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Assessing the effect of zoo closure on the soundscape using multiple acoustic indicators

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ABSTRACT

The zoo soundscape has important implications for animal welfare, management, and conservation. However, despite its importance, the zoo soundscape is yet to be examined in depth. Consistent human presence can influence the zoo soundscape. However, it is difficult to determine the specific impact of human presence, as visitors are usually present during the day when animals are active. The COVID-19 lockdown in 2020 provided a unique opportunity to study zoo soundscapes in the absence of visitors. The main aim of this study was to compare the sound environment across three zoo aviaries during the 2020 closure period to a comparable period in 2019 in which the zoo was open. We examined broad band frequency measures of sound pressure levels, sound pressure levels in defined frequency bands, and ecoacoustic indices (the Acoustic Complexity Index and Normalized Difference Soundscape Index) to describe the zoo soundscape. Ecoacoustic indices have not, to our knowledge, previously been used in the zoo setting, although they may provide a useful metric to assess zoo soundscapes. Therefore, we used this natural experiment to explore how successful these measures may be in assessing sound in zoo environments. We found that, during the zoo closure period, the overall sound pressure levels were lower (by 4.4 – 6.4 dB(Z) depending on aviary), and this effect was particularly pronounced in the lower frequency bands. The proportion of sound energy at low frequencies was also lower during the zoo closure period in two of the three aviaries. We argue that NDSI could be a useful index for determining the impact of human presence in zoos, although further information on how it is influenced by additional factors, such as human speech, would be beneficial. The use of multiple indices to assess the sound environment can provide additional information beyond traditional measures of sound levels in zoos, such as frequencies where sound energy is concentrated and characteristics of the soundscape, which could be used to better target management and mitigation.

1. Introduction

Zoos differ from wild environments in a number of aspects, such as the lack of predators, reductions in disease and parasites, and space constraints (Frankham, 2008). Perhaps the clearest difference between zoo environments and those in the wild is the consistent presence of human influences. The effect of the presence of human visitors, often measured by the overall number of visitors, on animal behaviour and welfare has been widely examined (Davey, 2007; Fernandez et al., 2009; Hosey, 2008, 2000; Sherwen and Hemsworth, 2019). However, the effect of human presence on other aspects of the environment, such as environmental sound, is less often considered.

Human presence can influence the soundscape experienced by animals in zoos. In general, sound sources in zoos can be separated into five broad categories (e.g., Clark & Dunn, 2022): 1) permanent sources of anthropogenic sound, such as heating, ventilation, and air conditioning (HVAC) systems; 2) temporary anthropogenic sound from maintenance, construction, and other events; 3) human speech and footfall; 4) sounds produced by other animals (Clark and Dunn, 2022); and 5) sound from abiotic sources such as weather patterns and running water. Three of these five categories are related to human presence and anthropogenic sound sources, suggesting that the constant presence of humans is likely to have a significant impact on the soundscape. Sound produced by other animals may also vary between wild and zoo environments due to

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novel species composition in zoos. As such, animals in zoos may experience soundscapes that differ from those in the wild (Lara and Vasconcelos, 2019). In addition, the contributions of different sound sources are likely to differ among zoos and enclosures, and, therefore, soundscapes are also likely to vary among zoo environments (Clark and Dunn, 2022).

The soundscape is an important consideration in zoos due to its potential effects on animal behaviour, communication, and welfare. Increases in sound from visitors have been associated with a wide range of behavioural changes across taxa, which are often interpreted as negative (reviewed in Sherwen & Hemsworth, 2019). As well as potential effects on animal behaviour, exposure to environmental sound can also affect physiology, development, neural functions, and genetics (Kight and Swaddle, 2011), and may even lead to hearing impairment (Wolfenden et al., 2019). Importantly for ex-situ breeding programmes, sound can also negatively affect reproductive success (Halfwerk et al., 2011; Kight et al., 2012). Increased background sound can obscure sounds that are important for survival and reproduction, an effect known as masking, which could reduce communication efficacy (Barber et al., 2010; Blickley and Patricelli, 2010; Brumm and Slabbekoorn, 2005). Many taxa are reported to alter vocal behaviour to reduce the effect of masking (Brumm and Slabbekoorn, 2005; Slabbekoorn and Ripmeester, 2008). As such, the soundscape in zoos may alter vocal behaviour, contributing to vocal divergence between populations, which may have knock-on effects for conservation programmes (Lewis et al., 2021; Passos et al., 2017). Given its potential effects on animal behaviour, welfare and conservation, understanding the soundscape has important implications for animal management in zoos.

Despite its importance, the study of sound in zoos has lagged behind that in wild environments (Clark and Dunn, 2022) and sound is less often considered than other features of the zoo environment (Binding et al., 2020). Past work has focused mostly on measuring maximum sound pressure levels, which provide a quantification of environmental sound in decibels, most often in dB(A) (Clark and Dunn, 2022). This metric is weighted to the human hearing range, and does not provide any additional information on how energy is spread over the frequency spectrum, including outside the human hearing range, which may be relevant for some species. However, there is increasing interest in the full spectrum of sound in zoos (Clark and Dunn, 2022; Pelletier et al., 2020; Rose et al., 2021). Due to recent technological advances, such as the development of low-cost autonomous recording units (ARUs), it is possible to collect large amounts of data with comparatively little effort (Brandes, 2008). This allows for a more in-depth study of the soundscape beyond traditional sound levels, such as the investigation of sound in specific frequency bands (Pelletier et al., 2020). There also is ample opportunity to use measures such as ecoacoustic indices, which were developed for use in the wild, in zoos (Bradfer-Lawrence et al., 2019; Clark and Dunn, 2022; Sueur et al., 2014). Ecoacoustic indices reduce multidimensional data into a single metric which provides information about the characteristics of sound in the environment, such as complexity or diversity, rather than just measuring sound intensity (Sueur et al., 2014). The addition of ecoacoustic indices to analysis of sound in zoos may provide a more well-rounded view of the soundscape, which will be beneficial for management.

As zoos are rarely closed for prolonged periods; visitors are present throughout the year. Therefore, it is difficult to determine the effects of human presence on the soundscape, as humans are constantly present during the day when many animals are active. However, the COVID-19 lockdown in 2020 provided a unique opportunity to study sound in the zoo in the absence of visitors and with reduced influences from other anthropogenic sound sources (e.g., road and air traffic). A number of studies have examined the effect of lockdown and the absence of visitors on animal behaviour in zoos (Carter et al., 2021; Finch et al., 2022; Jones et al., 2021; Masman et al., 2022; Podturkin, 2022; Williams et al., 2021b, 2021a; Williams et al., 2022), but, to our knowledge, the effect on the soundscape has not been explored. We aimed to determine the impact of zoo closure (or, more specifically, an absence of visitors and a reduction in human influences) on the soundscape by comparing the COVID-19 closure period to a comparable period when the zoo was open. Firstly, we investigated changes in sound pressure levels using broad frequency band measures (dB(A) and 10 Hz – 10 kHz dB(Z)), as well as in narrower, defined frequency bands (dB(Z)), to determine if there were changes in the volume of sound associated with human presence. Secondly, we examined the effect of human presence on aspects of the soundscape beyond volume using two ecoacoustic indices: the Acoustic Complexity Index (ACI) (Pieretti et al., 2011), which measures soundscape complexity, and the Normalized Difference Soundscape Index (NDSI) (Kasten et al., 2012), which quantifies soundscape naturalness (i.e., the ratio of low frequency anthropogenic sound to higher frequency biotic sound). As ecoacoustic indices have not previously been used in zoos, this natural experiment provides the opportunity to determine if these indices can usefully quantify the effect of human presence on the soundscape in zoos.

