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REVIEW

Defining Mechanistic Pathways for Anthropogenic Noise Impact on Avian Species

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Abstract

Purpose of Review This review collates and analyses data on noise exposure of birds in relation to avian hearing system performance. It provides new insights into the mechanistic pathways of anthropogenic noise impact on avian species.

Recent Findings Noise impacts both humans and wildlife. Birds are of conservation concern, given the recent reports of major global declines in bird populations and that one in eight bird species is threatened with extinction. Studies of noise impacts on birds have been, and continue to be, published. Whilst many of these studies report associations between noise and a response in birds, relatively few provide clear demonstration of the mechanisms of impact.

Summary Anatomical and physiological datasets were compiled for species representing nineteen avian orders. Information on noise sources, propagation path and habitat selection was also collated. Bird order was not a good predictor of bird hearing frequencies, but body dimensions were. In general, smaller birds were found to have higher peak hearing frequencies than larger birds. Cranium height was the strongest predictor of peak hearing frequency for birds. These findings provide mechanistic context to noise impacts on birds and a potential basis for predicting responses of avian species to different noise environments.

Keywords Mechanistic pathways · Noise impact · Birds · Avian hearing system · Avian hearing thresholds · Habitat selection · Propagation path

Introduction

Noisy environments have changed significantly and rapidly over the recent years. As demonstrated in a recent avian population report, around 48% (5245) of the world's species population declined, causing concerns about biodiversity loss [1]. Areas with animal abundance are now quieter and are presenting non-natural sound sources, e.g. electric vehicles, drones, wind farms, heat pumps, and human transportation and infrastructure [1, 2]. According to a recent international assessment, one in eight bird species are threatened with extinction [3]. As stated by Barton and Holmes [4], there is no place on Earth free from noise pollution. Not only humans are affected by noise pollution but also wildlife. It can affect the physiological, behavioural, communication, and sensory perception of wildlife.

Birds are important in several ecosystem services, such as habitat (1) regulating activities, e.g. pollinators, seed dispersers, and control of pets; (2) supporting activities, e.g. scavengers activities by nutrient cycling activities and ecosystem fluxes and processes through avian migration; [1] (3) cultural activities by physical health and mental wellbeing of humans, since avian son can be considered restorative [5].

In birds, communication, e.g. sending or receiving information, is essential for several behavioural characteristics and survival activities, such as territory defence, warning of danger, locating or attracting a mate, caring for offspring, prey capture, individual and species recognition, and vocal learning [6••, 7]. The variety of hearing ranges possessed by birds enhances their ability to localise sounds produced by mates, predators, humans and the environment, discriminating pitch, intensity, and temporal differences [6••].

Sound-source determination involves more than the auditory mechanism [8••]. Factors such as learning and attention, storage of information, and hypothesis testing are cognitive aspects

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linked to the acoustic signal localisation [9]. The sonic propagation path and habitat selection can also affect the reception of acoustic signals, influencing the hearing thresholds of species due to signal and spectral degradation [10, 11].

The present study aims to investigate the mechanistic pathways of anthropogenic noise impact on avian species. Key elements of the mechanistic pathways are explained, highlighting critical steps that should be considered in anthropogenic noise impact assessment for birds. Since biological factors are essential in a mechanistic pathway, this paper focuses on an analysis of the body and head dimensions, the avian hearing system, and the animal habitat selection linked to the sound propagation path.

Mechanistic Pathways

The term mechanistic pathway is commonly used in studies that are trying to identify the step-by-step of a biochemical process [12]. This study considers the process of emission–propagation–reception–outcomes that are widely studied on noise models for humans, but we are now focusing on avian species. The major differentiation between the traditional noise propagation models and a mechanistic pathway is the biological factor, including habitat selection and the body structure of each bird species. These aspects are determinants to the outcomes regarding the impacts caused by anthropogenic noise in the environment. Figure 1 shows the mechanistic pathway of the impact caused by anthropogenic noise on avian species. Some confounding factors, indicated in red, do not have a direct acoustic influence on the receptor but are important for mechanistic pathways due to avian habitat selection. Each step of the mechanistic pathway will be explained in detail in the text.

Sound Sources

Soundscapes comprise three significant sound source taxonomy components: biophony, geophony, and anthrophony. Biophony is sound produced by animals; geophony is non-biological sound and originates from atmospheric and geophysical sounds, e.g. wind, water, and rustling leaves [13]. Biophonic and geophonic sounds are classified in Schäfer's taxonomy as natural sounds [14]. In contrast, anthrophony is sound from human activities [13]. Schäfer [14] subdivided sounds from human activities into mechanical sounds, human sounds, and sounds and society, e.g. descriptions related to socio-cultural differences such as continents, towns, cities, maritime, domestic, trades, professionals, livelihoods, factories, offices, entertainments music, ceremonies

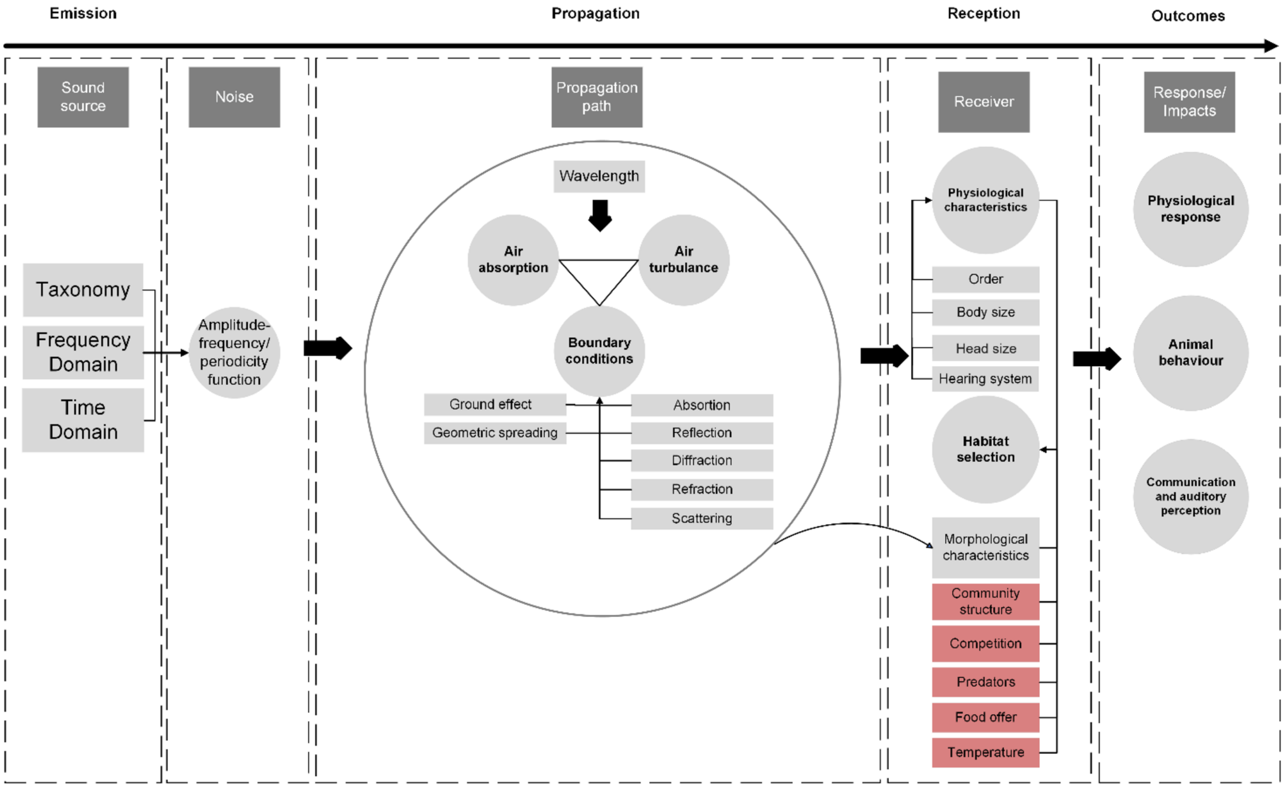

Fig. 1 Anthropogenic noise impact mechanistic pathway for avian species

and festivals, parks and gardens, and religious festivals. Farina and Gage [15] classify electromechanical sounds as technophony, which is usually associated with disturbance when there is an overabundance of technological sound sources. These are considered perceptually unpleasant, loud, or quantified disturbances, frequently rated as unwanted sounds or noise [16].

Anthropogenic noise is any human-produced sound considered unwanted or harmful to humans and wildlife [17]. The sound classification taxonomy started through Murray Schäfer, which classified the human-produced sounds as human-related (voice, body, and clothing), human activities (sounds related to general soundscapes, towns, cities, maritime, domestic, factories and offices, entertainments, music, ceremonies and festivities, parks and gardens, religious festivities), and mechanical sounds (machines, industrial and factory equipment, transportation machines, warfare machines, trains and trolleys, internal combustion engines, aircraft, construction and demolition equipment, mechanical tools, ventilators and air conditioners, instruments of war and destruction, farm machinery) [14]. The new sound sources provided by electrical transportation, drones, wind farms, and devices are not observed in Schäfer's sound sources taxonomy. Still, they can be classified, according to Brown et al. [18] and the International Organization for Standardization [19], as electro-mechanical sounds that can be stationary and mobile sounds. Background noise is the opposite of foreground noise or principal sound signal under investigation [14]. Schäfer describes the difference between foreground and background sounds through the description of hi-fi and lo-fi soundscapes. Hi-fi sounds have a favourable signal-to-noise ratio, where discrete sounds can be heard clearly due to low ambient noise, and sounds do not overlap frequently, making it easier to determine them at a distance, e.g. countryside, rural, and natural areas. Lo-fi sounds are obscure in a population of sounds which are amplified, and it is not possible to determine their localisation easily [14].

Despite the literature's emphasis on the sound source determination by humans through psychophysical (spectral and spatial–temporal) and perceptual attributes, many non-human species will also be able to recognise spectral and spatial–temporal content on sound signals. The spectral profile is an amplitude-frequency function and provides information about who or what emitted the sound, e.g. predator, prey, or sounds produced by safe activities that can be ignored [20]. Biophony predominates at 2 and 8 kHz [21–23], while geophony has a diffuse signal through the entire spectrum, being strong at the low frequencies [24], e.g. wind and rustling leaves around 200 Hz [25]. Sources like wind-generated waves (200 - 2 kHz) and rain (15–20 kHZ) also occur at mid and high frequencies [26, 27].

Table 1 Frequency range of sound sources that are disturbing to humans

Source type	Frequency range (Hz)	Dominant frequency (Hz)	Amplitude	References
Car	1000	1000		Rochat [28]
Heavy truck	500–1000	500		Rochat [28]
Motorcycle	1000–3000			Carley et al. [29]
Tractor	63–2000			Abd-El-Tawwab et al. [30]
Train	200–5000			Grassie et al. [31]
Tram	400–1000	500	75.5 dB	Panulinova et al. [32]
Aircraft	50–5000			Oakland International Airport [33]
Mining: surface diesel equipment	31.5–125		93–106 dB(A)	Giardino and Marracini [34]
Mining: drilling	1000–8000		93–115 dB(A)	Giardino and Marracini [34]
Mining: underground cutting equipment	125–500		95–107 dB(A)	Giardino and Marracini [34]
Lawnmower	75–300	7–300	95 dB	Villa [35]
Leaf blower	6–20,000	220	93–102 dB(A)	Cook [36], Pasanen et al. [37]
Construction: foundation-stage machinery	below 800			Lee et al. [38]
Construction: demolition-stage machinery	500–2000			Lee et al. [38]
Construction: breaker and bulldozer	4–5000			Lee et al. [38]
Electric vehicles	160–5000			UNECE [39], Soundproofist [40]
Drones	2000–4000	3000	65 dB(A)	Jokisch and Fischer [41], Torija and Clark [42]
Anthropogenic	below 2000			Dowling et al. [43]
Snowmobile	1000–1500			Padois and Berry [44]
Wind farm	20–200		93.2–110 dB	Chiu and Lung [45]

Table 1 shows the frequency range characteristics of technological sounds, which are considered disturbing by humans. Most of the demonstrated sound sources have low (up to 200 Hz) and mid-frequency (200–2000 Hz) components, and around 1/3 of them have high-frequency (above 2000 Hz) components. A great part of the demonstrated sound sources has mid-frequencies as the dominant frequency.

In contrast, the temporal domain provides through the amplitude envelope (AE) the maximum amplitude value of all samples in a frame, which can provide characteristics of onset detection (when the acoustic event started), an approximate idea of loudness, and sensitivity to outliers. The root mean square (RMS) is a stable indicator of loudness, which shows the sum of the acoustic energy of the sound sample. The zero-crossing rate (ZCR) shows how often the sound signal crosses a horizontal axis, representing the time domain and the signal's frequency. It helps to give a monophonic pitch estimation and is ideal for voice or communication detection [46]. In avian studies, time domain analysis is essential for sound source separation and syllable detection [47]. Bird species identification can be enhanced by combining time and frequency domain analysis [48]. Deep learning techniques make this possible [49]. Concerning the avian hearing perspective, the time domain can help to understand possible mechanisms regarding the physiology of avian hearing through the correlation of hearing processors, e.g. through rearrangement of the auditory nerves to follow the cycles of the stimulus tone [50, 51], and the interaural time difference [52, 53]. The time domain can help analyse animals' behaviour and physiology such as wingbeat coupling, respiration, mating preferences, or arousal coding interpretation, which can be analysed with the help of the amplitude envelope technique [54].

