates due to any effect as a prolonged stressor, whereas discrete larger visitor groups within the exhibit initiated lower alert responses, perhaps because the birds used other behaviours as a response to these larger discrete groups (e.g., by perching higher in the enclosure or seeking cover).

Movement behaviour (including walking and flight) increased with higher PF in the DH. Research into the effects of auditory enrichment on zoo-housed birds noted change to the number of occurrences of flight based on the music or sound the birds were exposed to (Robbins and Margulis, 2016). These authors suggested that birds may habituate to sound over time, but sudden changes or the presence of more naturalistic sounds may increase the performance of some behaviours. As change to the sound environment in the DH (an increase in LEQ) also increased the performance of social behaviour (including vocalisation) it may be that birds are responding to distinct calls or song patterns from other species, which in turn cause movement. Robbins and Margulis (2016) stated that naturalistic sounds increased vocalisation in some bird species, whereas human-created music increased calls in others. In our study, the mixture of species that all utilise a similar environment may have caused behaviour change in one species due to the response of sounds or visitors from another species, e.g., increased alarm calling due to loud groups of visitors increasing movement behaviour in others. However, further research into inter-specific associations and how individuals responded to the behaviour of others, as well as to the

behaviour of their own species plus humans, is required to fully validate this.

Responses of wild forest birds to human presence has identified species-specific differences in behavioural responses (Fernández-Juricic et al., 2004). These authors noted that larger bodied species retreated further from humans within a forest and were less tolerant of human presence overall. Time spent on alert behaviours significantly increased with higher PF and with higher total number of visitors to FOB, and the largest-bodied species (pied imperial and Victoria crowned pigeons) displayed the largest increase in alert as a state behaviour (Table 2). It may be that these species responded to any disturbance to the prevailing sound environment with alterations to behaviour as a primary defence strategy - to keep a watch and to judge the need for any further behavioural reaction. The large size of these pigeons may mean that use of cover could be limited and therefore vigilance is their best option when assessing where a potential stressor is coming from before retreating further. In our study, the Victoria crowned pigeons, the world's largest species of pigeon (Lint, 1977) showed an increase in vigilance rates with higher numbers of people and an increase in LEQ, suggesting that birds were disturbed by a more powerful sound environment and the presence of greater numbers of visitors. Research on wild Victoria crowned pigeons identified them as being a species intolerant of long-term disturbance by humans but able to tolerate moderate disturbance if suitable habitat is available (Keiluhu et al., 2019). Such wild traits may be apparent in captivity, with higher visitor number instigating more vigilance in this species, however, given that the pigeons were nesting during the observation period, the quality of the habitat provided in the enclosure may be suitable for the birds to perform normal behavioural changes to tolerate human presence overall.

An extended period of data collection would be useful to decipher individual species responses to visitors within this tropical rainforest environment. As noted in wild rainforest habitats (Retamosa Izaguirre et al., 2021), the conditions of this planted, climate-themed environment- temperature and humidity, dense planting and cover, the running stream and waterfall- will alter the way sound travels within the space occupied by the birds and therefore how they perceive sounds and respond to them. An extended period of study would further identify key sound predictors of bird behaviour and how such predictors correlate with other environmental and anthropogenic factors. This would be especially useful for any further comparison of different styles of indoor enclosure where the modelling of different habitats will not only influence the characteristics of the sound environment but also how visitors behave in the enclosure too.

4.3. Research extensions and areas for further study

Whilst this research has shown that zoo-housed birds respond differently to the presence of changes to the sound environment and to the presence of visitors at/in their enclosures, further developments are possible to improve the validity of these results. Calibration of the recording equipment could be considered for future research to enable further, precise identification of differences in sound measurements between enclosures. As temperature and humidity impact on how far sound can travel, future research should consider accurate measurement of temperature and humidity when attempting to quantify behavioural responses to sound (especially in climate-controlled indoor enclosures).

Consideration of microphone location and standardised distance between the microphone and species, plus evidence that identifies the audible threshold for frequencies within species-specific audiograms would add further support to conclusions drawn from behavioural data and species-specific responses to sound. Consolidation of recording periods, observing behaviour and recording sounds over sequential dates in the same season is also a relevant methodological change for a future project. This would provide more validity to the description of the overall characteristics of the sound environment at each zoo and help

further identify differences in the background sound environment between urban and suburban zoos.

For some behaviours, model r^2 values are low, suggesting that other sources of variation are impacting on the time spent on these behaviours. For example, time spent on feeding and foraging for the flamingo flocks may be further influenced by availability of flamingo pellet, the timing of when pellet was provided by keepers and the overnight weather conditions that can impact on bird energy requirements. These factors are worthy of measurement in any future study and could improve the r^2 value for this model (currently at 21%). Low r^2 values in the indoor bird houses, for example foraging (25%) and social behaviour (20%) may be similarly affected by other variables that have not been measured during this period of observation. The physiological need to preen, as a maintenance activity, and forage to maintain homeostatic demands will be important drivers of these behaviours- highly individual in how much time is proportioned to them. Consequently, further analysis of behavioural change at the individual level is likely to identify key predictors of such important maintenance or adaptive behaviours, and other activities where model r^2 values are currently low.