2. Methods

2.1. Data collection sites and periods

Data were collected from three aviaries at Chester Zoo, UK, between April 30th and May 21st 2019 and April 8th and May 9th 2020 (see Appendix A for precise dates). We decided to work in aviaries as acoustic communication plays a particularly prominent role in the life of many bird species, and many birds are most active during visitor hours (Catchpole and Slater, 2008). Changes in vocal behaviour associated with anthropogenic sound have been reported in a range of species (Patricelli and Blickley, 2006; Slabbekoorn, 2013), and these changes could have knock-on effects for conservation programmes (Lewis et al., 2021). Therefore, aviaries were chosen as understanding the human impact on sound in zoo aviaries provides a useful basis for further research on how human-induced soundscape change might impact birds and other animals in the zoo.

The Bali Temple aviary (Fig. 1) is an outdoor, walkthrough aviary located near the edge of the zoo, in an open area close to a main road (A41). The Sumatra aviary (Fig. 1) is also an outdoor, walkthrough aviary, but in a sheltered location surrounded by zoo buildings. In a walkthrough aviary, the visitor path is located inside the aviary, i.e., visitors and birds occupy the same space without barriers. The Dragons in Danger aviary (Fig. 1) is an indoor aviary located at the centre of the zoo. Although this aviary is not a walkthrough, the visitor path moves through the building with netted aviaries either side of the walkway, meaning that there is no sound barrier between visitors and birds. Each aviary contained a range of bird species, including various passerines, pigeons, pheasants and parrots, many of which are native to South East Asia (species lists for each aviary in each time period can be found in Appendix A).

2.2. Data collection method

Sound recordings (sample rate 24 kHz, 16-bit, stored as Wav files) were made using Wildlife Acoustics SM4 recorders (Wildlife Acoustics Inc., Maynard, MA, USA) placed within the enclosure. The built-in omnidirectional microphones with a sensitivity of -35 ± 4 dB (0 dB = 1 V/Pa at 1 kHz) of the SM4 were used for recording. Devices recorded in stereo (two channels), although only a single channel was used for analyses. For the Dragons in Danger aviary, the recording device was placed in a central location within the bird area, although this was outside of the netted aviaries. Device position and orientation were consistent between years. Devices were set to record continuously across the days, and were collected at a later date that was convenient for zoo staff. As a result, the devices often continued to record until either the batteries ran out or the memory card reached capacity, resulting in some differences in the total duration of recordings per year per aviary (Bali

Fig. 1. A) Location of Chester Zoo (Chester) within the UK, indicated by yellow star B) Map of aviaries included in the study: A) Bali Temple, B) Dragons in Danger, C) Sumatra. The zoo perimeter is marked in yellow. Scale bar on zoo map indicates 300 m. Copyright: Google Earth.

Temple 2019 ~ 167 h, 2020 ~ 101 h; Dragons in Danger 2019 ~ 163 h, 2020 ~ 182 h; Sumatra 2019 ~ 169 h, 2020 ~ 136 h). As the sampling frequency was 24 kHz we could reliably capture information on sounds up to 12 kHz following the Nyquist theorem, which is appropriate for birds, as biotic sound (and the frequency limits of many bird songs) is typically concentrated below 8 kHz (Kasten et al., 2012; Pijanowski et al., 2011; Slabbekoorn and Ripmeester, 2008). The 2019 recordings were not part of the initial design of this study, as it was prior to the 2020 closure period. As a result, microphones were not calibrated for the 2019 recordings. When the opportunity for this study occurred following zoo closure during the pandemic, we did not have the capacity in the zoo to calibrate the microphones on the recorders. To minimise the potential effects of differences in sensitivity, we counterbalanced recorders and microphones as much as possible across years and locations to reduce the impact of systematic differences between enclosures.

2.3. Data extraction

Data for sound pressure levels and ecoacoustic indices were extracted using Kaleidoscope Pro 5.4.7 (Wildlife Acoustics Inc., Maynard, MA, USA). Data were extracted for a single channel (left) of the stereo recording in all cases.

2.3.1. Broad frequency band measures

To assess sound pressure levels (broad and defined bands), we extracted the mean (L_{eq}) sound pressure level (SPL) for each 1-hour period during the day. Mean sound pressure level is a representative measure for sounds that remain more or less constant over time, and is only weakly affected by sharp bursts of sound that may occur e.g., slamming doors. Sound pressure levels used the standard reference of 20 μPa, where 1 Pa is equal to a sound pressure level of 94 dB.

We extracted two broad frequency band measurements, A-weighted decibels (dB(A)) across the recording, and Z-weighted decibels (dB(Z)) between 10 and 10,000 Hz. A-weighted sound level measurements apply a filter adjusted to the human hearing range with reduced weighting of infra- and ultra sounds (Kurra, 2021). A-weighted measurements are often used in acoustic studies in zoos, as most commercial sound level meters use this metric. Therefore, we included dB(A) values to allow for comparison with other studies. Moreover, birds' hearing ranges are broadly similar to that of humans (Catchpole and Slater, 2008) suggesting that dB(A) may be meaningful when examining sound in an aviary setting. Z-weighted dB uses a flat-frequency response, where all frequencies are given equal weight, providing a less anthropocentric measure of sound in the environment. Therefore, dB(Z) provides a broader measure of sound in the environment, which is not based on the hearing range of a particular species. Mean sound pressure levels for both A-weighted and Z-weighted dB were calculated within 60-minute intervals.

2.3.2. Defined frequency band measures

We also examined sound pressure levels (dB(Z)) in different frequency bands. Understanding how sound energy is distributed in the environment can help us to identify which sounds are prevalent, determine which species are most likely to be affected by sound, and appropriately target mitigations, which often act across a limited range of frequencies (Orban et al., 2017). We extracted information on sound pressure levels from 30 third-octave bands (central frequencies 19.7 – 10079.4 Hz). Mean sound pressure levels for each octave band were calculated within 60-minute intervals. We then combined the sound pressure level (SPL) from these bands into four larger frequency bands for analysis: very low frequency (17.6–111.4 Hz); low frequency (111.4 – 890.9 Hz); mid frequency (890–9 – 8979.7 Hz); and high frequency (8979.7 – 11313.7 Hz). Each third-octave band was given equal weighting, providing a measure in dB(Z), using the following equation, where the summation runs over all third-octave bands in the bin being created (Lin et al., 2021):

$$\mathrm{SPL_{total}} = 10\log\left(\sum\nolimits_i 10^{\frac{SPLi}{10}}\right)\ \mathrm{dB(Z)}$$

These divisions are meaningful for the study of sound in aviaries and elsewhere in zoological environments. The very low frequency band covers sound below 100 Hz, including some infrasound (<20 Hz), which can effect health in both humans and animals (Lousinha et al., 2018; Pereira et al., 2021; Persinger, 2014). Many bird taxa use frequencies below 1 kHz for communication (Slabbekoorn and Ripmeester, 2008), and therefore may contribute to and be impacted by sound in the 'Low' frequency band. The 'Mid' frequency band is biologically relevant for many species, covering a large proportion of biotic sounds (Kasten et al., 2012; Pijanowski et al., 2011) and the sensitive hearing ranges of most bird species (Dooling, 1992; Dooling et al., 2000). Some bird species may also use higher frequencies in songs and for alarm calls, so will contribute to and be impacted by the 'High' band. Our combined frequency bands also align with those calculated in Pelletier et al. (2020), which facilitates comparisons and increases repeatability (Clark and Dunn, 2022). However, unlike Pelletier et al. (2020), we only studied sounds below 12 kHz, as these are likely to be most relevant for birds.