Propagation Path

The sound propagation process in the air naturally degrades in amplitude, spectral, and temporal structure the acoustic energy of sound signals [10]. Regarding amplitude degradation, the main reasons for acoustic energy loss are spherical spreading and excess attenuation. Spherical spreading is one form of geometric spreading, dependent on the intensity of the sound source [55•]. Its attenuation has a relation of $I/r2$ (intensity divided by squared distance), where r represents the distance of the sound source, and by doubling the distance, there will be a decrease of 6 dB of sound intensity. For linear sound, sources will produce a cylindrical spreading. This decrease will be 3 dB when doubling the distance from the source [56, 57]. The excess attenuation occurs through air absorption, turbulence, and boundary conditions, e.g. scattering, diffraction, reflection, refraction, ground effect, and absorption of surfaces [10, 55•].

Regarding diffraction, narrowband wavelength sounds, like bird vocalisations, cannot diffract in dense vegetation [58]. Scattering occurs as a specular reflection on small segments of a rough surface [59]. Ground effects also influence animal signals with attenuations up to 20 dB [10]. Figure 2 shows each acoustic phenomenon for airborne sound propagation.

Some investigations with the blackbird, *Turdus merula*, the song thrush, *T. philomelos*, and the great tit, *Parus major*, showed an improvement in long-distance communication when they were singing on the top of trees [60, 61]. This observation depends on how dense the forest is, the ground effect, and animal behaviour patterns.

The spectral degradation occurs due to signal filtering. Animal signals are characterised by their frequency content, varying according to taxa [11]. High frequencies (narrowband signal) travel short distances, while low frequencies (broadband signal) can travel farther [62]. The evaluation of anthropogenic noise impact on avian species should consider the frequencies characteristics of the anthropogenic noise and the hearing abilities as well as communication frequencies of the investigated bird species. The relationship between anthropogenic noise and ambient sounds can be measured through signal-to-noise-ratio (SNR), aiming to reduce the noise level and increase the signal level [63]. SNR is the ratio between the signal's power and background noise's power.

Temporal characteristics of the acoustic signals are essential in mate selection and localisation [64]. Signal degradation in terms of the temporal domain occurs when overlapping signals are received from different paths, causing a temporal distortion of the signal [10].

Receiver—Birds

Since birds are considered the receivers in this study, it is important to observe how avian orders are classified due to specific characteristics, e.g. body dimensions and habituations, helping us to understand their auditory system and hearing capacities.

Avian Orders and Their Relatedness

The avian order presented in Table 2 follows the IOC World Bird List [65]. The following orders Phaethontiformes (Ph), Pterocliformes (Pt), Otidiformes (Ot), Gaviiformes (Ga), Procellariiformes (Pr), Ciconiiformes (Ci), Trogoniformes (Tr), and Bucerotiformes (Bu) will not be analysed in this work due to lack of information of their hearing capacities, e.g. hearing thresholds.

Habitat Selection

Habitat selection is a process of behavioural responses which influences the survival and fitness of individuals [66, 67].

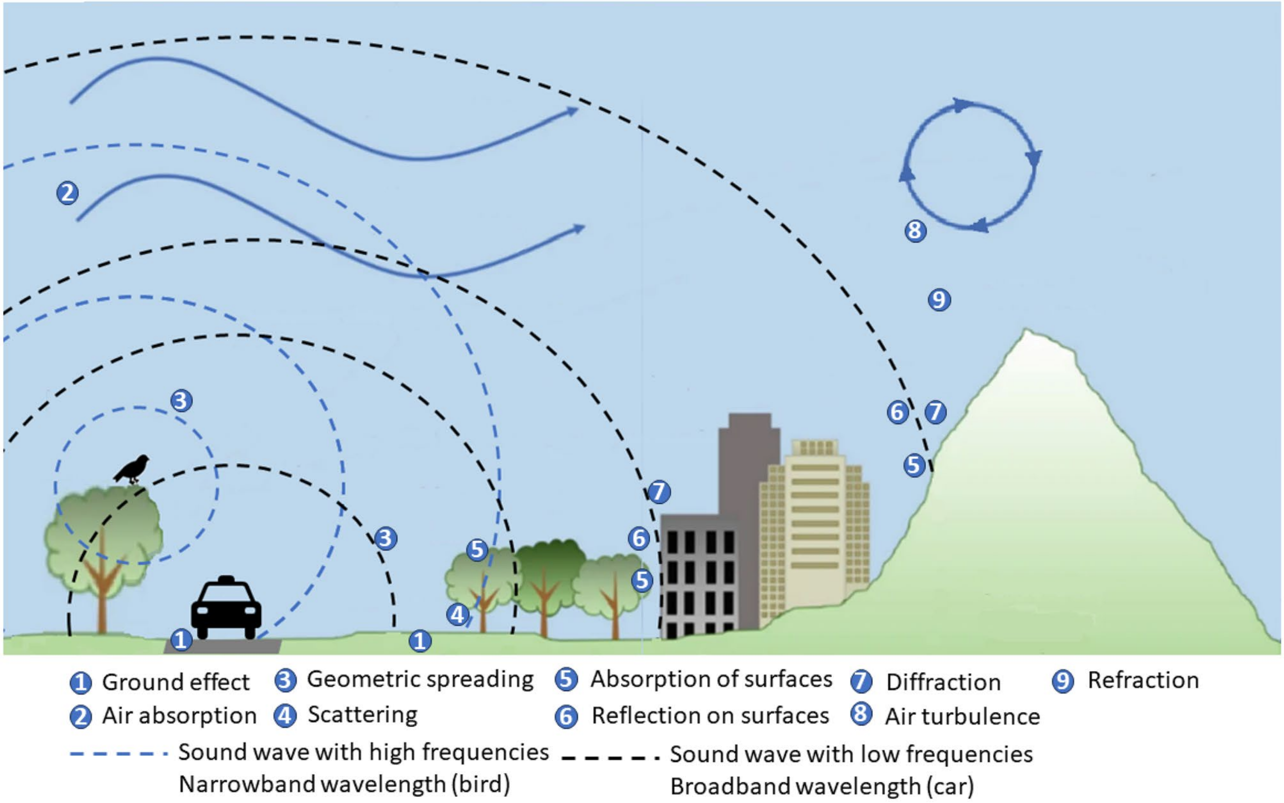

Fig. 2 Factors influencing sound propagation in airborne (adapted [55•])

Common factors for the habitat selection of avian species are food availability, community structural (competition and other synecological factors), functional characteristics of the species, shelter from enemies and adverse weather [68, 69]. Other factors that could influence avian habitat selection are landscape, terrain, nesting, communication, look-out, and avian internal motivations [70].

Morphological and physiological factors are also connected and can be a reason for habitat selection and hearing abilities. As a physiological aspect, it is possible to mention the body size of birds. Small birds like reed warbler (*Acrocephalus scirpaceus*) are often observed in dense vegetation, while larger birds from the same species prefer open areas. The competition of hole-nesting in breeding conditions is also associated with body size [71, 72]. Species like (*Acrocephalus arundinaceus*, *A. scirpaceus*) have adapted their body size, such as height and length, to improve survival in tall, erect vegetation with deep water. Others adapted their climbing abilities to live in areas with water and land [73].

Avian Hearing System

Birds and reptiles have some basic similarities in the design of their middle ears but diversity in the structural organisation. The similarities are related to the interaural pathway, which is tubes in the posterior and ventral portions of their skulls that connect the middle ear cavities in their heads; thereby, helping in the localisation of sound [74, 75••].

The columella is a thin bone structure in the interior position of the skull (middle ear) that transmits sounds from the eardrums. This bone structure is homologous to stapes in mammals. In contrast, the extracolumella is a cartilaginous structure associated with the columella [51]. The hearing threshold is highly associated with the size of the columellar footplate where larger footplates can lower the hearing thresholds of birds.

Like mammals and reptiles, birds also have sensory hair cells across the auditory papillae (the primary hearing organ—equivalent to the organ of Corti in mammals), transitioning short to tall hair cells over the immovable superior cartilaginous plate (Fig. 3I and J). Short hair cells' position orientation varies according to bird species, while in humans, they are fixed and have only one direction. Papillar morphology anatomic specialisations make hearing high or low-frequency sounds unique among different species [50, 75••, 76••].

Additionally, the auditory curves of different avian orders are related to their body sizes, such as weight and overall

Table 2 Avian orders and relatedness

Avian orders	Taxa	Relatedness
Anseriformes (An)	Ducks, geese, swans	Waterfowl (Anseriformes) are sister to the landfowl (Galliformes)
Galliformes (Ga)	Quails, partiriges, pheasants	Landfowl (Galliformes) are sister to the waterfowl (Anseriformes)
Phoenicopteriformes (Ph)	Flamingos	Flamingos and grebes (Podicipediformes) are ancient sister taxa, potentially related to shorebirds
Podicipediformes (Po)	Grebes	Grebes and flamingos (Phoenicopteriformes) are ancient sister taxa and members of the basal polytomy, potentially related to shorebirds (Charadriiformes)
Phaethontiformes (Ph)	*Tropic birds*	*Tropic birds together with Sun bittern and Kagu (Eurypygiformes) are sister to core waterbird clade*
Pterocliformes (Pt)	*Sandgrouse*	*Sandgrouse are sister to the mesites*
Columbiformes (Cl)	Doves, pigeons	Pigeons are the sister group to an Old-World clade consisting of sandgrouse (Pterocliformes) and the mesites (Mesitornithiformes). Together, they form the clade Columbimorphae at or near the base of Neoaves
Caprimulgiformes (Ca)	Nightjars	The nocturnal caprimulgiform birds and related Apodiformes define a spectacular basal adaptive radiation of Neoaves
Apodiformes (Ap)	Swifts	Swifts and hummingbirds and their relatives are ancient sister to the Caprimulgiformes and included together by some in that Order
Otidiformes (Ot)	*Bustards*	*Now in their Order, the bustards are the sister group to turacos (Musophagiformes) or cuckoos (Cuculiformes)*
Cuculiformes (Cu)	Cuckoos	Cuckoos are sister to bustards (Otidiformes) or the turacos (Musophagiformes)
Gruiformes (Gr)	Cranes, rails, coots	Long recognised as an artificial assemblage of taxa, the revised core Gruiformes represents the branches of the basal polytomy. This Order now includes seven families: rails (Rallidae), flufftails (Sarothruridae), finfoots (Heliornithidae), trumpeters (Psophiidae), cranes (Gruidae), and Limpkin (Aramidae)
Gaviiformes (Ga)	*Loons, dives*	*Loons are the sister group to penguins (Sphenisciformes) + tube-nosed seabirds*
Procellariiformes (Pr)	*Tube-nosed seabirds*	The tube-nosed seabirds are sisters to penguins (Sphenisciformes). Albatrosses are the sister group to all other tubenoses
Suliformes (Su)	Frigatebirds, cormorants	The Suliform waterbirds are sisters to the herons and pelicans (Pelecaniformes)
Pelecaniformes (Pe)	Pelicans, herons, egrets, spoonbills Ibis, herons, pelicans, hammerkop, shoebill	The relationships among Pelecaniform bird families remain uncertain
Ciconiiformes (Ci)	*Storks*	*The Order Ciconiiformes includes only the storks (Ciconiidae). Ibises and spoonbills (Threskiornithidae) and herons (Ardeidae) are members of the Pelecaniformes*
Charadriiformes (Ch)	Waders	Shorebirds and diving birds in the Charadriiformes are an ancient and diverse adaptive radiation of waterbirds
Accipitriformes (Ac)	Raptors	Raptors (Accipitriformes) are basal members of the core landbirds clade. New World vultures are a deep basal split and sister to the rest of the Accipitriformes
Strigiformes (St)	Owls	Owls are basal members of the core landbirds
Trogoniformes (Tr)	*Trogons*	*Trogons are embedded in the Core Landbirds as the sister group to the Bucerotiformes, Coraciiformes, and Piciformes*
Bucerotiformes (Bu)	*Hornbills, hoopoes*	*Separation of the hornbills and hoopoes from the Coraciiformes as the Order Bucerotiformes maintains monophyly of the Coraciiformes*
Coraciiformes (Co)	Rollers, kingfishers, bee-eaters	The kingfishers, rollers, and allies form the sister group to the Piciformes
Piciformes (Pi)	Woodpeckers, barbets	The diverse Piciformes include jacamars, puffbirds honeyguides, wrynecks, barbets and toucans, and woodpeckers worldwide
Falconiformes (Fa)	Falcons	The falcons and caracaras (Falconiformes) are not relatives of other raptors in the Accipitriformes, but rather are a separate lineage and Order in the terminal landbird clade Australaves which includes parrots and the Passeriformes

Table 2 (continued)

Avian orders	Taxa	Relatedness
Psittaciformes (Ps)	Parrots	Parrots (Psittaciformes) are the sister group to the Passeriformes
Passeriformes (Pa)	Songbirds	The Passeriformes, or perching birds, include most world bird species. The New Zealand wrens (Acanthisittidae) are the sister group to all passerines, including suboscines and oscines

Legend: Orders in italics are not included in the review of the present work

length, where small birds, like songbirds, can hear higher frequencies better, whereas larger birds hear lower frequencies better [76••, 78]. Rosowski and Graybeal [79•] state that these inversely and significant correlations are easily observed in high and mid-frequency ranges. Peacock et al. [77••] observed that a greater absolute mass of the middle ear ossicles could predict lower frequency peaks for birds with these hearing system characteristics. The avian nucleus mesencephalicus lateralis, pars dorsalis (MLd) is an auditory midbrain nucleus responsible for acoustically mediated behaviours, such as vocal learning, echolocation and prey localisation. The optic tectum (TeO) is related to flight behaviour in birds, providing visual cues. Since MLd and TeO occupy the same section of the avian midbrain and they are highly dependent and their ratio is used for on investigation related to avian auditory midbrain. Iwaniuk et al. [6••] investigated the size of the auditory midbrain of several birds and concluded that independent of MLd size, there is an overall similarity in hearing abilities across taxa.

