

## REVIEW

## Acoustic communication in terrestrial and aquatic vertebrates

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## ABSTRACT

Sound propagates much faster and over larger distances in water than in air, mainly because of differences in the density of these media. This raises the question of whether terrestrial (land mammals, birds) and (semi-)aquatic animals (frogs, fishes, cetaceans) differ fundamentally in the way they communicate acoustically. Terrestrial vertebrates primarily produce sounds by vibrating vocal tissue (folds) directly in an airflow. This mechanism has been modified in frogs and cetaceans, whereas fishes generate sounds in quite different ways mainly by utilizing the swimbladder or pectoral fins. On land, vertebrates pick up sounds with light tympana, whereas other mechanisms have had to evolve underwater. Furthermore, fishes differ from all other vertebrates by not having an inner ear end organ devoted exclusively to hearing. Comparing acoustic communication within and between aquatic and terrestrial vertebrates reveals that there is no 'aquatic way' of sound communication, as compared with a more uniform terrestrial one. Birds and mammals display rich acoustic communication behaviour, which reflects their highly developed cognitive and social capabilities. In contrast, acoustic signaling seems to be the exception in fishes, and is obviously limited to short distances and to substrate-breeding species, whereas all cetaceans communicate acoustically and, because of their predominantly pelagic lifestyle, exploit the benefits of sound propagation in a dense, obstacle-free medium that provides fast and almost lossless signal transmission.

**KEY WORDS:** Aquatic animals, Communication, Hearing, Land animals, Sound

## Introduction: the physics of sound propagation in water and on land

Sound is generated by the vibration of an object in an elastic medium, and it propagates easily in air and water. It was Aristotle (2016) who first reported that aquatic animals such as fishes and whales produce sounds. We now know that acoustic communication is widespread in invertebrates (insects, crustaceans) as well as vertebrates living in both media. How do the different physical properties of water and air – mainly the much higher density of water – affect sound transmission? Sound travels four to five times faster, has a much higher wavelength and a much lower absorption in water (Table 1). This raises the question of whether differences in sound propagation between media affect the way in which aquatic and terrestrial animals produce and detect sounds and communicate acoustically.

The acoustic communication of aquatic and terrestrial animals does differ because of the differences in physical characteristics

of the media (Hawkins and Myrberg, 1983). In particular, the propagation of low-frequency sounds is limited in shallow water but is facilitated in deep water as compared with air. The wavelength of a sound of a given frequency is four to five times longer in water compared with air (Table 1), and sound waves cannot propagate if the depth of the medium (water) is lower than the wavelength. Very shallow water (1–2 m) thus acts as a high-pass filter (see Glossary). Accordingly, in 1 m of water, sound frequencies below 1 kHz will not propagate; paradoxically, this is the frequency range most often used by fish for acoustic communication (Lugli, 2015). This cut-off frequency (see Glossary) phenomenon restricts communication distances in shallow water (Fine and Lenhardt, 1983; Rogers and Cox, 1988). In contrast, the low absorption and long wavelengths of sounds in water enable some aquatic animals to communicate over distances of 10 km and more – distances otherwise unknown in air. In air, ground effects set in when the sender is close to the ground and temperature gradients result in a waveguide-like effect (Bradbury and Vehrencamp, 2011).

There are also surprising similarities in the use of acoustic signals in both media. Infrasound and ultrasound (see Glossary) are used similarly in both media by different mammals. The largest mammals in both habitats, namely, elephants and baleen whales (mysticetes), utilize infrasound for long-distance communication over kilometres (Narins et al., 2016). In contrast, ultrasound is used for echolocation and hunting of small prey items (i.e. biosonar), e.g. insects by bats and fishes by toothed whales (odontocetes) such as dolphins (Au, 2000a; Akamatsu et al. 2005; Au and Simmons, 2007).

The aim of this Review is to describe and compare acoustic communication in terrestrial and aquatic vertebrates. The article will start by comparing mechanisms used for sound production and sound detection in both media. We will then compare and analyze acoustic behaviour and end by discussing whether there are fundamental differences in sound generation and detection, as well as communication, owing to physical differences between the media.

## Sound production in terrestrial and aquatic vertebrates

Both species inhabiting land and those living in the water have developed many ways to produce sounds. They have evolved specialized sound-generating mechanisms (also termed sonic or vocal organs), which are entirely devoted to the production of acoustic signals for communication. Here, we use the term 'vocalization' in a broad sense for all kinds of sounds generated by specialized mechanisms for communication purposes, independently of whether vocal folds (cords) are involved. In addition, both terrestrial and aquatic taxa can produce non-vocal acoustic signals, such as by hitting the substrate (Bradbury and Vehrencamp, 2011; Suthers et al., 2016). The main difference in sound production in air and underwater is the transfer of the signals from the vibrating structure to the medium. In air, this can be done directly, whereas in water, intermediate structures are typically involved.