2.3.3. Ecoacoustic indices

Eocacoustic indices are statistics that can be used to summarize aspects of the soundscape (Sueur et al., 2014; Towsey et al., 2014). Ecoacoustic indices have not previously been used in zoo environments (Clark and Dunn, 2022), but could be useful in understanding sound in zoos beyond sound pressure levels. We identified two indices, the Acoustic Complexity Index (ACI) (Pieretti et al., 2011) and the Normailized Difference Soundscape Index (NDSI) (Kasten et al., 2012), (detailed below), that may be particularly relevant to the zoo environment and examined how they behave in the different aviaries and situations in this study. Whilst ecoacoustic indices can be tuned to match individual habitats, we used the standard settings (Kasten et al., 2012; Pieretti et al., 2011), which are detailed below, during extraction. Ecoacoustic indices are yet to be used in zoo settings, so it is difficult to determine how standard settings perform and, if sub-optimally, how they should be adjusted. For each index (ACI and NDSI), we extracted index values for each 60-s section of recordings using Kaleidoscope Pro. An average of each index was then taken per hour to be used in analyses.

We extracted the Acoustic Complexity Index (ACI) (Pieretti et al., 2011), which is based on the observation that many biotic sounds are intrinsically variable, whilst anthropogenic sound is often more constant (Pieretti et al., 2011; but see Wolfenden et al., 2019). The index compares amplitude differences between time intervals within narrow frequency bands, and these measures are combined across frequency bands to calculate the overall index (Pieretti et al., 2011). The ACI in each minute of each recording was computed as

$$ACI = \sum_{f=1}^{F} \frac{\sum_{k=1}^{K} \left| I_{f,k} - I_{f,k+1} \right|}{\sum_{k=1}^{K} I_{f,k}}$$

where $I_{f,k}$ is the intensity of sound in band f in time step k, $K = 2812$ is the number of 0.021–s time steps in 60 s of recorded sound, and $F = 256$ is the number of frequency bins in the full frequency range. Natural soundscapes, e.g., those with high biophony (sounds of biotic origins e.g., birds), have higher ACI values (Pieretti et al., 2011). In wild environments, ACI values have been found to correlate with the number of bird vocalizations (Pieretti et al., 2011). Examining diel patterns in ACI could indicate whether the metric responds appropriately to increases in vocal activity during daylight hours in the zoo. In addition, by comparing ACI values in 2019 and 2020, we can assess whether soundscape complexity is affected predictably by human presence and anthropogenic disturbances. To calculate ACI, we used an FFT window size of 512, with non-overlapping windows. We considered the entire frequency range of the recording in the calculation of ACI.

The Normalized Difference Soundscape Index (NDSI) (Kasten et al., 2012) determines the relative ratio of anthropogenic compared to biotic sound, providing a useful metric to assess the dominance of anthropogenic sounds in zoo environments. Anthropogenic sounds are generally prevalent between 1 and 2 kHz, although many anthropogenic sounds also occur below 1 kHz, whereas biological sounds are more commonly found between 2 and 8 kHz (Kasten et al., 2012; Pijanowski et al., 2011). Therefore, these bands are used to represent anthropogenic (1 – 2 kHz) and biotic (2 – 8 kHz) sound in the index. Some sounds in our recordings, particularly at low frequencies, may fall outside of this range, but we chose to use the default values for ecoacoustic indices to aid comparison with other studies. Briefly, the NDSI calculates the power spectral density of the signal, and then an estimate of the power spectral density integral is computed for each of the specified frequency ranges, which are then compared using the formula NDSI $= (\beta - \alpha)/(\beta + \alpha)$, where β and α are the total estimated power spectral density for the largest 1 kHz biophony and anthrophony bins respectively (Kasten et al., 2012). The NSDI returns a value between -1 and $+1$, with positive values indicating relatively more biotic compared to anthropogenic sound and negative values indicating relatively more anthropogenic compared to biotic sound (Kasten et al., 2012). By comparing the 2019 and 2020 periods, we can assess how NDSI changes with human presence and determine its effectiveness as a metric for assessing sound disturbance in zoos. To calculate NDSI we used an FFT window size of 512 with 50 % overlap of windows, using the 1 – 2 kHz and 2 – 8 kHz bands detailed above.

2.4. Data analysis

To examine the effect of visitor absence on features of the soundscape we used a series of Generalized Additive Models (GAMs) implemented in the mgcv package (Wood, 2011) in R 4.1.2 (R Core Team, 2022). The use of GAMs allows us to account for the non-linear effect of time of day on the soundscape by fitting a spline to the variable. All models included fixed effects of year, time of day, and the interaction between year and time of day as predictors, and random effects of date. The effect of year (as a factor) compares sound during the 2020 zoo closure period to the period of zoo opening in 2019. Time of day was included in the model as a fitted spline. This accounts for non-linear changes in the response variables over the course of each day. The interaction between year and time of day allows for time of day to affect response variables differently in each year. The random effect of date accounts for non-independence of data points within days if days differ intrinsically. When studying dB(Z) computed for individual frequency bands, we used a model with the same fixed and random effects outlined above. To remove high order interactions and improve interpretability of our results, we studied the effect of year on dB(Z) separately within each frequency band. Models are formalized in Appendix B. As different aviaries are expected to behave differently both within and between years, the set of models described above were run separately for each aviary in the dataset. This aids interpretation of the results by removing high order interactions between factors.

2.5. Data availability statement

Data and code associated with this manuscript can be found at https://doi.org/10.48420/22921460.

3. Results

3.1. Broad frequency band measures

Broad frequency band measures of sound pressure levels varied significantly between years, although the effects differed among aviaries. When examining dB(A), Sound pressure levels (SPLs) measured in dB(A) were lower in the Dragons in Danger and Sumatra aviaries in 2020 (i.e., in the absence of visitors) compared to 2019 (Table 1; Fig. 2B). There was no significant difference in dB(A) in the Bali Temple aviary between years (Table 1; Fig. 2B). Sound pressure levels measured in dB (Z) were significantly lower in all 3 aviaries in 2020 compared to 2019 (Table 1; Fig. 2A). Across all models, the spline for time was significant ($p < 0.01$), meaning that sound pressure levels varied significantly over the course of the day (Fig. 2, Table 4).

3.2. Defined frequency band measures

Changes in SPLs within defined bands varied among aviaries and frequency bands. In all three aviaries, SPLs in the low and very low frequency bands decreased in 2020 compared to 2019 (Table 2; Fig. 3). However, SPLs in the mid frequency band decreased only in the Sumatra and Dragons in Danger aviaries. SPLS in the high frequency band decreased in the Sumatra and Dragons in Danger aviaries, but increased in the Bali Temple aviary (Table 2; Fig. 3). Across all models, the spline for time was significant ($p < 0.001$), meaning that SPLs varied significantly over the course of the day (Fig. 3, Table 4).