Outcomes—Birds' Response to Anthropogenic Noise

Anthropogenic noise can affect birds' physiology, behaviour, and acoustic perception responses [80, 81]. Common physiological impacts include physical damage to ears, stress responses, changes in reproductive success, and potential changes in birds' populations are observed. Behavioural impacts include fight-flight response, avoidance, and reduced foraging efficiency, along with changes in vocal communication and the ability to hear predators/other sound sources [82••].

Physiological Response

a. Physical damage to ears

The auditory hair cells can be damaged through exposure to loud sounds. For example, blasts with intensity over 140 dB(A), multiple blasts up to 125 dB(A), and continuous exposure with an intensity up to 110 dB(A), up to 72 h, can all cause permanent hearing cell damage in birds, consequently, the reduction of hearing capacity and possible deafness, while intensities between 93 and 110 dB(A) can cause temporary hearing damage to birds [83].

b. Stress responses

Chronic stress of noise causes elevated heart rate, increases in stress hormone levels, and weight loss in birds [84].

c. Changes in reproductive success and population size

The stressful conditions caused by anthropogenic noise alter birds' resistance to diseases, resulting in reduced reproductive success [84]. Consequently, changes in population size happen due to problems with egg production, incubation, brooding, predators, brood parasites, abandonment of nests, the ability to find or attract a mate, and the ability of parents to hear and respond to begging calls [4, 82••].

Animal Behaviour

a. Fight-flight response.

The fight-flight response is caused by stressful stimuli which affects the hormonal states of the birds. The affected hormones are epinephrine and norepinephrine, which are released by the adrenal gland, causing an elevation in birds' heart rates [85]. Noisy environments can cause fight-flight responses, which affect birds' mate attraction and territorial defence [82••].

b. Avoidance response.

Some species, like the house finch (*Carpodacus mexicanus*) and black-chinned hummingbird (*Archilochus alexandri*), avoid areas with anthropogenic noise [86]. According to Forman and Deblinger [87], the avoidance effect was observed through nesting location and birds' occupancy near roadways, with birds staying up to 300 m (about 984.25 ft) away from roadways.

c. Changes in foraging responses

Different behaviours can be observed as changes in foraging responses, such as latency on attack response from predators, were on great tit (*Parus major*) studies [88] and difficulty in detecting the prey on owl studies [89]. In the study of Burger and Gochfeld [90], it highlighted five species that usually forage in the presence of people.

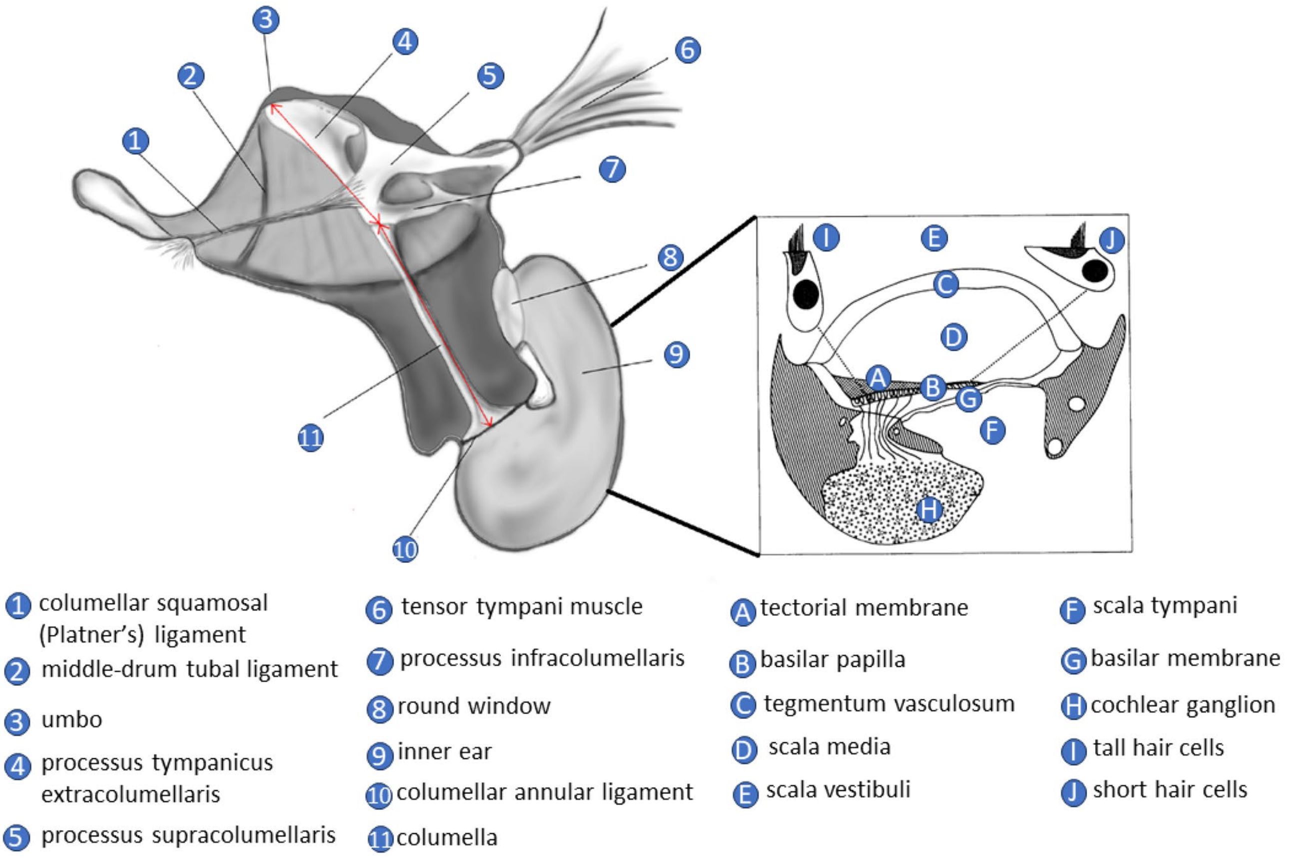

Fig. 3 Avian middle ear. Adapted from Peacock et al. [77••] and Gleich and Manley [50]

Acoustic Perception—Communication and Hearing

Birds' communication can be affected by the environment, body size, vocal apparatus, and masking caused by natural and anthropogenic sounds [82••]. Effects from the environment are observed easily in urban settings, which have acoustic similarities to cliffs, canyons, and other hard-surfaced natural environments [91–93]. As mentioned before, the body, through the vocal apparatus, also influences which frequencies the birds will sing and hear. Masking occurs when the communicated sound is hidden or interfered with by anthropogenic or natural sounds [82••, 94, 95]. To overcome this problem, birds may change frequency, amplitude, and song components through temporal shifts, e.g. changes in preferable hours to communicate (i.e. dawn chorus), avoiding rush hours [82••].

One well-studied mechanism of communication is the Lombard effect. This mechanism is usually observed in the communication of humans, other mammals, and several bird species [96]. The Lombard effect occurs when the animal increases vocal amplitude to cover background noise, avoiding a masking process, exercising vocal plasticity, and guaranteeing that their communication intentions can be achieved effectively [97, 98]. Vocal plasticity is considered a vital signal adaptation in the evolution of animal communication [99]. Despite this, there are different reasons for using the Lombard effect across taxa [97, 100, 101], such as changes in song composition over time, observed in historical records of bird songs were the minimum frequency increased [102], and cultural evolution of birds, noticed on frequency-dependent vocalisations for mate selection, where male birds with rare alleles most likely learn with common allele birds to attract females during breeding season [103].

Methodology

As highlighted in the mechanistic pathway description, this work focuses on biological factors, such as the body and head effect on avian hearing, hearing system dimensions, and habitat selection of the avian class. Since the hearing physiological and psychophysical aspects of birds are topics that few investigators conducted research, we selected papers with wide coverage of bird orders and species. The base work for selection on avian orders and species was the study by Peacock et al. [77••, 104••]. Not all species indicated in the works of

Table 3 Avian body size

Avian orders/ Nr	Species binominal name	Species common name	Body length (cm)			Body weight (kg)			References
			Min	Max	Avg	Min	Max	Avg	
An1	*Aix sponsa*	Wood duck	47.0	54.0	50.5	0.45	0.86	0.66	The CornellLab of Ornothology [110]
An2	*Anas platyrhynchos*	Mallard	50.0	65.0	57.5	0.72	1.58	1.15	íNaturalist [111]
An3	*Mergus merganser*	Common merganser	54.0	71.0	62.5	0.90	2.16	1.53	The CornellLab of Ornithology [112]
Ga1	*Pavo cristatus*	Indian peafowl	96.0	117.0	106.5	2.75	6.00	4.38	Denver Zoo [113]
Ph1	*Phoenicopterus chilensis*	Chilean flamingo	150.0	150.0	150.0	1.80	3.60	2.70	Associated with American Flamingo: *Phoenicopterus ruber* Smithsonian's National Zoo & Conservation Biology Institute [114]
Po1	*Podilymbus podiceps*	Pied-billed grebe	31.0	38.0	34.5	0.25	0.57	0.41	Muller and Storer [115]
Po2	*Aechmophorus occidentalis*	Western grebe	55.0	75.0	65.0	0.80	2.00	1.40	TheCornellLab of Ornithology [116]
Cl1	*Streptopelia decaocto*	Eurasian collared dove	30.0	33.0	31.5	0.20	0.20	0.20	Texas Invasive Species Institute [117]
Ca1	*Chordeiles minor*	Common nighthawk	22.0	24.0	23.0	0.07	0.10	0.08	University of Michigan. Museum of Zoology. Animal Diversity Web [118]
Ap1	*Aeronautes saxatalis*	White-throated swift	15.0	18.0	16.5	0.03	0.04	0.03	Collins and Johnson [119], Ryan and Collins [120]
Cu1	*Coccyzus americanus*	Yellow-billed cuckoo	32.0	34.0	33.0	0.11	0.13	0.12	The CornellLab of Ornithology [121]
Gr1	*Fulica americana*	American coot	34.0	43.0	38.5	0.43	0.85	0.64	Duning Jr. [122]
Su1	*Phalacrocorax auritus*	Double-crested cormorant	70.0	90.0	80.0	1.20	2.50	1.85	TheCornellLab of Ornithology [123]
Pe1	*Plegadis chihi*	White-faced ibis	46.0	56.0	51.0	0.45	0.53	0.49	The CornellLab of Ornithology [124]
Pe2	*Nycticorax nycticorax*	Black-crowned night heron	58.0	66.0	62.0	0.73	1.01	0.87	Smithsonian's National Zoo & Conservation Biology Institute [125]
Pe3	*Ardea herodia*	Great blue heron	115.0	138.0	126.5	1.82	3.60	2.71	Duning Jr. [122]
Ch1	*Charadrius vociferus*	Killdeer	20.0	28.0	24.0	0.07	0.12	0.10	Wiersma et al. [126]
Ch2	*Larosterna inca*	Inca tern	39.0	42.0	40.5	0.18	0.21	0.20	The CornellLab of Ornithology [127]
Ch3	*Uria aalge*	Common murre	38.0	46.0	42.0	0.95	1.04	0.99	Duning Jr. [122]
Ch4	*Larus delawarensis*	Ring-billed gull	43.0	54.0	48.5	0.30	0.60	0.45	University of Michigan. Museum of Zoology. Animal Diversity Web [128]
Ac1	*Cathartes aura*	Turkey vulture	76.0	76.0	76.0	1.36	1.36	1.36	Chattahoochee Nature Center [129]
St1	*Bubo virginianus*	Great horned owl	46.0	68.0	57.0	1.40	1.40	1.40	Canadian Raptor Conservancy [130]
Co1	*Megaceryle alcyon*	Belted kingfisher	28.0	35.0	31.5	0.11	0.18	0.15	The CornellLab of Ornithology [131]
Co2	*Dacelo novaeguineae*	Laughing kookaburra	41.0	47.0	44.0	0.19	0.47	0.33	Pizzey and Doyte [132], Woodfall [133]
Pi1	*Colaptes auritus*	Northern flicker	28.0	36.0	32.0	0.09	0.17	0.13	The CornellLab of Ornithology [134], Duning Jr [122]
Pi2	*Sphyrapicus nuchalis*	Red-naped sapsucker	19.0	21.0	20.0	0.03	0.07	0.05	The CornellLab of Ornithology [135]
Pi3	*Picoides villosus*	Hairy woodpecker	18.0	26.0	22.0	0.04	0.10	0.07	The CornellLab of Ornithology [136]

Table 3 (continued)

Avian orders/ Nr	Species binominal name	Species common name	Body length (cm)			Body weight (kg)			References
			Min	Max	Avg	Min	Max	Avg	
Fa1	*Falco sparverius*	American kestrel	22.0	31.0	26.5	0.08	0.17	0.12	TheCornellLab of Ornithology [137]
Ps1	*Melopsittacus undulatus*	Budgerigar	18.0	18.0	18.0	0.03	0.04	0.04	The Australian Museum [138]
Ps2	*Trichoglossus moluccanus*	Rainbow lorikeet	25.0	30.0	27.5	0.08	0.16	0.12	Collar [139]
Pa1	*Taeniopygia guttata*	Zebra finch	10.0	10.0	10.0	0.02	0.03	0.02	Animal Spot [140]
Pa2	*Sturnus vulgaris*	European starling	21.5	21.5	21.5	0.07	0.10	0.08	University of Michigan. Museum of Zoology. Animal Diversity Web [141]
Pa3	*Cyanocitta cristata*	Blue jay	25.0	30.0	27.5	0.07	0.10	0.09	Wheaton Park District. Cosley Zoo [142]
Pa4	*Quiscalus quiscula*	Common grackle	28.0	34.0	31.0	0.07	0.14	0.11	The CornellLab of Ornithology [143]
Pa5	*Corvus brachyrhnchos*	American crow	40.0	50.0	45.0	0.30	0.60	0.45	BirdLife International [144]
Pa6	*Pica hudsonia*	Black-billed magpie	45.0	60.0	52.5	0.17	0.02	0.09	Trost [145]
Pa7	*Corvus corax*	Common raven	54.0	67.0	60.5	0.69	2.00	1.35	Boarman et al. [146]
Pa8	*Cyanocitta stelleri*	Steller's jay	30.0	34.0	32.0	0.10	0.14	0.12	Walker et al. [147]

Peacock et al. [77••, 104••] had a complete dataset about the body, middle ear, and auditory midbrain dimensions, as well as hearing thresholds in Hertz and Decibels. Body dimensions of all referred species are added in Table 3. Head dimensions are available in Table 4. Avian middle ear dimensions are shown in Table 5 [76••, 77••], auditory midbrain dimensions in Table 6 [6••], and hearing thresholds in Hertz in Table 7 [104••] and in Decibels in Table 8 [105–109]. Table 9 shows the habitat selection and influence of the propagation path in some species investigated by Peacock et al. [104••].