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**Glossary**

**Acoustic impedance**  
The resistance that a medium presents to the flow of acoustic energy (in close analogy with electrical impedance).

**Cut-off frequency**  
Limits to the propagation of low sound frequencies (i.e. long wavelengths) in shallow water. Sound waves can only propagate if the wavelength is smaller than the water depth; e.g. in 1 m deep water, sound frequencies below 1 kHz cannot propagate.

**Electric organ discharge**  
Signals generated by the electric organs of electric fish. Weakly electric fish use these discharges for navigation and communication.

**Formants**  
Enhanced frequencies in harmonic sounds that are produced in the vocal tract independently of the larynx (see Fundamental frequency). The supralaryngeal vocal tract (from the larynx to the nostrils or lips) has natural resonance properties that selectively dampen or enhance specific frequencies of the source signal.

**Fundamental frequency (or fundamental,  $f_0$ )**  
The lowest frequency in a harmonic sound. The fundamental frequency is often termed the first harmonic, and higher harmonics are referred to as overtones. Overtones are usually integer multiples of the fundamental frequency. The fundamental frequency describes the vibration rate of some anatomical structure in sound-generating organs.

**Hearing curve (audiogram)**  
A graph that shows the range of frequencies an animal detects and which sound pressure level is necessary to detect sound at particular frequencies. These sound pressure levels are called hearing thresholds.

**High-pass filter**  
An electronic filter that transmits frequencies higher than a certain cut-off frequency and attenuates frequencies that are lower. In certain habitats it means that only sound frequencies above the cut-off frequency (or wavelengths smaller than that of the cut-off frequency) will propagate.

**Infrasound**  
Sound lower in frequency than 20 Hz and thus not detectable to humans.

**Otoliths (Greek: otos=ear, lithos=stone)**  
Tiny calcareous ovoid to stick-like structures in the ears of bony fishes that serve in hearing, detection of gravity and head movement.

**Tympanum (ear drum or tympanic membrane)**  
A thin membrane that separates the middle ear from the external ear or the surrounding. It is typically seen from the outside in frogs, but not birds and mammals. It transmits air pressure changes of sound to the middle ear ossicles.

**Ultrasound**  
High-frequency sound above 20 kHz, and thus not detectable to humans.

**Weberian ossicles**  
Auditory ossicles in otophysine fish similar to the middle ear ossicles in mammals but of different origin.

Sound production in terrestrial vertebrates

Terrestrial and semiaquatic mammals (e.g. seals, otters) primarily produce sounds with the larynx, located at the top of the trachea (Fitch, 2006; Fitch and Hauser, 2003; Fitch and Suthers, 2016; Taylor et al., 2016). Basically, the larynx of land mammals consists of four cartilages, a pair of vocal folds and a set of muscles (Fig. 1). The opening between the vocal folds is often defined as the glottis. During breathing, posterior cricoarytenoid muscles contract, pulling the arytenoid cartilages and vocal folds away from each other. Sounds, however, are produced when interarytenoid muscles contract, causing the vocal folds to close the glottis. The respiratory air flow through the glottal slit induces passive oscillations of

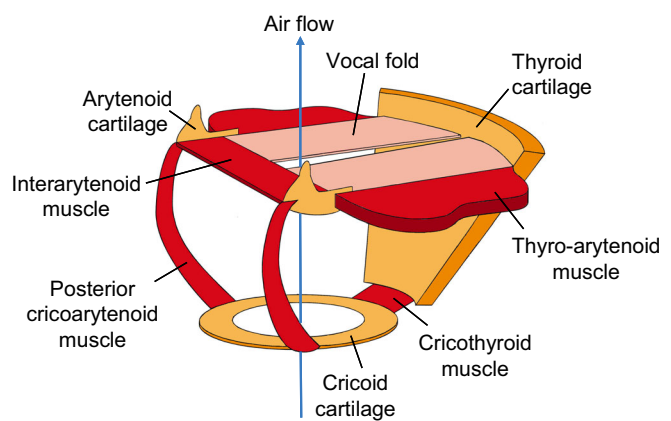
Table 1. Physical properties and sound characteristics in air and water