3.3. Ecoacoustic indices

There was a significant effect of zoo closure on the Acoustic Complexity Index (ACI), although the direction of this effect differed among aviaries (Table 3; Fig. 4A). ACI values were higher in 2020 than 2019 in the Bali Temple aviary, indicating a more complex soundscape. However, in the Dragons in Danger and Sumatra aviaries, ACI values were lower in 2020 than 2019, indicating reduced soundscape complexity in 2020. Across all models, the spline for time was significant ($p < 0.001$), meaning that ACI values varied significantly over the course of the day (Fig. 4, Table 4).

When considering the Normalized Difference Soundscape Index (NDSI), there was a significant effect of year in two out of the three aviaries examined. In the Bali Temple and Dragons in Danger aviaries, NDSI values were higher in 2020 than 2019 (Table 3; Fig. 4B). This indicates a greater proportion of biotic compared to anthropogenic sound in the soundscape. However, there was no significant difference in NDSI values between years in the Sumatra aviary. Across all models, the spline for time was significant ($p < 0.001$) meaning that NSDI values varied significantly over the course of the day (Fig. 4; Table 4).

4. Discussion

We found significant differences in the soundscape of zoo aviaries between the zoo closure period in 2020 and a similar period of normal zoo operation in 2019. During the closure period, no visitors were present on the zoo site, and human activity surrounding the zoo was reduced due to the COVID-19 lockdown. Given the substantial reductions in human activity during 2020, it is apparent that chronic human presence in and around the zoo has a significant effect on the zoo soundscape, with aviaries being quieter, with less low frequency sound, and greater soundscape naturalness during the closure period.

Overall sound pressure levels (SPLs) across the whole frequency spectrum decreased during the zoo closure period. This pattern is similar to that reported by Quadros et al., (2014), who found that sound levels were higher on days when the zoo was open compared to when the zoo was closed across enclosures measured. Results were similar, but not identical, when considering A-weighted (dB(A)) and Z-weighted (dB(Z)) metrics; all three aviaries were significantly quieter in 2020 when considering dB(Z), but only two of the three aviaries showed a significant decrease in dB(A). These differences can be understood in more detail using the narrower frequency bands examined in our study. Low and very low frequency sound, which is down-weighted when calculating dB(A) to reflect human hearing sensitivity (Kurra, 2021), was a significant component of the soundscape in all aviaries, and decreased significantly during the zoo closure period. Mid and high frequency sounds, which are given a larger weighting when calculating dB(A) (Kurra, 2021), also decreased in two of the aviaries. However, mid frequency sound showed no difference and high frequency sound increased in the third aviary, which may contribute the differences between aviaries when using dB(A). Our results suggest that an unweighted metric, such as dB(Z), may be more useful when characterizing the effect of human presence on the zoo soundscape, especially as weighted metrics, such as dB(A) may be inappropriate for assessing sound perceived by species with different hearing ranges to humans (Pater et al., 2009).

The use of defined, narrow frequency bands in addition to traditional, broad-band measures of SPLs provides a more detailed overview of where sound energy is concentrated in the environment. This can help us to further explore information provided by other metrics, such as dB (A) and dB(Z), as well as identifying which species may be impacted most by sound disturbances. Species with sensitive hearing ranges or vocal ranges in frequency bands impacted by human presence may be disproportionately affected. The frequencies of sound examined (17.6 – 11313.17 Hz) in this study were appropriate for birds (Catchpole and Slater, 2008; Dooling, 1992; Dooling et al., 2000). However, many animals are sensitive to frequencies outside of this range, including infrasound (e.g., elephants (Payne et al., 1986)) and ultrasound (e.g., rodents (Sales, 2010)), and defined bands could be tailored as necessary. Across aviaries, the frequency band with the greatest power differed, although low and very low frequency sounds were prominent across aviaries during both years. Sound in these bands significantly decreased

Table 1
Generalized Additive Models (GAMs) examining the effect of year (as a factor) on mean sound pressure level (SPL) in dB(A) and dB(Z) in three Chester Zoo aviaries. Estimates represent the difference in 2020 (zoo closure) compared to 2019 (zoo open).

	Mean Sound Pressure Level (dB(A)) Year (2020 vs. 2019)			Mean Sound Pressure Level (dB(Z)) Year (2020 vs. 2019)		
	Estimate	Standard Error	p-value	Estimate	Standard Error	p-value
Bali Temple	−0.165	0.515	0.750	−5.349	0.902	<0.001
Dragons in Danger	−6.806	0.674	<0.001	−4.409	0.347	<0.001
Sumatra Aviary	−3.637	0.341	<0.001	−6.362	0.333	<0.001

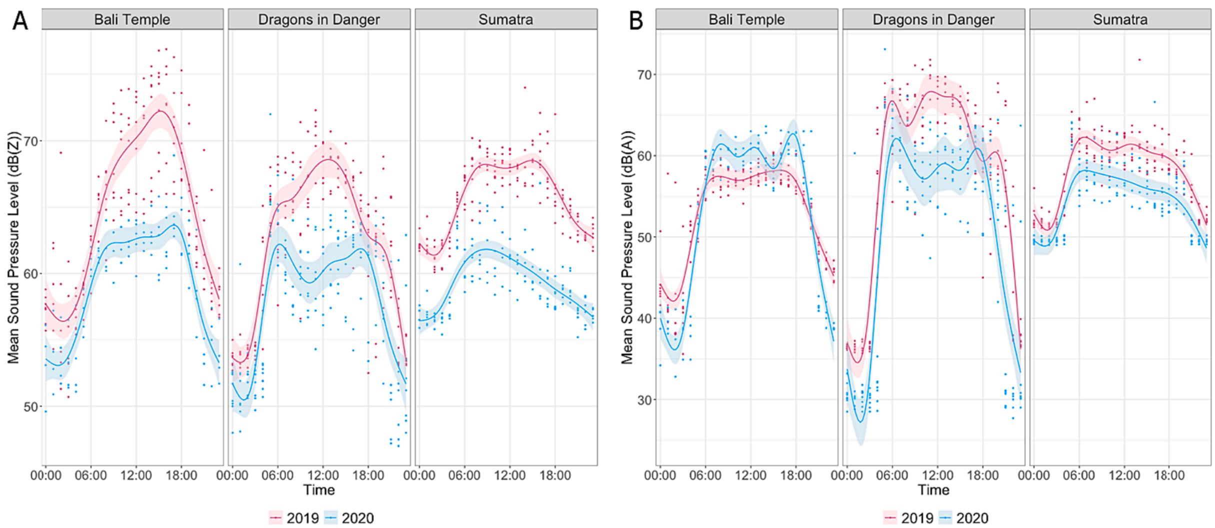

Fig. 2. Daily patterns of sound pressure levels (broad frequency band) for zoo closure (2020, blue) and zoo open (2019, red) periods across three zoo aviaries. Panel A shows the mean sound pressure levels in dB(Z). Panel B shows mean sound pressure levels in dB(A). Lines show the predicted values (using GAMs) and the shaded area shows the standard error around the prediction. Individual points show raw data values.