After gathering all the data, the relationships of body weight vs body length, peak hearing frequency vs body length, peak hearing frequency vs body weight, and avian hearing frequency ranges were plotted. Related to head dimensions, the width, length, and height from the cranium had their relation analysed together with the peak hearing frequencies. Additionally, it analysed the influence of the culmen length (beak). In support of the physiological findings, we calculated Pearson's correlations for sizes of the avian middle ear and hearing frequency range, avian auditory midbrain, and avian frequency range.

Results

This study does not cover the following avian orders: Phaethontiformes, Pterocliformes, Otidiformes, Gaviiformes, Procellariiformes, Ciconiiformes, Trogoniformes, Bucerotiformes.

Influence of Avian Body Size on Peak Hearing Frequency

The indicated bird species in the work of Peacock et al. [77••, 104••] were analysed in this section. Complementary information about body dimensions, e.g. weight and height, was collected and displayed in Table 3. Figure 4 shows a linear regression of the normalised dataset presented in Table 3. It adopted the min–max normalisation method. The strong positive linear regression of avian body length and body weight shows an adjusted $R^2 = 0.7722$, $p < 0.001$. The observations indicated as points are each bird species investigated by Peacock et al. [77••, 104••] but indicated as their respective bird order. As observed in this figure, the bird order of Passeriformes (Pa) concentrates its observations on the bottom left side of the plot due to its small body length and weight. The smallest bird observed in Fig. 4 is a zebra finch (*Taeniopygia guttata*), order Passeriformes (Pa1), with a 10-cm length and 0.02-kg weight. Bigger birds are observed on the upper right side of the figure, e.g. from the order Phoenicopteriformes (Ph1), the Chilean flamingo (*Phoenicopterus chilensis*), with 150 cm and 2.7 kg, and from the order Pelecaniformes (Pe3), the Great blue heron (*Ardea herodia*), with a length of 126.5 cm and 2.71 kg. There are also heavier birds indicated on the graph as an outlier: from the order Galliformes (Ga1), the Indian peafowl (*Pavo cristalus*) has a body length of 106.5 cm and a weight of 4.38 kg.

Table 4 Avian head size

Avian orders/ Nr	Species binominal name	Species common name	Cranium			Cranium + culmen	References
			Width (mm)	Length (mm)	Height (mm)	Length (mm)	
Ac1	*Cathartes aura*	Turkey vulture	39.00	61.00	30.00	94.00	Skulssite [148]
An1	*Aix sponsa*	Wood duck	27.00	49.00	27.00	85.00	Skulssite [149]
An2	*Anas platyrhynchos*	Mallard	30.00	60.00	27.00	110.00	Skulssite [150]
An3	*Mergus merganser*	Common merganser	36.00	52.00	24.00	118.00	Skulssite [151]
Ca1	*Chordeiles minor*	Common night-hawk	22.00	21.00	16.00	34.00	Skulssite [152]
Ch1	*Charadrius vociferus*	Killdeer	18.00	24.00	17.00	48.00	Skulssite [153]
Ch2	*Larosterna inca*	Inca tern	42.00	22.00	17.00	71.00	Based on *Sterna vittata* (Antarctic Tern) Skullsite [154]
Ch3	*Uria aalge*	Common murre	36.00	46.00	24.00	114.00	Skulssite [155]
Ch4	*Larus delawarensis*	Ring-billed gull	32.00	43.00	24.00	100.00	Skulssite [156]
Cl1	*Streptopelia decaocto*	Eurasian collared dove	12.50	31.00	17.46	51.00	Plateau and Foth [157], Skullsite [158]
Co1	*Dacelo novaeguineae*	Megaceryle alcyon	38.00	39.00	25.00	109.00	Skullsite [159]
Cu1	*Coccyzus americanus*	Yellow-billed cuckoo	21.00	-	19.00	50.00	Bone Clones Inc. [160]
Fa1	*Falco sparverius*	American kestrel	26.00	31.00	20.00	43.00	Skullsite [161]
Ga1	*Pavo cristatus*	Indian peafowl	38.00	48.00	34.00	86.00	Skullsite [162]
Gr1	*Fulica americana*	American coot	20.00	31.00	19.00	57.00	Based on purple gallinule (*Porphyrula martinica*) Skullsite [163]
Pa1	*Taeniopygia guttata*	Zebra finch	14.00	18.00	12.00	28.00	Based on painted finch (*Passerina ciris*) Skullsite [164]
Pa2	*Sturnus vulgaris*	European starling	19.00	24.00	14.00	52.00	Skullsite [165]
Pa3	*Cyanocitta cristata*	Blue jay	25.40	-	25.40	57.15	Darwin and Wallace [166]
Pa4	*Quiscalus quiscula*	Common Grackle	21.00	28.00	17.00	53.00	Skullsite [167]
Pi1	*Colaptes auritus*	Northern flicker	23.00	30.00	19.00	69.00	Skullsite [168]
Pa5	*Corvus brachyrhnchos*	American crow	36.00	39.00	26.00	87.00	Skullsite [169]
Pa6	*Pica hudsonia*	Black-billed magpie	13.33	-	22.03	-	Based on Eurasian magpie (*Pica pica)* Plateau and Foth [157]
Pa7	*Corvus corax*	Common raven	24.01	-	31.25	-	Plateau & Foth [157]
Pe1	*Plegadis chihi*	White-faced ibis	24.00	35.00	25.00	167.00	Skullsite [170]
Pe2	*Nycticorax nycticorax*	Black-crowned NIGHT heron	37.00	57.00	24.00	136.00	Skullsite [171]
Pe3	*Ardea herodia*	Great blue heron	35.00	74.00	28.00	196.00	Skullsite [172]
Ph1	*Phoenicopterus chilensis*	Chilean flamingo	36.00	53.00	31.00	150.00	Skullsite [173]

Table 4 (continued)

Avian orders/ Nr	Species binominal name	Species common name	Cranium			Cranium + culmen	References
			Width (mm)	Length (mm)	Height (mm)	Length (mm)	
Pi2	*Sphyrapicus nuchalis*	Red-naped Sapsucker	19.00	20.00	14.00	46.00	Based on yellow-billed sapsucker (*Sphyrapicus varius*) Skullsite [174]
Pi3	*Picoides villosus*	Hairy woodpecker	23.00	23.00	18.00	58.00	Based on three-toed woodpecker (*Picoides tridactylus*) Skullsite [175]
Po1	*Podilymbus podiceps*	Pied-billed grebe	19.00	28.00	16.00	53.00	Based on Slavonian grebe (*Podiceps auritus*) Skullsite [176]
Po2	*Aechmophorus occidentalis*	Western grebe	26.00	48.00	21.00	125.00	Skullsite [177]
Ps1	*Melopsittacus undulatus*	Budgerigar	15.25	13.60	14.20	21.95	Bartels et al. [178]
Ps2	*Trichoglossus moluccanus*	Rainbow lorikeet	19.00	30.00	19.00	45.00	Skullsite [179]
St1	*Bubo virginianus*	Great horned owl	61.00	50.00	38.00	86.00	Skullsite [180]

To verify the influence of body length against the peak hearing frequency, it was plotted in Fig. 5 a linear model of avian body length (cm) from Table 3 and peak hearing frequency (Hz) from Table 7, with a descending curve showing the relationship between body length and peak hearing frequency. It adopted the min–max normalisation method. The weak negative linear regression of avian body length and peak hearing frequencies shows an adjusted $R^2 = 0.2765$, $p < 0.001$. As expected, birds with smaller body lengths presented higher peak hearing frequencies, e.g. the zebra finch (*Taeniopygia guttata*), order Passeriformes (Pa1), with the smallest body length, can hear 1879 Hz as peak hearing frequency (upper left side of the plot). The point presented as an outlier on the same side of the plot represents the white-throated swift (*Aeronautes saxatalis*) from the Apodiformes (Ap1) order, which can hear a peak hearing frequency of 2249 Hz. As an example of a bird with a greater length which hears lower frequencies, it is observed that the Chilean flamingo (*Phoenicopterus chilensis*, Ph1) at the right side of the plot hears a peak hearing frequency of 973 Hz.

Figure 6 shows a linear model of avian body weight (kg) from Table 3 and peak hearing frequency (Hz) from Table 7, also with a descending tendency. It adopted the min–max normalisation method. The weak negative linear regression of avian body weight and peak hearing frequencies shows an adjusted $R^2 = 0.2182$, $p < 0.01$. On the bottom right side of the plot, it is possible to see heavier birds, e.g. the Indian peafowl (*Pavo cristalus*) from the Galliformes (Ga1) order, with a weight of 4.38 kg and a peak hearing frequency of 862 Hz. The linear, smooth model on the left side of the graph shows the results of the zebra finch (*Taeniopygia guttata*) from the Passeriformes (Pa1), with a weight of 0.02 kg and a peak hearing frequency of 1879 Hz. As mentioned in Rosowski and Graybeal [79•], these inversely and significant correlations are more predominantly observed in high and mid-frequency ranges when compared to body weight and length. Figures 4, 5, and 6 were produced with the help of the software R, using the packages ‘tidyverse’ and ‘ggplot’.

Avian Head Size Relation with Hearing Frequencies

Additional regression analysis was conducted with avian head measures (Table 4) and peak hearing frequencies (Table 7). It considered the following avian head dimensions: cranium width, length, and height. The influence of the beak (culmen) was also considered through the combination of the cranium and culmen length. To complete the physiological measures, it also calculated the cranium volume, as well as the cranium in combination with the culmen volume.

Figure 7 shows a linear model of avian cranium width (mm) from Table 4 and peak hearing frequency (Hz) from Table 7, also with a descending tendency. It adopted the min–max normalisation method. The weak negative linear

Table 5 Avian middle ear dimensions [76••, 77••]

AO	Species common name	Interaural distance (mm) [a]	Columellar mass (mg) [a]	Columellar length (mm) [a]	Footplate area (mm^2) [a]	Footplate diameter [a]		Tympanic membrane area (mm^2) [a]	Tympanic membrane [a]		Extracolumellar length (mm) [a]	Papilla length (mm) [b]
						Diam. 1 (mm)	Diam. 2 (mm)		Diam. 1 (mm)	Diam. 2 (mm)		
An	*Mallard*	-	*0.183*	*2.27*	*1.00*	*1.35*	*0.94*	*28.05*	*6.25*	*5.72*	*1.77*	*3.00*
	Wood duck	20.95	0.093	1.71	0.66	1.07	0.79	16.01	5.07	4.02	1.49	
	Common merganser	27.67	0.265	2.42	0.83	1.15	0.92	15.62	5.10	3.90	1.43	
Ga	Indian peafowl	32.20	0.405	2.70	1.22	1.54	1.01	27.37	7.59	4.59	1.50	
Ph	Chilean flamingo	29.86	0.378	3.12	1.09	2.00	0.92	29.59	7.42	5.08	1.68	
Po	Western grebe	27.68	0.493	2.44	1.81	1.43	1.20	22.96	6.96	4.20	2.05	
	Pied-billed grebe	21.46	0.202	1.93	0.94	1.42	0.84	8.36	4.70	2.26	1.71	
Cl	Eurasian collared dove	16.70	0.112	1.79	0.88	1.40	0.80	16.33	5.53	3.76	1.24	
Ca	Common nighthawk	18.59	0.095	2.83	0.61	1.02	0.76	12.69	4.90	3.30	1.73	
Ap	White-throated swift	13.92	0.106	1.52	0.59	1.13	0.67	4.76	2.58	2.35	0.91	
Cu	Yellow-billed cuckoo	17.34	0.109	1.89	0.60	1.16	0.66	9.71	4.52	2.73	1.38	
Gr	American coot	19.02	0.154	1.82	0.71	1.16	0.78	16.03	5.57	3.67	1.64	
Su	Double-crested cormorant	31.37	0.742	4.04	0.99	1.26	1.00	14.65	5.94	3.14	1.84	
Pe	Great blue heron	26.11	0.572	3.57	1.42	1.81	1.00	33.17	8.28	5.10	2.07	
	White-faced ibis	18.75	0.125	1.88	0.81	1.30	0.80	14.08	5.98	3.00	1.30	
	Black-crowned night heron	30.73	0.483	2.95	1.78	2.02	1.27	34.87	8.74	5.08	2.37	
Ch	Common murre	29.33	0.444	2.86	0.89	1.29	0.88	36.42	8.84	5.25	1.79	
	Killdeer	11.91	0.063	1.20	0.54	1.02	0.67	11.67	4.22	3.52	1.15	
	Ring billed gull	26.77	0.291	2.62	0.76	1.09	0.89	17.45	6.80	3.27	1.44	
	Inca tern	21.16	0.116	1.79	0.57	0.96	0.76	9.23	4.36	2.70	-	
Ac	Turkey vulture	38.40	0.820	3.89	1.64	1.90	1.10	22.53	7.21	3.98	1.05	
St	Great horned owl	61.66	1.478	4.97	3.02	2.27	1.70	66.82	11.10	7.67	3.65	
Co	Belted kingfisher	22.26	0.204	2.23	1.32	1.73	0.97	19.93	5.90	4.30	1.51	
	Laughing kookaburra	38.47	0.692	3.19	2.41	2.00	1.15	26.59	7.73	4.38	1.20	