Sound characteristics	Air	Water
Density $\rho$ (kg m <sup>-3</sup> )	1.2	1.000
Speed of sound $c$ (m s <sup>-1</sup> )	343	1480
Wavelength $\lambda$ at 100 Hz (m)	3.43	14.8
Wavelength $\lambda$ at 1 kHz (m)	0.343	1.48
Absorption at 1 kHz (dB 100 m <sup>-1</sup> )	1.2	0.008
Particle velocity $v$ at 1 W m <sup>-2</sup> sound intensity (m s <sup>-1</sup> )	0.49	0.08
Acoustic impedance $\rho c$ (g m <sup>-2</sup> s <sup>-1</sup> )	0.4×10 <sup>-6</sup>	1480×10 <sup>-6</sup>

Values may vary slightly depending on humidity, temperature, salinity and water depth. From Hawkins and Myrberg (1983).

the vocal folds, and the number of these oscillations determines the fundamental frequency (see Glossary) of sounds (e.g. 130 Hz in men, 200 Hz in women). Fundamental frequency may increase when the tension on the vocal folds is increased by contracting the cricothyroid and thyro-arytenoid muscles. The source signal generated by the larynx is subsequently modified in the supralaryngeal vocal tract. Some frequencies will be enhanced (formants; see Glossary) and others dampened because of resonance properties (source-filter theory) (Titze, 2000; Fitch and Suthers, 2016; Herbst, 2016; Taylor et al., 2016).

A large diversity in the anatomy of the larynx enables land mammals to produce a variety of sounds, from infrasound in elephants up to ultrasound in mice and bats. Vocal fold length determines, within limits, the fundamental frequency of sounds. This enables elephants to produce infrasonic vocalizations with a larynx that has anatomy similar to that of humans (Herbst et al., 2012). Bats generate biosonar frequencies up to 150 kHz with a thin membrane along the edge of the vocal folds (Au and Simmons, 2007). The location of the larynx varies in mammals and can even change during calling. For example, red deer stags can pull their larynx downward towards the sternum with a pair of laryngeal retractor muscles. This increases the vocal tract length, lowers the formant frequencies of roars and exaggerates the size of the bellowing stag (Fitch and Reby, 2001). Besides laryngeal sounds,



**Fig. 1. Schematic drawing of the terrestrial mammalian larynx.** The typical larynx consists of four tiny cartilages, four sets of muscles and two vocal folds. The vocal folds are stretched by the thyroid and arytenoid cartilages when the cricothyroid and thyro-arytenoids muscles contract. Contraction of the interarytenoid muscle blocks the air flow and sets the vocal folds into vibration when mammals exhale air. Contraction of the posterior cricoarytenoid muscles pulls the vocal folds back and allows free air flow. Modified from Bradbury and Vehrencamp (1998). For clarity, this schematic drawing differs from the actual mammalian larynx, which has fleshy vocal folds, a thyroid cartilage almost entirely surrounding the larynx and a ring- not disc-shaped cricoid cartilage.

land mammals can generate communication sounds using non-specialized mechanisms, such as stamping on the ground (deer, moose), rattling with spines (porcupine), beating one's chest (gorilla) or tree drumming (chimpanzee) (Arcadi et al., 1998).

As in other vertebrate groups except fishes, sound production in birds is tightly coupled with the respiratory system. Birds possess a sound-generating structure at the junction of the trachea and the bronchi, the syrinx. The syrinx comprises several pairwise structures, which may result in the two sound sources in several bird taxa (Suthers and Zollinger, 2004). Like the mammalian larynx, the structure is made of muscles, cartilages and vibrating tissue (labia), but may also include additional sound-generating membranes (Fig. 2) (Gaunt and Wells, 1973; Goller and Larsen, 1997). In contrast to mammals, the air flow is maintained by air sacs, which act like a bellows system and thus also aid in efficient sound production (Duncker, 2000, 2004). The remaining vocal tract and associated structures (e.g. vocal sacs) play a significant role in shaping the spectral composition of the sounds released to the environment. The structural diversity of these mechanisms is particularly high among non-passerines. Parrots, for example, can use their tongue to modulate the sounds produced by their simple syrinx (two pairs of intrinsic syringeal muscles in contrast to four to nine pairs in oscines) (Gaunt, 1983). Much of the functionality of the sound-producing system of birds is shared with the mammalian system (Elemans, 2014; Elemans et al., 2015). All these anatomical features underlie the ability of birds to modulate frequency and amplitude of vocal output, yielding their exceptional diversity in vocal communication (Riede and Goller, 2010). Instead of vocal sound production, some birds may use other bodily structures, such as beaks and wing and tail feathers, to produce sounds (e.g. Clark, 2016). The drumming of woodpeckers involves the beak and an external resonating body such as a tree (Winkler et al., 1995).