Table 2
Generalized Additive Models (GAMs) examining the effect of year and frequency band (Very Low (17.6–111.4 Hz), Low (111.4 – 890.9 Hz), Mid (890–9 – 8979.7 Hz), High (8979.7 – 11313.7 Hz)) on sound pressure levels (dB(Z)) in three Chester Zoo aviaries. Values represent pairwise differences illustrating the change in the mean sound pressure level (SPL) within each frequency band during zoo closure in 2020 compared to zoo opening in 2019.

	Year (2020 vs. 2019) Estimate	Standard Error	p-value
	Bali Temple		
Very Low	−7.471	0.853	<0.001
Low	−7.066	0.860	<0.001
Mid	0.148	0.545	0.787
High	4.188	0.552	<0.001
	Dragons in Danger		
Very Low	−3.071	0.635	<0.001
Low	−10.068	1.301	<0.001
Mid	−5.727	0.713	<0.001
High	−3.042	0.724	<0.001
	Sumatra Aviary		
Very Low	−8.098	0.408	<0.001
Low	−4.390	0.2859	<0.001
Mid	−3.808	0.347	<0.001
High	−2.100	1.064	0.049

in 2020, indicating a significant effect of human presence. Due to the opportunistic nature of this study, microphones were not calibrated prior to deployment, although microphones were deployed in different enclosures in 2019 and 2020 to minimize the potential impacts of differences in microphone sensitivities between units. Despite these steps, some of the variation in our measurements of sound pressure levels may have resulted from the lack of microphone calibration. However, the pattern of soundscape changes across the 3 aviaries combined with the rotation of microphones provides evidence for an effect of zoo closure and human presence on the soundscape. Future research should ensure that microphones are calibrated prior to deployment to obtain a more accurate estimate of the soundscape and changes therein.

We also examined the use of ecoacoustic indices in zoo environments. Although ecoacoustic indices can provide information about the characteristics of sound in the environment beyond its intensity (Sueur et al., 2014), they are not generally considered in zoo environments (Clark and Dunn, 2022). The Acoustic Complexity Index (ACI) is a measure of soundscape complexity, and correlates with animal vocal activity in wild environments (Pieretti et al., 2011). We did not find consistent differences in patterns of soundscape complexity between the two periods, with complexity increasing in one aviary and decreasing in the other two. This suggests that soundscape complexity, and the ACI, may not be a suitable measure to assess anthropogenic sound disturbances and the response of zoo-housed birds. Although not suitable as a measure of sound disturbance, ACI showed similar diel patterns to SPLs, increasing in the morning as more animals become active and decreasing towards the end of the day, indicating that peaks in ACI may still relate to vocal activity. In addition, the direction of change for ACI reflected changes in SPLs in the mid and high frequency bands. Where ACI values decreased, SPLs in both mid and high bands also decreased, and when the ACI value increased there was a corresponding increase in SPLs in the high frequency band. Most biotic sound is concentrated between 2 and 8 kHz (Kasten et al., 2012; Pijanowski et al., 2011), although some birds use higher frequencies in the vocal repertoire, so these changes in SPLs, and associated changes in ACI may indicate differences in biotic sound and vocal activity. Although vocal activity can shift due to anthropogenic sound disturbance (Brumm and Slabbekoorn, 2005; Ortega, 2012; Slabbekoorn and Ripmeester, 2008), a number of other factors could have influenced our results. Vocal activity is likely to be affected by the time of year (Amrhein et al., 2002; Digby et al., 2014; Koloff and Mennill, 2013; Sierro et al., 2023), weather (Digby et al., 2014; O'Connor and Hicks, 1980; Vokurková et al., 2018), and number of birds in and around the aviary. Furthermore, in complex and frequently disturbed zoo environments, soundscape complexity may be influenced by additional factors beyond birds' vocal activity, in particular the presence of human voices. Whilst soundscape complexity and the ACI could be useful for detecting peaks in vocal activity in birds, e.g., during breeding, to inform management decisions, further investigation is required to fully understand possible factors that influence the ACI in zoos and the relevance of soundscape complexity in zoo environments.

The Normalized Difference Soundscape Index (NDSI) is a measure of soundscape 'naturalness' (Kasten et al., 2012). NDSI values were higher in 2020 for two of the three aviaries, indicating a more natural soundscape, with a greater proportion of 'biotic' (2–8 kHz) compared to 'anthropogenic' (1–2 kHz) sound. Given the decrease in human activity in 2020, the NDSI appears to be a successful indicator of disturbance associated with human presence in zoos, and could be used to determine the relative impact of human-generated sound. Whilst NDSI appears to be potentially useful in zoos, there are some potential limitations. In particular, our analyses of sound pressure levels in defined bands

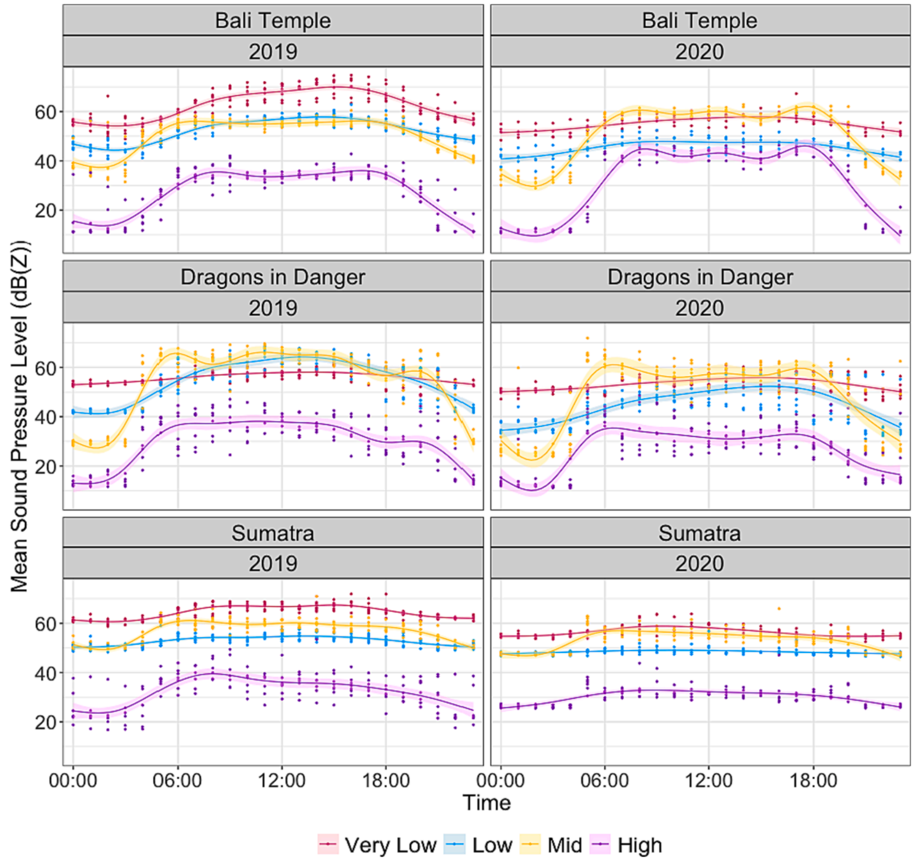

Fig. 3. Mean sound pressure levels (dB(Z)) within frequency bands (Very Low (17.6–111.4 Hz), Low (111.4–890.9 Hz), Mid (890-9–8979.7 Hz), High (8979.7–11313.7 Hz)) for zoo closure (2020) and zoo open (2019) periods in three zoo aviaries. Lines show the predicted values and the shaded area (using GAMs) shows the standard error around the prediction. Individual points show raw data values.