Table 5 (continued)

AO	Species common name	Interaural distance (mm) [a]	Columellar mass (mg) [a]	Columellar length (mm) [a]	Footplate area (mm^2) [a]	Footplate diameter [a]		Tympanic membrane area (mm^2) [a]	Tympanic membrane [a]		Extracolumellar length (mm) [a]	Papilla length (mm) [b]
						Diam. 1 (mm)	Diam. 2 (mm)		Diam. 1 (mm)	Diam. 2 (mm)		
Pi	Northern flicker	21.90	0.129	2.10	0.81	1.26	0.82	17.63	6.18	3.65	1.40	
	Hairy woodpecker	16.44	0.074	1.53	0.46	0.83	0.71	12.30	4.79	3.27	1.05	
	Red-naped sapsucker	14.65	0.048	1.29	0.39	0.82	0.61	9.10	4.33	2.68	1.08	
Fa	American kestrel	15.75	0.147	1.86	0.79	1.27	0.80	17.06	6.73	3.23	1.30	
Ps	Rainbow lorikeet	21.80	0.230	2.13	0.77	1.06	0.92	8.97	4.23	2.70	1.13	
	Budgerigar	13.82	0.056	1.34	0.30	0.69	0.55	7.13	3.24	2.80	0.80	2.60
Pa	Zebra finch	12.36	0.041	1.15	0.26	0.67	0.49	7.61	3.56	2.72	0.77	2.10
	European starling	15.56	0.114	1.59	0.56	1.00	0.70	9.58	4.33	2.82	1.07	2.86
	Common grackle	21.44	0.144	1.64	0.68	1.11	0.78	14.93	6.30	3.02	1.20	
	Common raven	27.89	0.728	4.78	1.99	2.06	1.23	53.58	9.94	6.68	2.94	
	American crow	32.28	0.390	3.39	1.07	1.42	0.96	31.86	7.80	5.20	2.43	
	Black-billed magpie	26.32	0.257	2.67	1.10	1.50	0.94	19.36	5.70	4.33	2.02	
	Steller's jay	20.97	0.146	2.04	0.81	1.26	0.82	20.72	6.91	3.82	1.62	
	Blue jay	22.32	0.167	2.59	0.90	1.27	0.90	23.01	7.00	4.19	-	

Table 6 Avian auditory midbrain dimensions (adapted from [6••])

AO	Species binominal name	Species common name	Auditory category	Brain volume (mm^3)	TeO volume (mm^3)	MLd volume (mm^3)	MLd:TeO
An	*Anas platyrhynchos*	Mallard	Generalists	6065	187.48	7.916	0.042
Ga	*Pavo cristatus*	Indian peafowl	Generalists	7355	284.95	15.141	0.053
Gr	*Fulica americana*	American coot	Generalists	2719	127.65	5.454	0.043
Ch	*Charadrius vociferus*	Killdeer	Generalists	1073	100.92	1.817	0.035
Co	*Dacelo novaeguineae*	Laughing kookaburra	Generalists	4027	333.48	5.116	0.015
Ps	*Trichoglossus moluccanus*	Rainbow lorikeet	Vocal learners	3728	123.42	2.578	0.021
	Melopsittacus undulatus	Budgerigar	Vocal learners	1220	43.53	2.386	0.055
Pa	*Taeniopygia guttata*	Zebra finch	Vocal learners	328	20.90	0.771	0.034

regression of avian cranium width and peak hearing frequencies shows an adjusted $R^2 = 0.2029$, $p < 0.01$. The smallest observed cranium width was from the Eurasian collared dove (*Streptopelia decaocto*, Cl1), which correlated with mid to low-peak hearing frequencies. Other birds from the order Passeriformes also presented small cranium widths, as observed through 'Pa1', zebra finch (*Taeniopygia guttata*), and 'Pa6', black-billed magpie (*Pica hudsonia*), which correlated with high and mid-peak hearing frequencies, respectively. Furthermore, birds with large cranium width, e.g. 'St1', great horned owl (*Bubo virginianus*), are correlated with low-peak hearing frequencies.

Figure 8 shows a linear model of avian cranium length (mm) from Table 4 and peak hearing frequency (Hz) from Table 7, also with a descending tendency. It adopted the min–max normalisation method. The weak negative linear regression of avian cranium length and peak hearing frequencies shows an adjusted $R^2 = 0.3314$, $p < 0.001$. The smallest observed cranium length was from the budgerigar (*Melopsittacus undulatus*, Ps1), which correlated with high-peak hearing frequencies. Birds with greater cranium length, e.g. 'Pe3', great blue heron (*Ardea herodia*), are correlated with low-peak hearing frequencies.

Figure 9 shows a linear model of avian cranium height (mm) from Table 4 and peak hearing frequency (Hz) from Table 7, also with a descending tendency. It adopted the min–max normalisation method. The weak negative linear regression of avian cranium height and peak hearing frequencies shows an adjusted $R^2 = 0.4498$, $p < 0.001$. The smallest observed cranium height was from the zebra finch (*Taeniopygia guttata*, Pa1), which correlated with high-peak hearing frequencies. Birds with greater cranium height, e.g. 'St1', great horned owl (*Bubo virginianus*), are correlated with low-peak hearing frequencies.

Figure 10 shows a linear model of avian cranium + culmen length (mm) from Table 4 and peak hearing frequency (Hz) from Table 7, also with a descending tendency. It adopted the min–max normalisation method. The weak negative linear regression of avian cranium + culmen length and peak hearing frequencies shows an adjusted $R^2 = 0.1019$, $p < 0.05$. The smallest observed cranium + culmen length was from the common raven (*Corvus corax*, Pa7) and black-billed magpie (*Pica hudsonia*, Pa6), which correlated with mid to low and peak hearing frequencies, respectively. Birds with greater cranium + culmen length, e.g. 'Pe3', great blue heron (*Ardea herodia*), are correlated with low-peak hearing frequencies.

Avian Hearing System Size Relation with Hearing Frequencies

To analyse the influence of avian middle ear dimension on the hearing frequency thresholds, a Pearson correlation with standardised values of the following parameters was conducted: (a) avian middle ear dimensions from the dataset presented in Table 5, where interaural distance (mm), ID; columellar mass (mg), CM; columellar length (mm), CL; footplate area (mm^2), FA; footplate diameter 1 (mm), FD1; footplate diameter 2 (mm), FD2; tympanic membrane area (mm^2), TMA; tympanic membrane diameter 1 (mm), TMD1; tympanic membrane diameter 2 (mm), TMD2; extracolumella (mm), EL, and (b) bird hearing thresholds in frequency (Hz) in Table 7, where peak hearing frequency is equal to frequency of peak in transfer function (PF), and frequencies where it achieved the thresholds of 3 dB, 6 dB, and 10 dB.

In this statistical analysis, the following species were removed due to missing values of some parameters: mallard, double-crested cormorant, Inca tern, blue jay, common murre, and hairy woodpecker.

Figure 11 shows the results of the Pearson correlations, where dimensions of the avian middle ear correlate positively with each other, and the same occurs with avian hearing frequency thresholds (blue-coloured results). These correlations are considered strong correlations due to coefficients over 0.5, with an exception on the relation of 'CM' vs 'FD1'. Negative correlations occurred when avian middle

Table 7 Bird hearing thresholds in frequencies (Hz) [104••]

AO	Species binominal name	Species common name	Frequency of peak in transfer function (Hz)	Frequencies (Hz) where it achieved the thresholds of:			
				3 dB	6 dB	10 dB	20 dB
An	*Anas platyrhynchos*	Mallard	1138	431	710	1381	6667
	Aix sponsa	Wood duck	1106	470	794	1179	-
	Mergus merganser	Common merganser	802	290	802	1541	-
Ga	*Pavo cristatus*	Indian peafowl	862	337	544	911	3612
Ph	*Phoenicopterus chilensis*	Chilean flamingo	973	395	685	1199	5142
Po	*Aechmophorus occidentalis*	Western grebe	1906	1019	1992	4352	-
	Podilymbus podiceps	Pied-billed grebe	1141	503	981	1872	-
Cl	*Streptopelia decaocto*	Eurasian collared dove	1269	658	1572	4203	-
Ca	*Chordeiles minor*	Common nighthawk	1081	297	803	1170	5084
Ap	*Aeronautes saxatalis*	White-throated swift	2249	1097	1765	3949	-
Cu	*Coccyzus americanus*	Yellow-billed cuckoo	1462	552	954	2050	4536
Gr	*Fulica americana*	American coot	1301	384	621	1045	5486
Pe	*Ardea herodia*	Great blue heron	895	440	684	1118	6185
	Plegadis chihi	White-faced ibis	1076	361	605	1052	8792
	Nycticorax nycticorax	Black-crowned night heron	677	233	454	937	2845
Ch	*Uria aalge*	Common murre	1928	1085	3026	-	-
	Charadrius vociferus	Killdeer	1747	632	1427	2154	-
	Larus delawarensis	Ring-billed gull	1637	630	1024	2246	-
	Larosterna inca	Inca tern	1801	762	1293	8271	-
Ac	*Cathartes aura*	Turkey vulture	1165	713	1810	3129	-
St	*Bubo virginianus*	Great horned owl	798	218	362	672	-
Co	*Megaceryle alcyon*	Belted kingfisher	947	339	597	1134	9384
	Dacelo novaeguineae	Laughing kookaburra	928	502	826	3010	-
Pi	*Colaptes auritus*	Northern flicker	1511	1258	2048	3913	-
	Picoides villosus	Hairy woodpecker	1706	534	850	-	-
	Sphyrapicus nuchalis	Red-naped sapsucker	2089	754	1522	2719	-
Fa	*Falco sparverius*	American kestrel	1174	464	745	1394	-
Ps	*Trichoglossus moluccanus*	Rainbow lorikeet	1764	647	1320	2391	-
	Melopsittacus undulatus	Budgerigar	1672	905	1648	3499	-
Pa	*Taeniopygia guttata*	Zebra finch	1879	1333	2351	6027	-
	Sturnus vulgaris	European starling	2018	947	1723	3075	-
	Quiscalus quiscula	Common grackle	1604	607	988	1700	-
	Corvus corax	Common raven	793	193	310	654	6006
	Corvus brachyrhnchos	American crow	1062	539	936	2562	5620
	Pica hudsonia	Black-billed magpie	1426	940	1467	2915	-
	Cyanocitta stelleri	Steller's jay	1257	458	907	1384	8359
	Cyanocitta cristata	Blue jay	1480	609	1024	1522	7560

ear dimensions were analysed with hearing frequency thresholds (red-coloured results). Strong correlations occurred in almost all middle ear dimension relations with the peak hearing frequency (PF), especially when observed values of − 0.7 correlating with the tympanic membrane diameter 1 (TMD1/2), footplate diameter 1 (FD1), and columellar length (CL), indicating the smaller the respective parts are, the higher was the peak hearing frequency. An exception occurred on the columellar mass (CM) correlation, which presented a weak Pearson coefficient (0.2). It also observed the moderate descendent coefficients for 3 dB, 6 dB, and 10 dB in the correlations with the avian middle ear dimensions. As an overall result related to the negative correlations, it is possible to observe that the smallest the avian middle ear component is, the most suitable is the hearing of higher frequencies, and the opposite is true.

Regarding the avian midbrain correlation results presented in Fig. 12, the dataset of Table 6 about avian auditory midbrain

Table 8 Bird hearing thresholds in dB

AO	Species common name	Absolute threshold sensitivity (In dB.RE 20 µN/m^2)											Ref
		250 Hz	500 Hz	710 Hz	1 kHz	1.4 kHz	2.0 kHz	2.8 kHz	4.0 kHz	5.7 kHz	8.0 kHz	8.5 kHz	
An	Mallard	35.1	27.2	-	21.2	-	12.6	-	16.4	28.6	64.9	-	Hill [105]
Ga	Indian peafowl	33	25	21	13	14	17	23	27	34	73	82	Heffner et al. [106]
St	Great horned owl	5	−6	-	−20	-	−17	-	-	17	60	80	Dyson et al. [107]
Ps	Budgerigar	35.5	18.1	9.4	8.7	8.2	2.8	0.25	6	18.5	61.4	67.8	Okanoya and Dooling [108]
Pa	Zebra finch	64.9	52.5	-	32.5	25	24.8	22.5	24	30	72.5	-	Okanoya and Dooling [108]
	European starling	35	24.8	-	20	-	10	7.5	14.8	24.8	61	-	Okanoya and Dooling [108]
	American crow	-	44.6	-	18.6	-	12	-	15.3	-	27.3	-	Cohen et al. [109]
	Blue jay	-	38.6	-	22.6	-	13.33	-	28	-	62	-	Cohen et al. [109]

dimensions, together with part of the data from Table 7 about bird hearing thresholds in frequency (Hz), was used. Since the dataset presented in Table 6 is limited, the results shown in Fig. 12 refer to the following species: mallard duck, Indian peafowl, American coot, killdeer, laughing kookaburra, rainbow lorikeet, budgerigar, and zebra finch. The dataset used in this correlation was standardised using *Z*-scores.