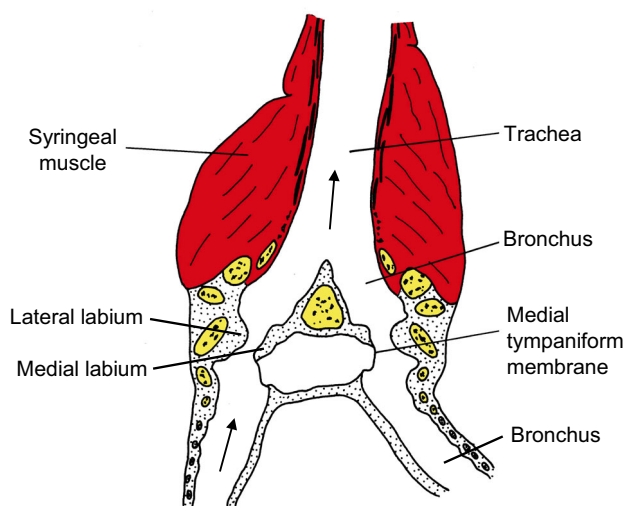
### Sound production in aquatic vertebrates

Virtually all amphibious and aquatic tetrapods utilize vibrating tissues in an air flow to produce sounds, similar to terrestrial tetrapods. This is the case in amphibious tetrapods, such as frogs, toads and pinnipeds, as well as in entirely aquatic taxa such as

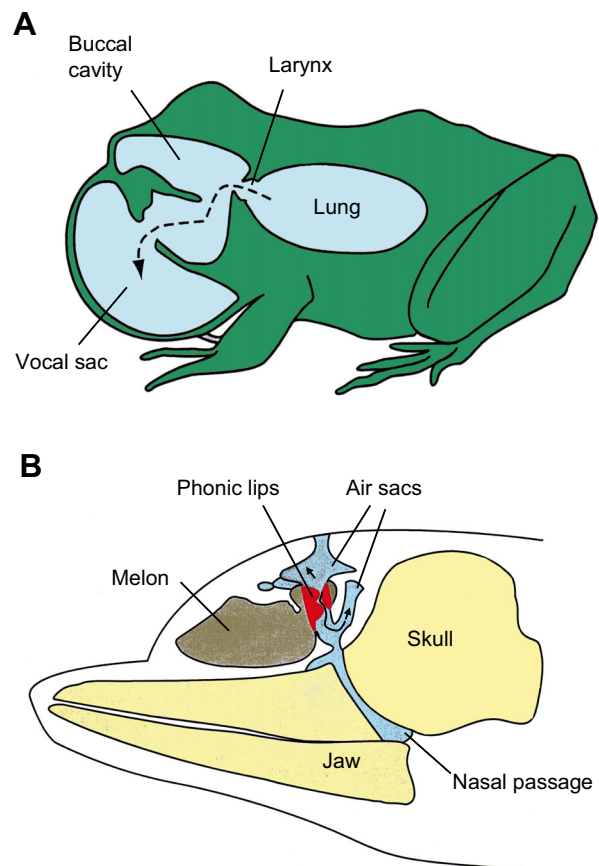
cetaceans. Because of the impossibility of inhaling and exhaling air underwater, the sound-producing mechanisms of these animals have been modified to avoid frequent trips to the surface.

In frogs and toads (Anura), the terrestrial laryngeal sound-producing mechanism has been modified basically in two ways. These animals have vocal sacs to help radiate sound energy effectively (like a speaker membrane) and they use an air-recycling system to pump air between the lungs and the vocal sacs across the larynx (vocal folds). This air pumping is independent of air breathing, because the nostrils and mouth are closed (Gerhardt and Huber, 2002; Kime et al., 2013; Colafrancesco and Gridi-Papp, 2016) (Fig. 3A). Among Anura, an exception to the normal tetrapod mechanism of sound production is found only in the fully aquatic pipid frogs, such as the African clawed frog *Xenopus*. Instead of vocal folds, pipids possess ossified disc-shaped rods of the arytenoid cartilage, which are separated by the action of laryngeal muscles. According to Yager (1992a), this produces an implosion of air that results in clicking sounds.