Table 3

Generalized Additive Models (GAMs) examining the effect of year (as a factor) on Acoustic Complexity Index (ACI) and Normalized Difference Soundscape Index (NDSI) in three zoo aviaries Estimates represent the difference in 2020 compared to 2019.

	ACI Year (2020 vs. 2019)			NDSI Year (2020 vs. 2019)		
	Estimate	Standard Error	p-value	Estimate	Standard Error	p-value
Bali Temple	5.412	0.817	<0.001	0.244	0.054	<0.001
Dragons in Danger	−3.566	1.219	0.004	0.460	0.065	<0.001
Sumatra Aviary	−8.507	1.163	<0.001	−0.027	0.031	0.375

indicate that sounds below 1000 Hz are a significant component of the zoo soundscape, and these sounds decreased during the zoo closure period. However, when using the default settings, these frequencies are not used in the calculation of the NDSI, and so are not captured by the index, which may limit our understanding of overall impacts on the soundscape. Despite this, NDSI values suggested a similar, but not identical, pattern of human presence on the soundscape as the SPLs in two of the three aviaries, but did not differ between years in the third. However, the NDSI provides information about relative changes in the soundscape, rather than changes in absolute values. So, if sound in both the 'biotic' and 'anthropogenic' bands change in the same way relative to one another, NDSI values will not change despite an overall change in SPLs. One of the most important limitations of the NDSI in zoos is the potential impact of human voices, as, although human voices are a biotic sound, human speech covers a broad range of frequencies (Fant, 2004) spanning both the 'anthropogenic' and 'biotic' bands defined in the default NDSI settings. Whilst this does not preclude the use of NDSI, further investigation would be beneficial to understand the usefulness of NDSI in monitoring zoo sound.

Across all measures, aviaries varied in terms of the soundscape and changes therein. Such differences may relate to aviary position within the zoo, setting (indoor or outdoor), popularity, and species composition. Previous studies have reported that indoor environments differed significantly from those outdoors (Pelletier et al., 2020). However, we did not find consistent differences between the indoor and outdoor aviaries. Changes in species composition and number of birds in aviaries between years may have significantly impacted our measures. For example, in the Bali Temple aviary, high frequency sound and ACI values increased, and mid frequency sound remained unchanged, despite SPLs in these bands decreasing in the other aviaries. Compared to the other aviaries, the Bali Temple had the largest population increase (73 birds in total in 2019 vs. 83 birds in total in 2020), which may have impacted biotic sound and vocal activity. In order to identify specific features that could impact changes in the soundscape, a larger sample size of aviaries would be required. However, it is possible that enclosures are uniquely impacted by different factors, in which case, generalizations would not be possible and enclosures would need to be studied on a case-by-case basis.

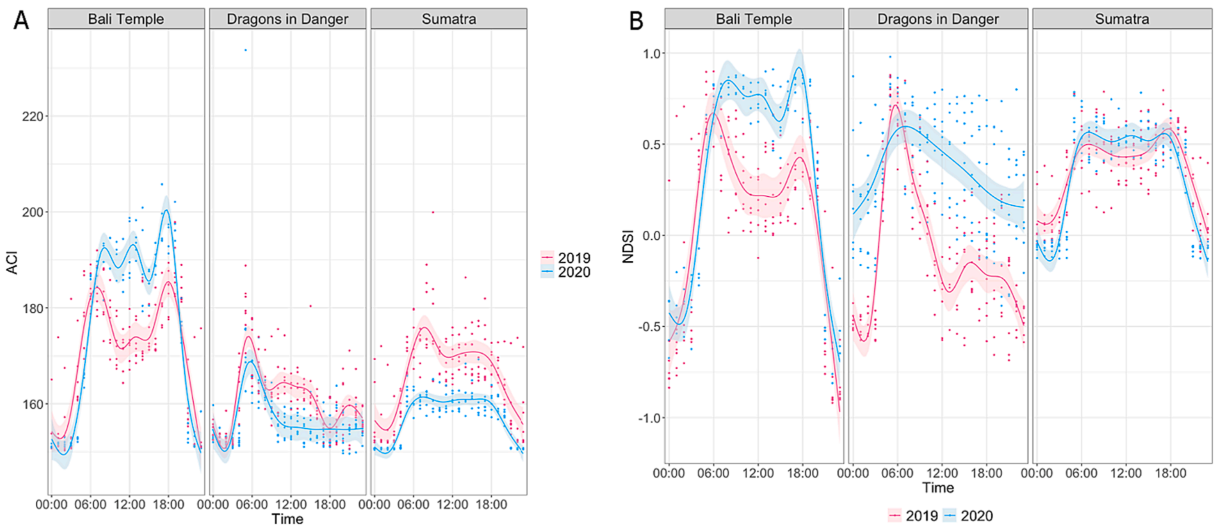

Fig. 4. Daily patterns of ecoacoustic indices in zoo aviaries for zoo closure (2020) and zoo open (2019) periods in three zoo aviaries. Panel A shows the Acoustic Complexity Index (ACI). Panel B shows the Normalized Difference Soundscape Index (NDSI). Lines show the predicted values and the shaded area shows the standard error around the prediction. Individual points show raw data values.

Table 4
Estimated degrees of freedom and smoothing parameters for fitted GAM models.

	Time (2019) Effective degrees of freedom	Smoothing parameter	p-value	Time (2020) Effective degrees of freedom	Smoothing parameter	p-value	Date Effective degrees of freedom	Smoothing parameter	p-value	Deviance	D^2 (%)
dB(A)											
Bali Temple	8.238	0.00317	<0.001	8.685	0.000676	<0.001	6.373	13.999	0.006	1645.746	90.0
Dragons in Danger	8.420	0.00219	<0.001	8.582	0.00167	<0.001	1.128	242.991	0.369	11743.190	81.6
Sumatra	8.166	0.00357	<0.001	7.645	0.00564	<0.001	4.124	41.293	0.105	1575.349	76.6
dB(Z)											
Bali Temple	7.501	0.00819	<0.001	6.970	0.00830	<0.001	9.569	2.784	<0.001	1492.115	86.4
Dragons in Danger	7.545	0.00756	<0.001	8.158	0.00389	<0.001	0.162	1824.504	0.44	3382.275	73.4
Sumatra	7.712	0.00650 (0.0064995)	<0.001	6.877	0.0121	<0.001	9.661	6.144	<0.001	534.070	90.2
Defined Frequency Bands (dB(Z))											
Bali Temple											
Very Low	7.575	0.00756	<0.001	4.645	0.0657	<0.001	9.442	3.080	<0.001	1468.56	87.2
Low	7.729	0.00636	<0.001	6.944	0.00850	<0.001	9.900	2.061	<0.001	1034.942	88.1
Mid	8.325	0.00272	<0.001	8.665	0.000725	<0.001	5.240	21.429	0.027	2330.833	90.0
High	7.976	0.00477	<0.001	8.591	0.000906	<0.001	0.00101	220051.10	0.520	4886.702	87.4
Dragons in Danger											
Very Low	4.339	0.143	<0.001	5.646	0.0477	<0.001	12.311	3.702	<0.001	1684.036	58.8
Low	6.793	0.0157	<0.001	6.709	0.0189	<0.001	12.397	3.542	<0.001	6755.53	80.9
Mid	8.540	0.00167	<0.001	8.584	0.00167	<0.001	0.472	611.573	0.416	13884.77	82.2
High	7.713	0.00627	<0.001	8.116	0.00414	<0.001	1.920	133.725	0.297	12700.06	67.9
Sumatra											
Very Low	7.593	0.00743	<0.001	6.162	0.0228	<0.001	10.591	3.977	<0.001	568.2058	92.1
Low	7.845	0.00555(45)	<0.001	3.254	0.403	<0.001	8.850	8.463	<0.001	504.1438	81.1
Mid	8.133	0.00375	<0.001	7.696	0.00533	<0.001	3.890	45.054	0.120	1747.47	76.8
High	7.568	0.00764	<0.002	3.771	0.217	<0.001	10.089	5.099	<0.001	4762.057	60.0
ACI											
Bali Temple	8.609	0.00143	<0.001	8.703	0.000634	<0.001	2.149	82.328	0.255	8363.015	86.8
Dragons in Danger	8.445	0.00208	<0.001	8.208	0.00359	<0.001	11.031	6.247	0.001	9259.291	57.7
Sumatra	8.187	0.00345	<0.001	6.044	0.0252	<0.001	10.423	4.337	<0.001	4937.955	78.9
NDSI											
Bali Temple	8.283	0.00293	<0.001	8.311	0.00167	<0.001	7.835	7.674	<0.001	12.306	84.5
Dragons in Danger	8.549	0.00163	<0.001	7.774	0.00650	<0.001	12.857	2.787	<0.001	13.783	78.3
Sumatra	7.850	0.00551	<0.001	8.347	0.00211	<0.001	9.796	5.797	<0.001	4.357	78.9