The analysed parameters from avian auditory midbrain were 'brain volume (mm^3), BV'; 'tectum opticum (TeO) volume (mm^3), TeOV'; 'nucleus mesencephalicus lateralis, pars dorsalis (MLd) volume (mm^3), MLdV'; and 'ratio MLd:TeO, MLd_TeO'. The same bird hearing thresholds of the previous correlation were also used in this correlation.

As observed in Fig. 11, the tendency of the same results presented in Fig. 12 occurred regarding the positive and negative correlations. The only parameter that is not relevant is the ratio between MLd:TeO, with weak or not significant correlations (bright colours). All correlation plots were made with the help of the software R, using the 'corrplot' package, 'colour' method, and 'upper' type as correlation configurations.

Avian Hearing Frequencies

With the data presented in Table 7, it was possible to show a possible hearing frequency of 37 bird species. Figure 13 shows the avian frequency range of birds investigated in this study, using as the threshold of low frequencies the results presented on the 3 dB level, and since not all birds presented 20 dB level results, we are plotting as high-frequency thresholds the 10 dB level for those species without results on the 20 dB level, with an exception for the common murre and hairy woodpecker which are showing the 6 dB level results as high-frequency threshold.

Frequencies below 300 Hz are in the low-frequency range, and above 5000 Hz are in the high-frequency range. Based on this information, it is possible to see that some species can hear low frequencies, such as common raven, Pa (193 Hz); great horned owl, Str (218 Hz); black-crowed night heron, Pa (233 Hz); and common merganser, An (290 Hz). The species that can hear up to high frequencies are American crow, Pa (5620 Hz); common raven, Pa (6006 Hz); zebra finch, Pa (6027 Hz); great blue heron, Pe (6185); mallard duck, An (6667 Hz); blue jay, Pa (7560 Hz); Inca tern, Ch (8271 Hz); Steller's jay, Pa (8359 Hz); and white-faced ibis, Pe (8792 Hz). The other birds comprise their hearing frequencies in the mid-frequency range. The frequency range plot was possible through the software R, with the package 'tidyverse', constructing the plot with the geometry line range.

Habitat Selection and Influence of Propagation Path

Table 9 shows the influence of habitat selection and propagation path for avian species. Based on the selected bird species

Table 9 Habitat selection of avian species

AO	Species binominal name	Species common name	Habitat type	Selection characteristics	References
Ph	*Phoenicopterus chilensis*	Chilean flamingo	Zoo environment	Space selection according to human presence	Rose et al. [181]
Cl	*Streptopelia decaocto*	Eurasian collared dove	Mediterranean urban environment	Food availability, protection from weather, avoidance of predators and human disturbance, security level, presence of competitors, and landscape composition	Eddajjani et al. [182]
Ch	*Uria aalge*	Common murre	Naturally complex and noisy acoustic environment	Acoustic niche diversity	Smith et al. [183]
Pi	*Picoides villosus*	Hairy woodpecker	Mature woodlands	Physical characteristics	Rottenborn [184]
Pa	*Quiscalus quiscula*	Common grackle	Roost in forested areas	Physical characteristics	Bodenchuck and Bergman [185]
Pe	*Ardea herodia*	Great blue heron	Quiet forest areas and foraging habitats	Propagation path	Carlson and McLean [186]
Ps	*Trichoglossus moluccanus*	Rainbow lorikeet	Avoidance of road areas	Propagation path	Uebel et al. [187]

from the work of Peacock et al. [104••, 77••] identified seven peer-reviewed works of seven avian species of seven different avian orders, e.g. Chilean flamingo (Ph), Eurasian collared dove (Cl), common murre (Ch), hairy woodpecker (Pi), common grackle (Pa), great blue heron (Pe), and rainbow lorikeet (Ps). Regarding habitat type, most of the works refer to natural environments ($n=5$; 71.42%), followed by urban and zoo environments ($n=1$; 14.28%) each. It identified 13 habitat selection characteristics, e.g. physical characteristics ($n=3$; 23.07%), propagation path, and human presence

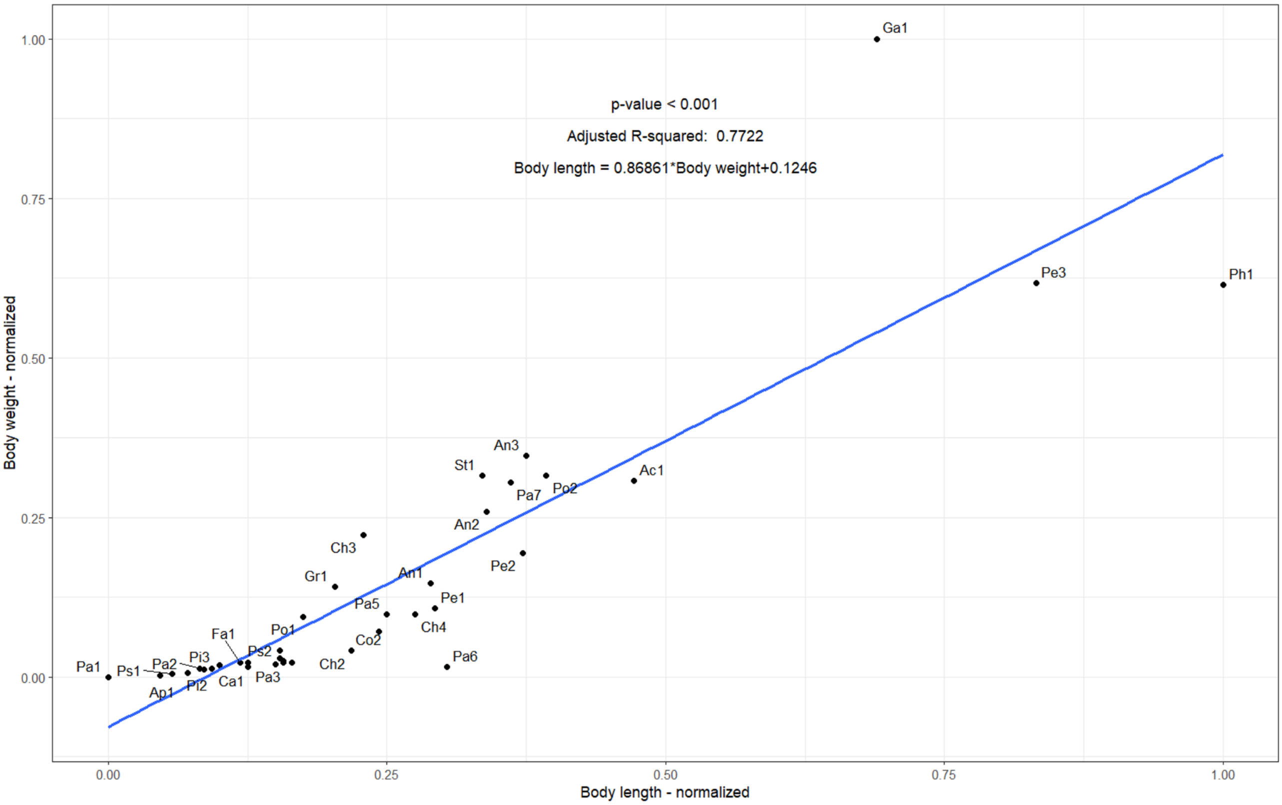

Fig. 4 Linear regression with normalised body length and body weight of avian species

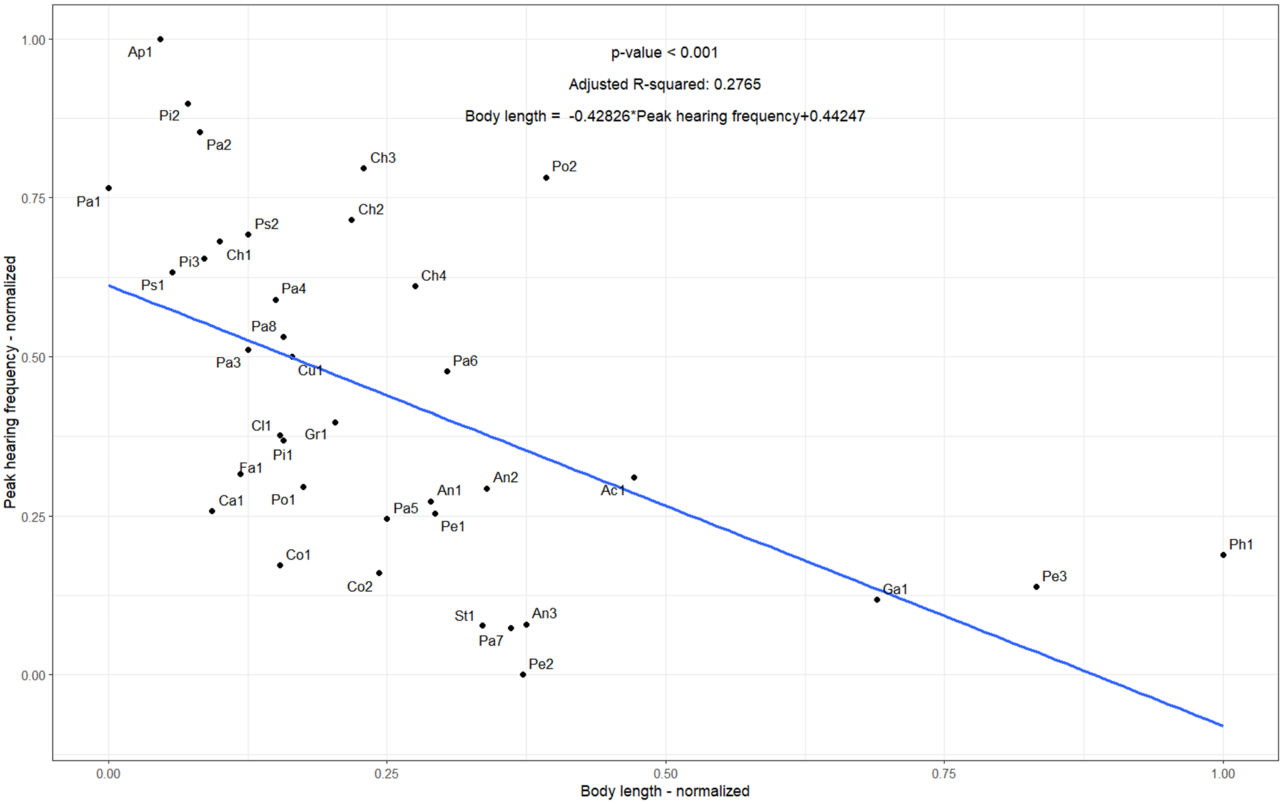

Fig. 5 Linear regression with normalised body length and peak hearing frequencies of avian species

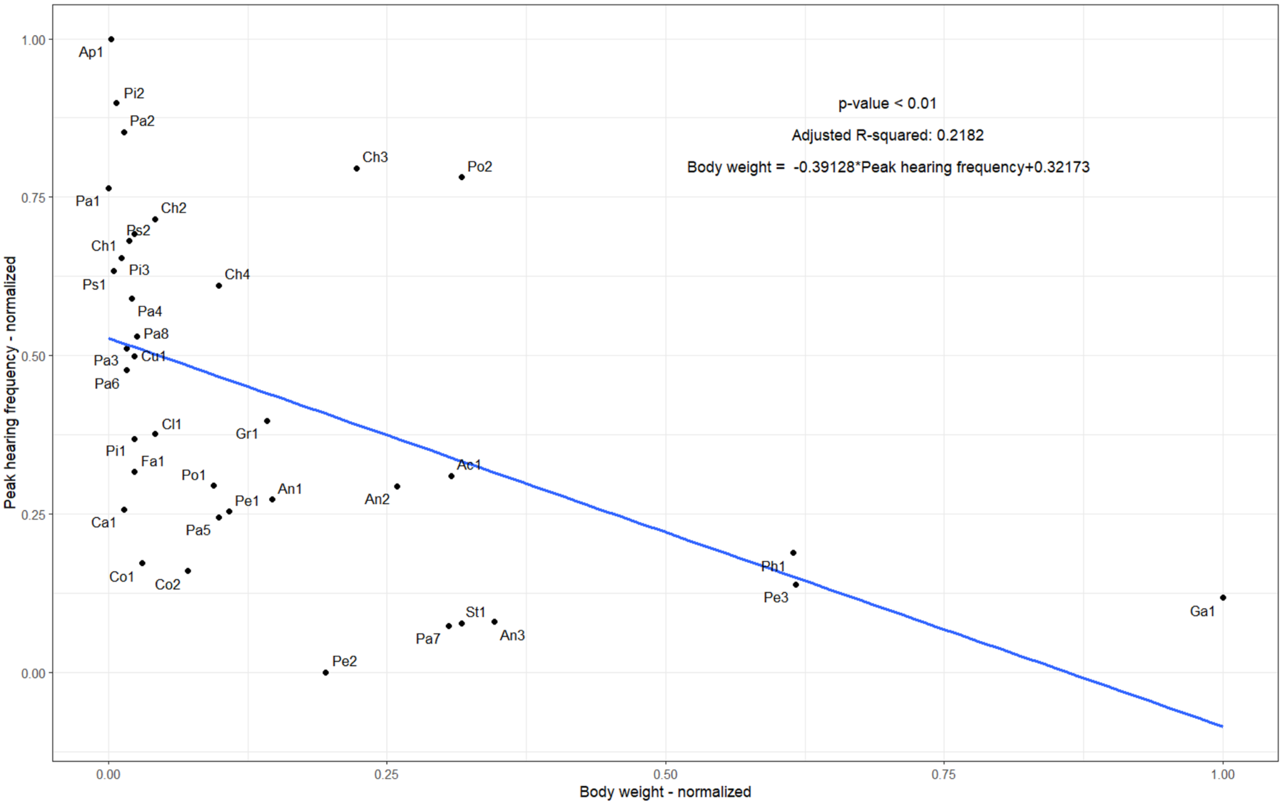

Fig. 6 Linear regression with normalised body weight and peak hearing frequencies of avian species