Like anurans, cetaceans use an air-recycling system for sound production. Baleen whales (mysticetes) seem to use their larynx and vocal folds for sound production, but experimental evidence is lacking (Reidenberg and Laitman, 2007). Much more is known in toothed whales (odontocetes) such as dolphins (Madsen et al., 2004). Cranford et al. (1996) and Cranford (2000) hypothesized that



**Fig. 2. Drawing of the syrinx of a songbird (brown thrasher).** Sounds are produced with membranes, e.g. medial tympaniform membranes, and the labia when exhaling, and in rare cases when inhaling. The separate labia allow songbirds to open and close each bronchial tube independently. Arrows indicate air flow. Modified from Catchpole and Slater (1995).



**Fig. 3. Drawings of sound-generating mechanisms in tetrapods.** (A) The vocal system in frogs consists of vocal cords that vibrate when air flows between the lungs and the buccal cavity/vocal sacs. (B) Dolphins produce sounds with their phonic lips, which are vibrated when air is pumped between air sacs within the nasal passage. Sounds are transmitted via the fatty tissue of the melon into the water. Dashed lines and arrows indicate air flow. Modified from Cranford et al. (1996), Gerhardt and Huber (2002) and Suthers (2010).



echolocation clicks and whistles are produced in the nasal passage between the larynx (which is not used for sound production) and the single blowhole (Fig. 3B). The nasal passage possesses several nasal air sacs, which can be compressed by associated muscles, and phonic lips (also known as monkey lips or sonic lips) protruding into the lumen. Sounds are produced when air is pressed out of the nasal sacs into the nasal passage through the phonic lips, which are pressed together by muscles. Although the exact mechanism is not known, it is assumed that the sound is transmitted through specialized fatty tissue (anterior and posterior bursae) adjacent to the phonic lips. The anterior bursa (often referred to as the melon) radiates the sound energy forward and acts as an ‘acoustic lens’ (Zimmer et al., 2005). Toothed whales produce a wide variety of whistles and broadband sounds (clicks) with main energies at a few kilohertz (thus well detectable for humans) up to ultrasonic frequencies of >100 kHz, used for echolocating prey. Whales can also communicate acoustically in unspecialised ways; sounds produced by baleen whales when hitting the water surface during breaching are considered to be a communication signal (Dunlop et al., 2010).

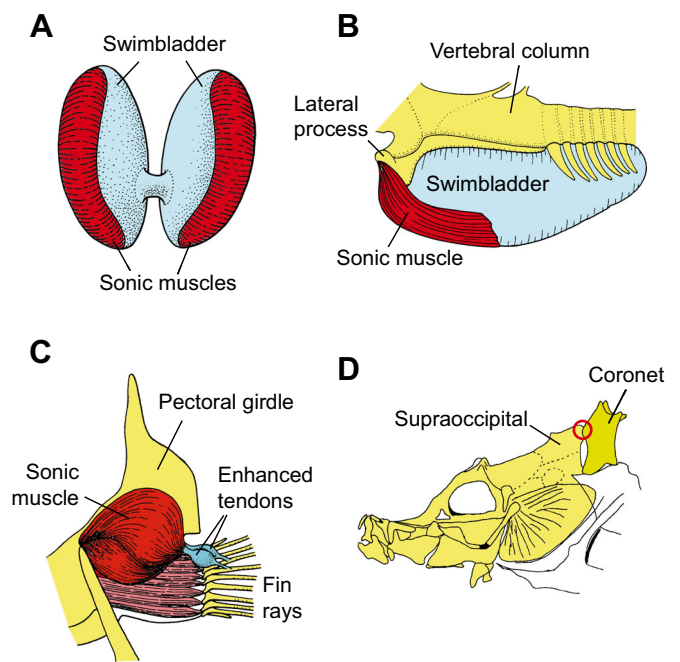
Comparing the air-recycling system of frogs and dolphins raises the question of why fully aquatic frogs do not utilize this system for sound production. Why did pipid frogs abandon their vocal cords and develop a bony implosion mechanism? Yager (1992a) argues that the laryngeal box in *Xenopus* radiates sound to the water like a fish’s swim bladder (see below). Whales use the fatty tissue of the bursae for this purpose; this tissue is often regarded as ‘acoustic fat’ (Madsen et al., 2003; Zimmer et al., 2005).