5. Conclusions

Differences in multiple measures of sound between a closure period in 2020 compared to a period of normal operation in 2019 indicated that human presence significantly affects the soundscape in the aviaries examined.

Our results have several implications for how sound is measured and managed in the zoo. Firstly, our findings indicate that a single measure (traditionally dB(A)) may not sufficiently capture the impact of human presence on the sound environment experienced by animals. Although the measures used in this study provide similar qualitative information about soundscape, different measures showed different patterns within and between aviaries. In particular, dB(A) failed to fully capture the impact of human presence on low frequency sound, so may not be the most suitable measure for assessing sound disturbance, especially for species with hearing sensitivities significantly different from humans. Therefore, examining multiple features of the soundscape, can provide more complete information for use in management decisions.

The use of narrow, defined frequency band measures provided additional information about the sound frequencies where most energy is concentrated, allowing us to identify the species most likely to be affected by human sound disturbance and target sounds for mitigation. Our results indicated that human impacts on the soundscape were most pronounced at lower frequencies, particularly those below 1000 Hz. Birds (or other taxa) that hear and vocalize in this range may be particularly susceptible to human disturbance, with sound potentially masking important vocal signals or contributing to vocal change. For this reason, incorporating species biology into the assessment of sound disturbance will be vital when considering the need for interventions. Our results also indicated heterogeneity between aviaries in the type and extent of human impacts on the soundscape, with measures differing between aviaries and years. Determining areas of low disturbance in this was may be relevant when choosing areas to place sensitive species.

Ecoacoustic indices have not previously been used in the zoo setting. but our results indicate that these measures provide useful information to guide zoo management. In particular, the NDSI, which measures the ratio of low to high frequency sound in the environment, could be used to identify areas more or less affected by human presence and inform decisions about the need for mitigation measures (e.g., sound barriers, moving equipment or machinery away from enclosures, or moving animals to more suitable locations). The ACI, which is a measure of soundscape complexity did not show clear patterns associated with human presence in the zoo, but may still be useful for determining peaks of vocal activity for birds in the zoo. Before deploying ecoacoustic indices more widely for zoo management purposes, further investigation into how they are affected by aspects of the zoo environment are required. In particular the impact of human speech, should be investigated more thoroughly, as speech is not commonplace in the environments where these indices were developed or the animals naturally occur.

Although we have demonstrated the potential for information on soundscapes to be used in a zoo setting, our study is limited to three aviaries within a single zoo. Wider exploration of the sound environment, encompassing taxa beyond birds and a larger number of zoos, would provide a stronger evidence base for management decisions. In addition, as bird vocalization patterns change over the course of the year (Amrhein et al., 2002; Digby et al., 2014; Koloff and Mennill, 2013; Sierro et al., 2023), the slight differences in the data collection dates within aviaries between year may contribute to soundscape differences. Recording soundscapes over longer time periods, for example, at set intervals across the year, would provide a more detailed picture of how the zoo soundscape changes over time. There were also some changes in species composition within aviaries over the course of our study, which could affect the contribution of avian vocalizations to the soundscape. Measuring the soundscape before and after changes in aviary composition could provide more information on how the numbers of individuals and species-specific presence could affect sound pressure levels and, in particular, ecoacoustic indices.

Finally, whilst we find an effect of human presence on the soundscape, we did not investigate whether these differences impacted animals' biology. Changes in the sound environment may result in shifts in behaviour, such as altered activity budgets (e.g., Steinbrecher et al., 2023)) or enclosure usage (e.g. Wark et al., 2023), or physiological changes (e.g., Powell et al., 2006). Soundscape differences may also impact the acoustic communication of animals in the zoo, as is the case in other environments, both by masking important vocal signals (Barber et al., 2010; Blickley and Patricelli, 2010; Brumm and Slabbekoorn, 2005) or by driving changes in vocal behaviour (e.g., Brumm & Slabbekoorn, 2005; Slabbekoorn & Ripmeester, 2008)). Further research is necessary to determine the impacts of sound on animal biology to identify sensitive species and the extent of required mitigations.

Author Contributions

RL and LW conceptualized the study, with all authors contributing to refining data extraction protocols. RL and LW were involved in data collection for the project. RL completed the extraction of sound measures. RL and TG were responsible for data analysis. RL wrote the initial draft of the manuscript, including data visualizations, with all authors contributing to editing the manuscript. LW, SdK, and TG provided supervision to RL throughout the course of the project.

CRediT authorship contribution statement

Rebecca N. Lewis: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing, Project administration, Funding acquisition. **Leah J. Williams:** Conceptualization, Investigation, Methodology, Project administration, Supervision, Writing – review & editing, Funding acquisition. **Selvino R. de Kort:** Methodology, Supervision, Writing – review & editing. **R. Tucker Gilman:** .