Measuring the characteristics of the sound environment at each end-of-sample point (rather than from the start to end of each minute sampling period) was used to correspond with data analysed for the study of enclosure usage and sound and visitors at these two zoos (Rose et al., 2021). As a single sound measure at the end of the sampling period may be more influenced by extraneous or unusual sounds that occur on the sample point and therefore any repeat of this work could consider a longer behavioural sampling time to link with continuous calculation of sound measures across the same time period. More meaningful LEQ values may be computed using this approach. The potentially limited variation in LEQ (Table 1) may suggest that LEQ is not the most appropriate measure for describing average sound level over time at/in these exhibits, as LEQ is most useful when sound levels are varying quickly (NoiseNews, 2015); therefore more work is needed to refine the recording of continuous sound levels within the zoo in the future. The wide range in PF measures per time period (Table 1) may result from acute sounds made by animals or specific human activities and therefore we cannot say how this has impacted the bird's response at a specific time point. Calculation of average sound power and frequency could also reduce any bias in these sound measures as this may capture a wider range of characteristics of the sound environment that animals are responding to. This approach has been used to determine effects of time spent visible during periods of heightened "noise" at and around a zoo enclosure (Wark et al., 2022) and could therefore be developed for further longitudinal study of sound and (any) associated zoo animal behavioural responses.

As well as further investigation of individual birds, so each zoo is worthy of wider evaluation. Individual zoo as a predictor of differences in occurrence of alert behaviour for the flamingo flocks is noted, with more time spent on alert at PZ (mean flock %). Husbandry routine, approach of visitors to the enclosure and their patterns of movement around it, management of the nesting site at BZ (habituating flamingos to human presence) and the presence of wild birds in the PZ open-topped enclosure may all account for the observed difference. Increased time spent on observations at each zoo, counts of the presence of wild birds and the way in which flamingos respond to keepers may provide further data to see if there is a significant influence of zoo on the bird's behaviours.

Trends toward a significant impact on inactivity caused by sound (reduced inactivity with increased sound power) would be further validated with a larger dataset on flamingo behaviour. Wild flamingos are responsive to the pressures of tourist presence, moving away if they feel disturbed (Yosef, 2000) and therefore increasing the number of recording periods throughout the day may further illuminate any relationship between sound, the source of sound, and flamingo movement patterns. Increasing the number of days of study would also capture wider variation of weather and climatic conditions, which are known to

influence flamingo activity (Rose et al., 2018) and bias any VE on captive flamingo flocks (Kidd et al., 2022; Rose et al., 2021).

Extension of this research to multiple zoos would also be of use. We are unable to provide replication for each species of bird and therefore our results may be very specific to each zoo. Whilst general trends may be considered useful to other facilities housing these species (e.g., the overall lack of visitor effect for two very closely related species of flamingo), observation on other populations at other zoos will provide a more complete picture of how these species of birds respond to visitors and variation in environmental sounds. Further study of the VE is encouraged in indoor bird walk-through aviaries. It appears from our results that a VE is likely in such enclosed zoo exhibits, with the birds being affected by people and by the sounds that visitors to these indoor spaces create. Our results showed that the way birds moved around their enclosure was affected by visitor presence, with increased movement at higher PF and changes to vigilance and alert behaviours apparent when visitor number increased. These findings mirror what can be found in research on wild bird responses to increased presence of bird watchers (Collins-Kreiner et al., 2013), with free-living birds moving away from larger groups of birdwatchers and maintaining a greater minimum distance from observers. A key point in the research of Collins-Kreiner et al. (2013) is that with increasing bird numbers comes an increasing number of birdwatchers, which are then more likely to disrupt the birds and impact on their activity and habitat usage. Such findings are likely important for zoos to consider. Increased visibility of birds within an exhibit will draw larger crowds of visitors (as the animals and their exhibit are perceived as more interesting) but this larger number of people will increase the likelihood of birds moving away or their behaviour being negatively impacted. Therefore, zoos need to design and structure enclosures to ensure that adequate cover is available, with retreat spaces (appropriate to the species held) and perches at height to enable natural anti-threat responses to be performed by the birds, which therefore allows them to have control over the presence of visitors and a choice in how they respond to them. A balance needs to be struck between engagement with the visitor, to ensure that the animal collection fulfils the key aims of the zoo, and that of animal welfare, avoiding long-term negative states and allowing animals the opportunity to thrive within the environments created and managed for them.

The complex relationships identified in our zoo-based study are reflected in work on wild bird population densities, activities and species richness in urban parks of varying sizes, across seasons and different levels of human presence (Zhou and Chu, 2012). These authors noted that noise from park visitors had little impact on the presence of birds, but numbers of visitors reduced bird presence at certain times of the year. We should be mindful of population, species, and individual animal differences in responses to human presence, as well as consider the effects of the environment and season on how birds may perceive changes to the sound environment and the behavioural responses, they show because of variation to the sounds around them. For example, from this study, we can recommend changes to the enclosures for the species that have been observed: change to the substrate of the DH in some areas to increase opportunities for behavioural diversity in the bush stone-curlew, and provision of leaves and branches on the ground to aid camouflage and expand foraging options. This may reduce the time this species spent alert and provide a greater sense of security when visitors are present.

5. Conclusions

Our research has identified that species of birds housed at two zoos, in different styles of enclosure, responded very differently to changes to the sound environment. Whilst there are elements of the sound environment that have been beyond our measurements, and whilst it may be hard to decipher precisely how specific species and individual birds responded to and interpreted sound, we have noted that some species altered their behaviour patterns according to increased power of sound around them. We have also illustrated that visitor presence in and around an enclosure can also change bird behaviour, potentially in conjunction with changes to the sound environment that the birds may be withdrawing from. This study highlights the multifactorial nature of any visitor effect and that different species, even though housed in the same environmental conditions, will respond in unique ways to variation in sound and human presence, and the interaction between the two. Zoos should consider further measurement of the sound environment when mixing species together in enclosures and consider ways to mitigate the potential effects of visitor presence on bird behaviours.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2022.104763.

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