Bony fishes have evolved perhaps the largest diversity of sound-generating organs among vertebrates (Ladich and Fine, 2006; Fine and Parmentier, 2015; Parmentier and Fine, 2016). Their mechanisms of sound production are independent of air flow and breathing, because fishes (with a few exceptions, e.g. lungfishes, labyrinth fishes) do not breathe air. Cartilaginous fishes (sharks and rays) and many bony fishes are not known to possess sonic organs or to produce sounds. In fishes, the large diversity of sound-producing mechanisms may be classified according to the organs involved into swim bladder, pectoral and head mechanisms. Of these, swim bladder mechanisms are the most common (Ladich and Bass, 2011; Ladich, 2014). Fast-contracting muscles, called drumming (or sonic or vocal) muscles, vibrate the swim bladder. The fundamental frequency of drumming sounds depends on the muscle contraction rate (50–250 Hz). This mechanism contrasts with the vibrations of mammalian vocal folds, which oscillate passively (see above). Drumming muscles can be entirely attached to the swim bladder (Fig. 4A), only partly attached (Fig. 4B) or even entirely detached, instead being attached to other structures within the fish’s body. The second major group of sonic mechanisms in fishes depends on vibrations of the pectoral girdle or those generated by tendon plucking or rubbing a pectoral fin friction process within the shoulder girdle (i.e. stridulation, as in crickets) (Fig. 4C). The third group of mechanisms is located in the head, e.g. in seahorses (Syngnathidae) and clownfish (Fig. 4D).

Fish vocalizations are usually brief (<1 s) low-frequency pulsed sounds with main energies of a few hundred hertz, corresponding to the contraction rate of drumming muscles. Broadband sounds with main energies close to or above 1 kHz may be generated by pectoral or head mechanisms in croaking gouramis, catfishes and seahorses (Ladich and Bass, 2011).

#### Comparison between sound production in air and underwater

A comparison of the main sonic mechanisms among vertebrates reveals no clear distinction between terrestrial and aquatic taxa



**Fig. 4. Drawings of sound-generating mechanisms in bony fishes.**

(A) Intrinsic drumming (sonic) muscle in the Lusitanian toadfish *Halobatrachus didactylus*, entirely attached to the swim bladder. (B) Extrinsic drumming muscles in the pimelodid catfish *Pimelodus* sp., originating at the lateral process of the vertebral column and inserting on the swim bladder ventrally. (C) Pectoral sound-producing mechanisms in the croaking gourami *Trichopsis vittata*. Two enlarged fin tendons are stretched by an enlarged adductor muscle and snapped over enhanced bases of two pectoral fin rays. (D) Head friction mechanism in the seahorse *Hippocampus* sp. The posterior margin of the supraoccipital bone is rubbed in a groove of the coronet (red circle). Modified from Colson et al. (1998), Ladich and Bass (2011) and Ladich (2014).

except in one trait. Vibrations of vocal tissue (vocal folds, labia, etc.) are directly transmitted to the air in land mammals and birds but not in frogs, cetaceans or fishes. Fishes differ from all other vertebrates by not relying on air or water flow for sound production. This differs from amphibious and fully aquatic tetrapods, which primarily utilize the terrestrial respiratory system for sound production but may be able to decouple sound production from air breathing (frogs, dolphins).

#### Ears and hearing in aquatic and terrestrial vertebrates

All vertebrates use the dorsal part of the inner ear (the vestibular system) to gain information about their body position and motion in three-dimensional space (Straka and Baker, 2011). The vestibular system consists of three semicircular canals (except in agnathans, which have only one or two; Ladich and Popper, 2004), which detect body rotation (angular acceleration), and the utricle, which that detects static changes in the position of the head or the body relative to the Earth’s gravitational vector (linear acceleration) (Straka and Baker, 2011). The ventral part of the inner ear consists of the saccule and a diversity of end organs that are used as sound detectors (although to different extents in different vertebrate species). The anatomy and physiology of the ventral part of the vertebrate ear do not reveal a clear distinction between vertebrate taxa living in aquatic versus terrestrial habitats (Ladich, 2017). The main difference between hearing in air and water is the transmission of sound pressure (or particle) oscillations to the inner ear auditory end organs.