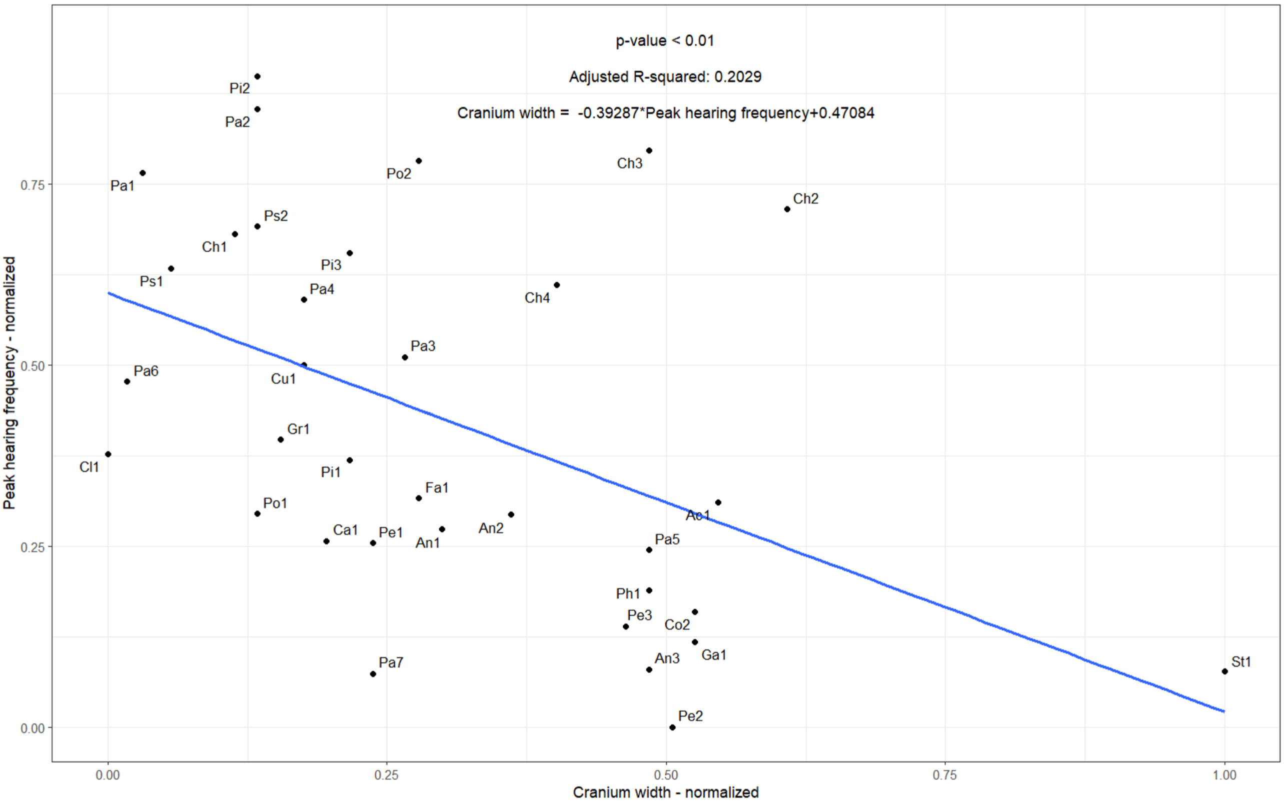

Fig. 7 Linear regression with normalised cranium width and peak hearing frequencies of avian species

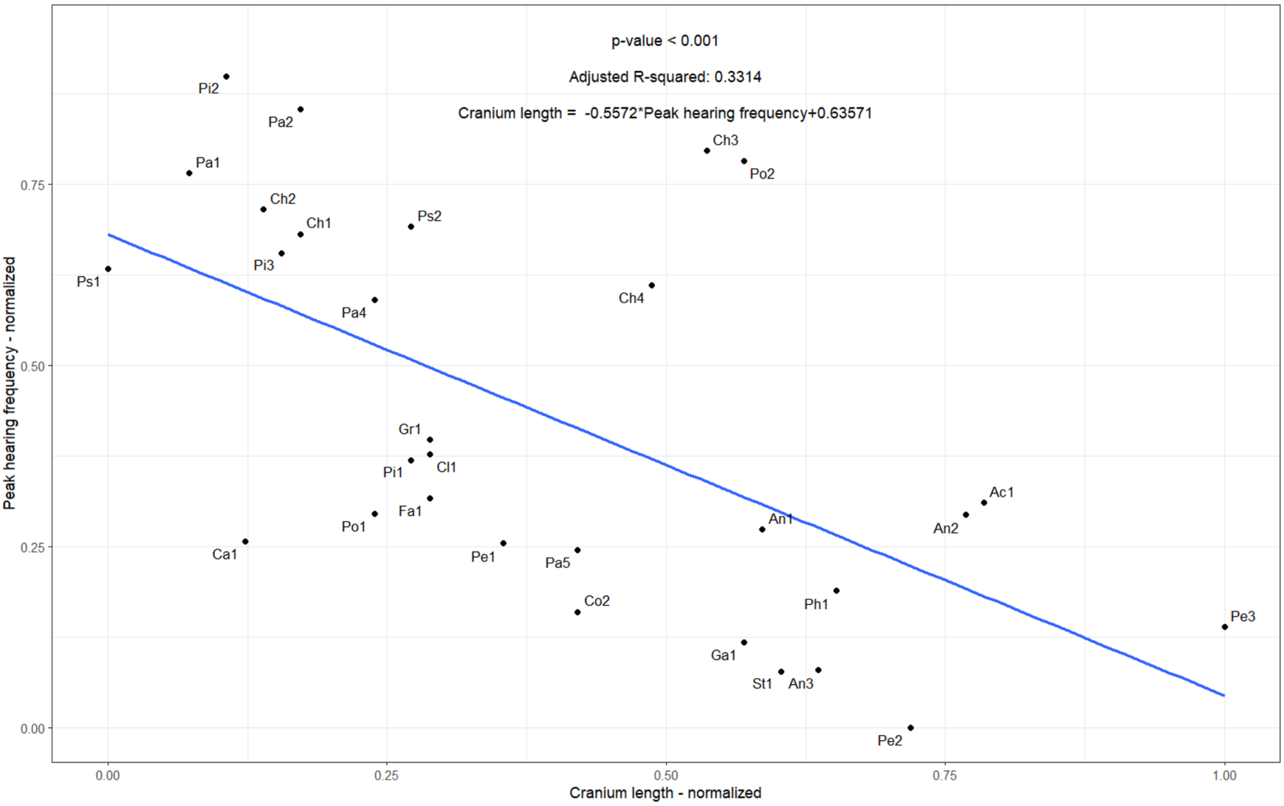

Fig. 8 Linear regression with normalised cranium length and peak hearing frequencies of avian species

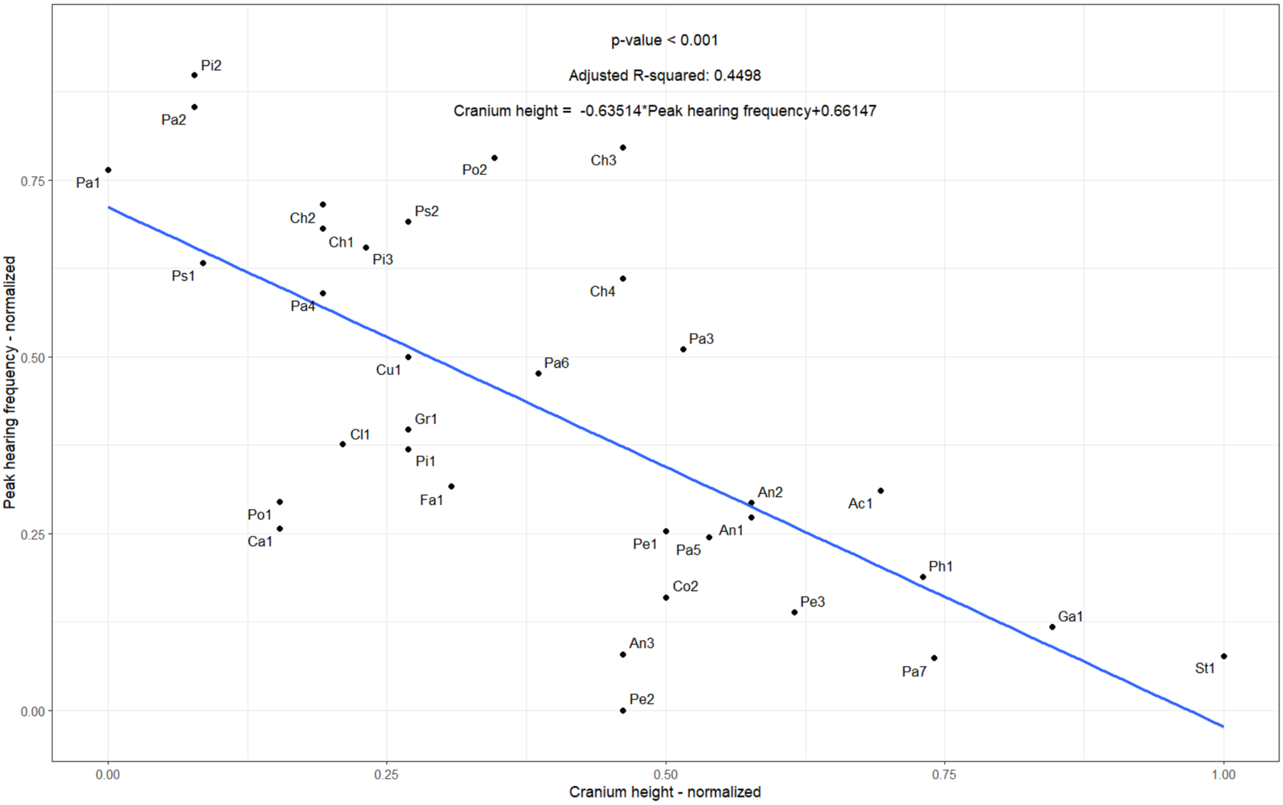

Fig. 9 Linear regression with normalised cranium height and peak hearing frequencies of avian species

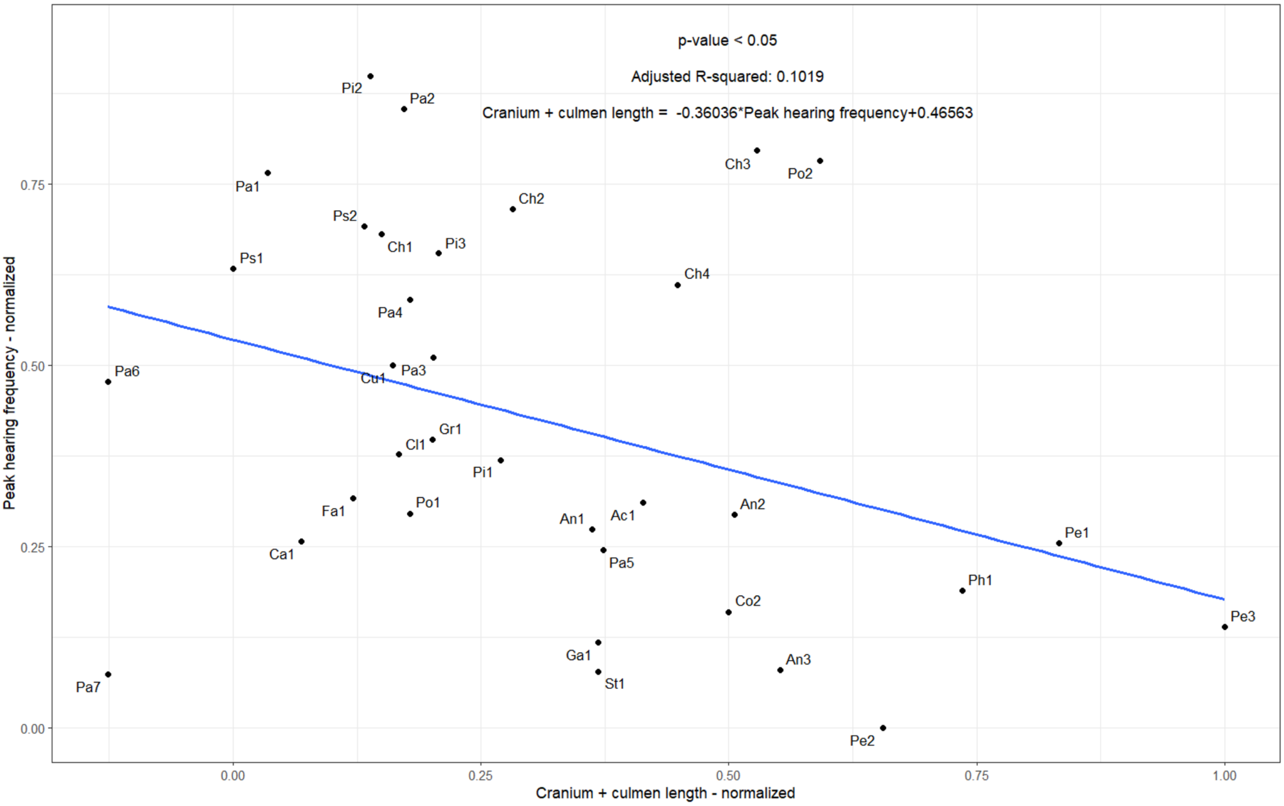

Fig. 10 Linear regression with normalised cranium + culmen length and peak hearing frequencies of avian species