Declaration of competing interest

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

Data availability

A link to an online repository containing data and code is provided within the manuscript

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Appendix

Appendix A:. Species lists for the three zoo aviaries in which the sound environment was investigated (Bali Temple, Dragons in Danger, Sumatra Aviary) in 2019 during zoo opening and 2020 during zoo closure. Date ranges of recordings are indicated in brackets

Bali Temple					
2019 (30/4/2019 – 7/5/2019)			***2020 (08/04/2020—12/04/2020)***		
Species Name	***Latin Name***	***Number***	***Species Name***	***Latin Name***	***Number***
Bali myna	*Leucopsar rothschildi*	9	Bali myna	*Leucopsar rothschildi*	5
Java sparrow	*Lonchura oryzivora*	55	Java sparrow	*Lonchura oryzivora*	65
Pied imperial pigeon	*Ducula bicolor*	5	Magpie robin	*Copsychus saularis*	2
Purple-naped lory	*Lorius domicella*	2	Pied imperial pigeon	*Ducula bicolor*	5
Sumatran laughing thrush	*Garrulax bicolor*	1	Purple-naped lory	*Lorius domicella*	4
Yellow-backed chattering lory	*Loris garrulus flavopalliatus*	1	Sumatran laughing thrush	*Garrulax bicolor*	1
			Yellow-backed chattering lory	*Loris garrulus flavopalliatus*	1
Total		**73**	**Total**		**83**
Sumatra aviary					
2019 (07/05/2019 – 14/5/2019)			***2020 (22/04/2020 – 28/04/2020)***		
Species Name	***Latin Name***	***Number***	***Species Name***	***Latin Name***	***Number***
Asian glossy starling	*Aplonis panayensis*	24	Asian glossy starling	*Aplonis panayensis*	26
Bronze-tailed peacock pheasant	*Polyplectron chalcurum*	2	Bronze-tailed peacock pheasant	*Polyplectron chalcurum*	2
Chestnut-backed thrush	*Geokichla dohertyi*	4	Chestnut-backed thrush	*Geokichla dohertyi*	5
Chestnut-bellied tree partridge	*Arborophila javanica*	1	Chestnut-bellied tree partridge	*Arborophila javanica*	1
Emerald dove	*Chalcophaps indica*	9	Emerald dove	*Chalcophaps indica*	6
Fairy bluebird	*Irena puella*	1	Fairy bluebird	*Irena puella*	1
Fire-tufted barbet	*Psilopogon pyrolophus*	1	Fire-tufted barbet	*Psilopogon pyrolophus*	1
Javan green magpie	*Cissa thalassina*	3	Javan green magpie	*Cissa thalassina*	2
Magpie robin	*Copsychus saularis*	1	Salvadori's pheasant	*Lophura inomata*	2
Salvadori's pheasant	*Lophura inomata*	2	Silver-eared mesia	*Leiothrix argentauris*	7
Silver-eared mesia	*Leiothrix argentauris*	3			
Total		**51**	**Total**		**53**
Dragons in Danger					
2019 (14/05/2019 – 21/05/2019)			***2020 (30/4/2020 – 08/05/2020)***		
Species Name	***Latin Name***	***Number***	***Species Name***	***Latin Name***	***Number***
Black-naped fruit dove	*Ptiliopus melanospilus*	3	Black-naped fruit dove	*Ptiliopus melanospilus*	4
Cinnamon ground dove	*Gallicolumba rufigula*	4	Cinnamon ground dove	*Gallicolumba rufigula*	3
Fairy bluebird	*Irena puella*	3	Fairy bluebird	*Irena puella*	2
Great argus	*Argusianus argus*	2	Great argus	*Argusianus argus*	2
Luzon bleeding heart dove	*Gallicolumba luzonica*	6	Javan green magpie	*Cissa thalassina*	2
Malayan great argus	*Argusianus argus argus*	1	Luzon bleeding heart dove	*Gallicolumba luzonica*	6
Mindanao bleeding heart dove	*Gallicolumba criniger*	2	Malayan great argus	*Argusianus argus argus*	1
Montserrat oriole	*Icterus oberi*	2	Mindanao bleeding heart dove	*Gallicolumba criniger*	3
Palawan peacock pheasant	*Polyplectron superbus*	2	Palawan peacock pheasant	*Polyplectron superbus*	1
Philippine mouse-deer	*Tragulus nigricans*	1	Philippine mouse-deer	*Tragulus nigricans*	1
Pink-headed fruit dove	*Ptilinopus porphyrea*	1	Pink-headed fruit dove	*Ptilinopus porphyrea*	1
Sumatran laughing thrush	*Garrulax bicolor*	2	Superb fruit dove	*Ptilinopus superbus*	5
Superb fruit dove	*Ptilinopus superbus*	4	Victoria crowned pigeon	*Goura victoria*	1
Visayan tarictic hornbill	*Penelopides panini panini*	5	Visayan tarictic hornbill	*Penelopides panini panini*	2
White-naped pheasant pigeon	*Otidiphaps aruensis*	2	White-naped pheasant pigeon	*Otidiphaps aruensis*	2
Total		**40**	**Total**		**36**

Appendix B:. Model formalization for analysing acoustic features

Studying sound pressure levels in narrow frequency bands.

For narrow band frequency measures, sound pressure levels (dB(Z)) were calculated within 4 defined frequency bands. Let y_i be the sound pressure level in frequency band b_i at time t_i on date d_i, and let a_i be an indicator that is 1 if d_i is in the year 2020 and is 0 otherwise. Let ^{i}B, ^{i}D, ^{i}G, and ^{i}C be row vectors that indicate the frequency band, date, year, and combination of frequency band and year, respectively, of observation i. In particular, ^{i}B is a row vector of length n_b, where n_b is the number of bands in the study, and in which entry $^{i}b_j$ is 1 if b_i is the j^{th} band and is 0 otherwise; ^{i}D is a row vector of length n_d, where n_d is the number of dates in the study, and in which entry $^{i}d_j$ is 1 if d_i is the j^{th} date and is 0 otherwise; $^{i}G=(1-a_i,a_i)$; and ^{i}C is a row vector of length 2 n_b where entry $^{i}C_j$ is 1 if b_i is the j^{th} band and $a_i=0$, $^{i}c_{j+}n_b$ is 1 if b_i is the j^{th} band and $a_i = 1$, and all other entries are zero. We fit the model.

$$y_i = \beta_0 + \beta_a a_i + {}^{i}BR_B + {}^{i}DR_D + {}^{i}CR_C + {}^{i}GF(t_i) + \varepsilon_i \tag{1}$$

where β_0 is the expected value of y across all observations in year 2019 (i.e., the intercept) and β_a is the estimated effect of being in year 2020. Vectors represented by the form R_X capture random effects. In particular, R_B, R_D, and R_C are column vectors of lengths n_b, n_d, and 2 n_b, respectively, with entries drawn from normal distributions with mean 0 and variances ν_b, ν_d, and ν_c, respectively. F is a vector-valued function in which entries $f_1(t)$ and $f_2(t)$ are smoothed functions of time of day in years 2019 and 2020, respectively, and $\varepsilon_i\ N(0,\nu_\varepsilon)$. The model parameters $\beta_0, \beta_0, \nu_b, \nu_d, \nu_c$ and ν_ε were estimated by restricted maximum likelihood and the smoothing parameters of f_1 and f_2 were estimated by penalized maximum likelihood.

If the interaction between band and year (ie, the estimated value of ν_c) is significantly different from 0, then the effect of year differs among bands, and when studying the effect of year it makes sense to consider each band independently. Thus, we fit the model.

$$y_i = \beta_0 + \beta_a a_i + {}^i BR_B + {}^i DR_D + {}^i CR_C + {}^i GF(t_i) + \varepsilon_i \quad (2)$$

where variables maintain the definitions from the full model, but where i runs over only those observations in the band being modelled.

Studying all other response variables

Broadband measures of dB(A) and dB(Z) were calculated across the full frequency spectrum, rather than in specific frequency bands as described above. Similarly, the ecoacoustic indices measured, ACI and NDSI, were measured using the full frequency spectrum. As a result, these measures produced a single value per time period. To study these features, we fit the model in Eq (2), where y_i represents the response variable in observation i.

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