### Fishes, amphibians and birds

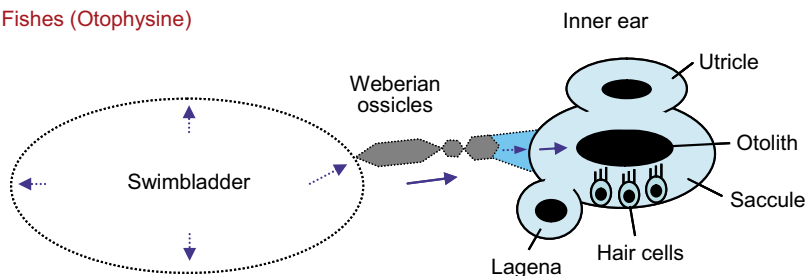
The ear of bony fishes (cartilaginous fishes will not be discussed further because they are not known to communicate acoustically) consists of three otolithic end organs, namely, the utricle, saccule and lagena (Ladich and Popper, 2004; Ladich and Schulz-Mirbach, 2016). Each otolithic end organ consists of a dense structure of calcium carbonate, the otolith (see Glossary), which is in close contact with a field of sensory hair cells termed maculae (Fig. 5A). Such an arrangement is not known in any tetrapod, but can be explained by physical constraints that fishes encountered during their evolution, namely, that they live in a medium that has the same density as the fish's body. Fishes in general lack a sound-pressure-detecting device and instead need a sensor that responds to tiny particle movements (particle velocity, acceleration, displacement), which, paradoxically, are much smaller in water than in air (Table 1). To overcome this problem, the sensory cells are coupled to the otolith, which is denser than the surrounding tissue. The otolith oscillates with a lag relative to the sensory hairs and the whole fish, which excites sensory cells (Hawkins, 1993; Ladich, 2017).

Fishes, in contrast to all other vertebrates, do not possess an auditory end organ solely devoted to hearing. Most fishes appear to use the saccule, a gravity sensor in most tetrapods, for hearing. However, in some taxa (e.g. herrings and marine catfishes), the utricle seems to be the main auditory end organ (Blaxter et al., 1981; Fay and Popper, 1999). The function of the lagena remains to be

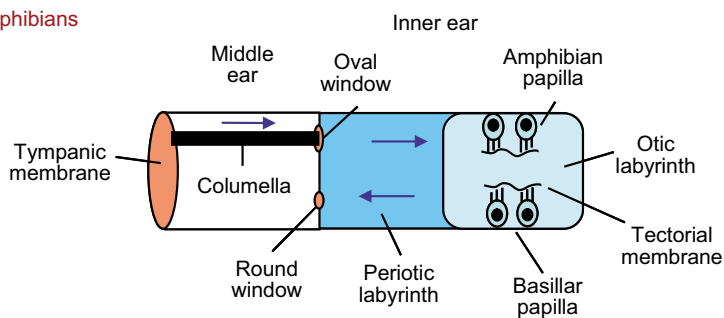
investigated. Thus, fishes differ from tetrapods in that they do not possess a sensory structure exclusively devoted to hearing and in detecting particle motion rather than sound pressure. Consequently, their hearing is limited to low frequencies of a few hundred hertz.

Interestingly, approximately one-third of fish species have mechanisms to detect sound pressure in addition to particle motion, thus improving their hearing abilities. These mechanisms involve accessory (or ancillary or peripheral) hearing structures, consisting of an air-filled chamber that undergoes volume changes in a sound-pressure field and transmits these oscillations to the inner ear (Popper and Fay, 1999; Ladich and Popper, 2004; Braun and Grande, 2008). The anterior walls of these air chambers (e.g. the swimbladder) therefore function very similarly to tympana (ear drums). In otophysines (carps and minnows, catfishes, characins and tetras, knifefishes), which comprise >8000 species, a series of tiny ossicles (Weberian ossicles; see Glossary) transmits oscillations of the swim bladder to the inner ear (Fig. 5A). Accessory hearing structures extend the detectable frequency range up to several kilohertz and increase the absolute auditory sensitivity (Fay, 1988; Ladich and Fay, 2013) (note that ultrasound detection up to 180 kHz is known in a few herring species; Narins et al., 2014). Besides ossicles, air-filled cavities can be connected to the inner ears via tube-like anterior swim bladder extensions (as seen in some squirrelfishes, drums, cichlids and all herrings). In mormyrids and labyrinth fishes, air bubbles close to the inner ear fulfil the same role (Ladich, 2016).

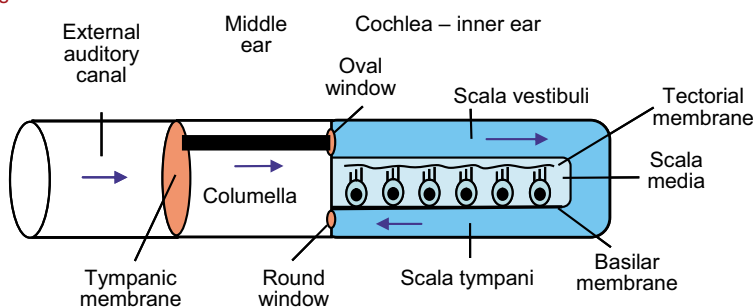
#### A Fishes (Otophysine)