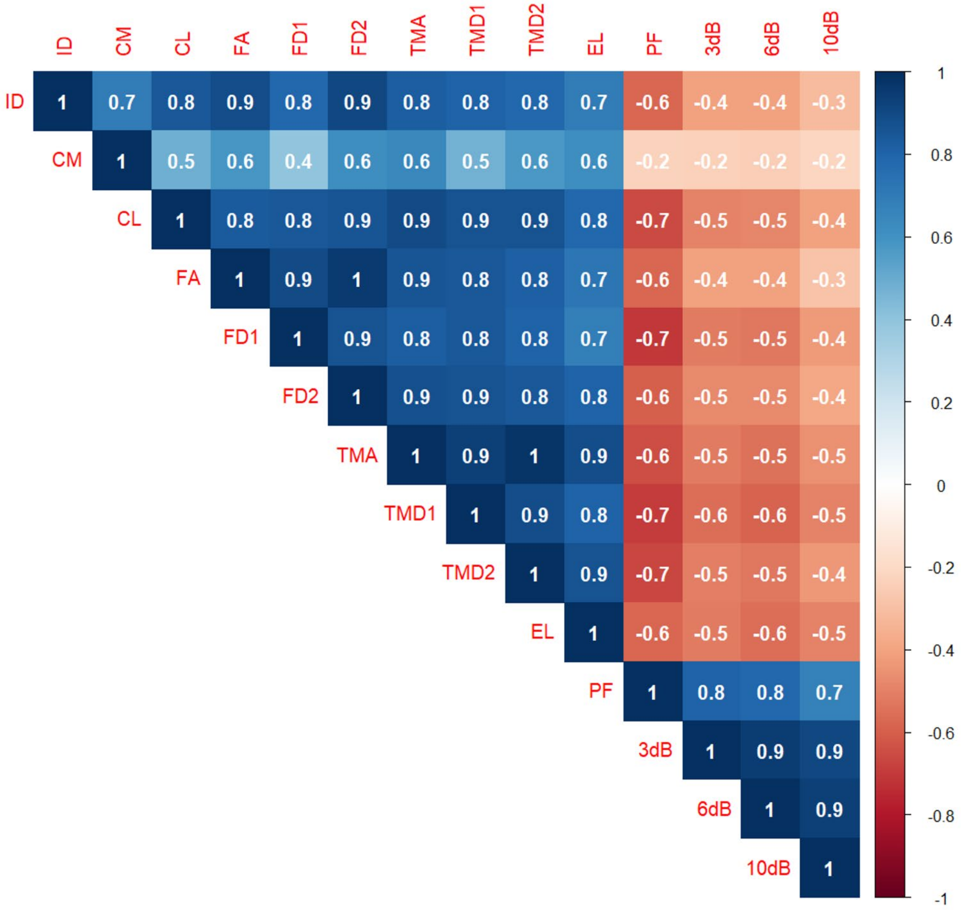

Fig. 11 Pearson correlations between sizes of avian middle ear parts and their hearing frequency range

(*n* = 2; 15.38%) each, followed by food availability, protection from weather, avoidance of predators, security level, presence of predators, and acoustic niche (*n* = 1; 7.69%) each.

Discussion

Influence of Avian Body Size on Peak Hearing Frequency

Using the hearing frequency dataset collected by Peacock et al. [77••, 104••] (Table 7) and avian body dimensions (Table 3), it was possible to observe through Figs. 5 and 6 the same findings stated by Rosowski and Graybeal [79•], Dooling et al. [78], and Gleich et al. [76••] related to the relation of the auditory curves of different avian order and their body sizes. Birds with small body sizes tended to hear better high frequencies, while species with large body sizes could hear more low frequencies.

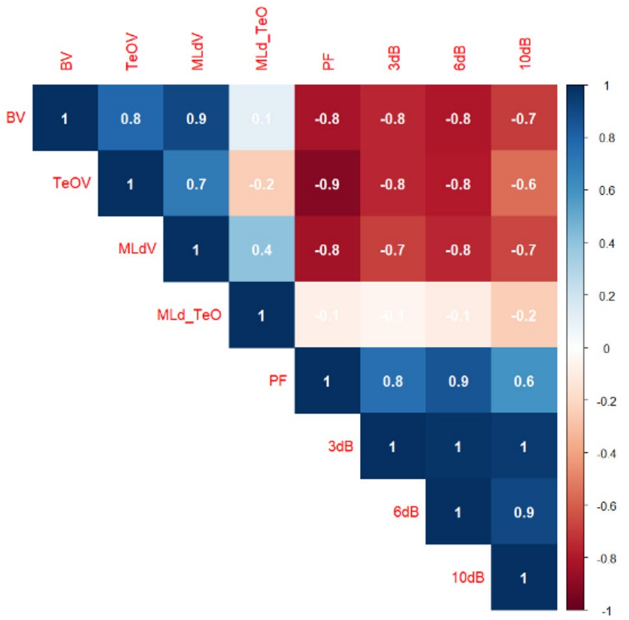

Fig. 12 Pearson correlations between dimensions of avian auditory midbrain and their hearing frequency range

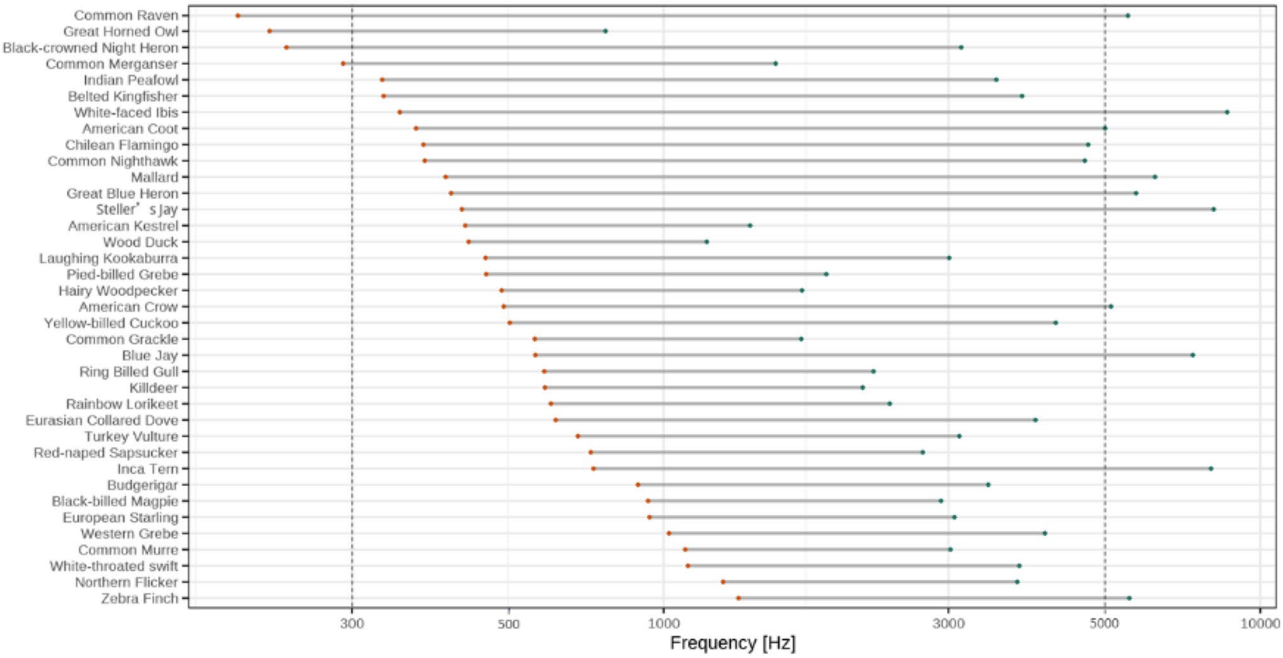

Fig. 13 Avian frequency ranges of 37 avian species

Influence of Avian Head Size on Peak Hearing Frequency

Through the hearing frequency dataset collected by Peacock et al. [77••, 104••] (Table 7) and avian head dimensions (Table 4), it is possible to see in Figs. 7, 8, and 9 that birds with smaller head dimensions could hear better high peak hearing frequencies, while birds with larger head dimensions heard better low frequencies. A similar observation was observed through the functional head size of mammals in the work of Heffner and Heffner [188].

Greater adjusted *R*-squared was presented in results related to cranium height, followed by length, width, and cranium and culmen length.

Avian Hearing System Size Relation with Hearing Frequencies

Rosowski and Graybeal [79•] stated that these inversely and significant correlations are easily observed in high and mid-frequency ranges. This was observed in great negative correlations of tympanic membrane diameter 1 and 2 (TMD 1–2), footplate diameter 1 (FD1), and columellar length (CL) with the peak hearing frequency (PF) in Fig. 8. Peacock et al. [77••] stated that a greater absolute mass of the middle ear ossicles, e.g. columellar mass (CM), could predict lower frequency peaks for birds with these hearing system characteristics. This was also observed in the figure on the low negative correlations with PF.

In general, it is possible to affirm that if the midbrain volume is large, the most suitable is the possibility of hearing low frequencies, and birds with small midbrains are able to hear higher frequencies.

Avian Hearing Frequencies

The avian hearing frequencies demonstrated in Fig. 10 are shown in ascending order, the species which concentrate their hearing frequencies on low to high frequencies. This distribution did not follow the avian orders, but there is a significant influence on the body size of the shown species. Corroborating the findings of the influence of avian body size on peak hearing frequency. There are some exceptions, like the belted kingfisher with a medium-small body size hearing better lower frequencies. Other species, like the Chilean flamingo, great blue heron, and turkey vulture with larger body sizes, could hear better mid-frequencies.

Habitat Selection and Influence of Propagation Path

Cody [69] informed that community structure, competition, and other synecological factors influence habitat selection, as observed in Eddajjani et al. [182], which investigated the Eurasian collared dove. This species prefers habitats with food availability, protection from weather, avoidance of predators and human disturbance, security level, presence of competitors, and landscape composition.

The acoustic influence is more evident in the habitat selection when observing morphological (vegetation) and physiological factors [71–73]. Species that selected their habitat according to morphological factors were the hairy woodpecker [184], common grackle [185], great blue heron [186], and rainbow lorikeet [187]. Physiological factors, e.g. stress caused by the visitor in a zoo, were observed in the work of Rose et al. [181], which investigated Chilean flamingos and reported a space selection inside the enclosures, according to human presence.

Regarding habitat selection, preferences in natural and non-natural environments were observed. Rose et al. [181] reported that the Chilean flamingo is using the enclosure space according to the presence of humans in the surroundings during the day. The Eurasian collared dove gives preference to habitats according to food availability, protection from weather, avoidance of predators and human disturbance, security level, presence of competitors, and landscape composition [182]. Some species, such as the common murre, are selecting acoustically complex environments. This suggests that niche diversity could be a reason for habitat selection [183]. Others are more concerned with the physical characteristics, e.g. the hairy woodpecker prefers mature woodlands [184], and the common grackle is known to roost in forested areas [185]. The great blue heron is selecting quiet forest areas and foraging habitats. This was highlighted in the observations regarding sound propagation path, where this species was highly annoyed at altitudes below 60 m and when the source was 30- to 267-m radius [186]. The propagation path of noises along roads can be damped by dense vegetation, as observed in the work of Uebel et al. [187], which investigated the rainbow lorikeet presence near roads.

Limitations

The main limitations observed in this study are finding works with a complete dataset of the investigated species over taxa, since there are over 11,000 bird species. The information related to the relevant aspects of the mechanistic pathway, such as noise sources, propagation path, habitat selection, and physiological data (body and head dimensions, hearing system, and thresholds), is totally fragmented, covering several fields of acoustics, turning this sort of literature review time-consuming and demanding.

Another relevant factor for the actual state-of-art is that few studies realised acoustic measurements and playback reproductions to ensure that the reported outcomes are associated with the indicated noise sources. Still, most of the findings collected in the literature review of this work are coming from peer-reviewed papers that use observational data as a major data collection method [189].

Conclusion

The presented work aimed to investigate mechanistic pathways of anthropogenic noise impact on avian species. This work adopted the database of Peacock et al. [77••, 104••] regarding birds, and complementary data was added to the dataset providing findings related to the physiological aspects. Additionally, an extensive literature report provided information related to propagation path and habitat selection.

This work showed that the avian hearing thresholds are related to body and head size, indicating that birds with a larger body and head size hear better mid and low frequencies, while those with a smaller body and head dimension could hear better higher frequencies.

Regarding habitat selection and propagation path, birds have specific preferences according to natural and non-natural environments, e.g. the presence of humans, selection of acoustically complex environments, due to niche diversity, and physical characteristics, such as vegetation morphology and avoidance of areas with the dominance of traffic noise sources.

This form of study is essential to show how avian species hear and how the frequency range of the noise sources overlaps with avian hearing frequencies, as well as their influence on physiological and habitat selection. This rich information can contribute to assertive noise control and mitigation measures which also consider the biodiversity, turning the sonic environment healthy for all.

Author Contributions M.S.E., R.J.Y and M.D.W. designed the study; M.S.E. screened the works; M.S.E. analysed the data; M.S.E. wrote the manuscript; R.J.Y., W.J.D, D.W. and M.D.W. edited and revised the manuscript.

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Data Availability All datasets used to produce the statistical analysis are disposed on the tables in this work.

Declarations

Conflict of Interest The authors declare no competing interests.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

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- • Of importance
- •• Of major importance

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