#### B Amphibians



#### C Birds



**Fig. 5. Schematic drawings of the ears of fishes, amphibians and birds.** (A) Fishes possess no outer or middle ear but detect sound with otolithic end organs of the inner ear, mainly the saccule. The swimbladder is shown as an accessory structure for hearing improvement in otophysine fish (minnows and carps, catfishes, tetras and piranhas). Oscillations of the swimbladder wall (arrows in swimbladder) in the sound pressure field are transmitted via a chain of tiny ossicles (Weberian ossicles) and a perilymphatic sinus to the endolymph of the inner ear. (B) The amphibian ear consists of an external tympanic membrane (ear drum), a middle and an inner ear. Sound pressure changes are transmitted via a middle ear ossicle (columella) to the oval window of the inner ear. The ear possesses several auditory end organs entirely devoted to hearing. The amphibian and basilar papilla consist of hair cells covered by tectorial membranes. (C) The bird ear consists of an outer ear canal that conducts sound to the tympanic membrane but lacks a pinna. The middle ear possesses a columella and the inner ear has a single auditory end organ, the cochlea. The cochlea is stretched in birds and consists of three fluid-filled canals. Movements of the fluids cause bending of the basilar membrane and relative motion between the tectorial membrane and the cilia/microvilli of hair cells, thus stimulating the sensory cells. Dark blue, perilymphatic spaces; light blue, endolymphatic spaces. Arrows indicate movement of ossicles and inner ear fluids. Drawings modified from Bradbury and Vehrencamp (1998) and Ladich (2017).

The ear of all adult tetrapods possesses an external tympanum (see Glossary), a middle ear with auditory ossicles, a perilymphatic labyrinth and auditory end organs devoted solely to hearing. The tympanic membrane enables tetrapods (except cetaceans) to detect sound pressure fluctuations in air and transmit these oscillations via auditory ossicles and the perilymphatic labyrinth to the endolymphatic fluid of the inner ear (Fritzsche, 1992). Amphibious tetrapods such as frogs, turtles and pinnipeds have ears that enable the animals to hear in both media (Hetherington and Lombard, 1982; Christensen-Dalsgaard et al., 2012; Reichmuth et al., 2013).

Frogs and toads lack an outer ear, which is why the tympanum is clearly visible immediately behind the eyes. The middle ear contains a column-like ossicle, the columella (Fig. 5B). This arrangement conducts airborne (and sometimes waterborne) sound pressure changes to the inner ear in adult anurans. Amphibians also have a second sound transmission pathway – the opercular system – to detect signals through the ground (Smotherman and Narins, 2004; Narins et al., 2016). In addition, the amphibian ear is unusual in the number of auditory end organs it contains. All anurans and some salamanders possess three end organs (sacculi, amphibian papilla and basilar papilla), which appear to have acoustic roles (Lewis and Narins, 1999). The sacculi differ from the amphibian and basilar papillae because it is an otolithic end organ (like in other vertebrates) in which calcium carbonate crystals called ‘otoconia’ cover the apical part of the sensory hair cells. The amphibian and basilar papillae have tectorial membranes instead of otoconia (similar to other tetrapods).

The acoustic frequency range is apparently divided among the auditory end organs. The sacculi are thought to detect vibrations up to 100 Hz, whereas the amphibian and basilar papillae respond to higher frequencies (Fay and Megela-Simmons, 1999). In general, amphibian hearing curves (see Glossary) show the highest sensitivity between 600 and 1000 Hz (similar to those of sound pressure-sensitive fishes) and upper frequency limits of 6000 Hz (except for ultrasound-detecting species; Narins et al., 2014).

In birds, the outer ear consists of an external auditory canal (meatus) but lacks the pinna found in mammals (see below). However, owls possess feathery structures of analogous function. Barn owls (*Tyto alba*), for example, have an asymmetric external ear canal that offers the functionality of asymmetric positions of the mammalian pinnae in directional hearing. The middle ear of birds resembles that of amphibians, having a columella (stapes), but the inner ear differs considerably. The avian inner ear has only one sensory epithelium, the cochlea, which serves only acoustical functions (Fig. 5C). The cochlear duct is not coiled like that of mammals, but is bent and consists of a sensory epithelium (basilar membrane). In birds, hair cells are densely spaced, not arranged in rows as in mammals. In addition, discrete types of hair cells (as observed in mammals) are not found. Birds have tall and short hair cells but they are difficult to define (Gleich and Manley, 2000; Gleich et al., 2004; Gleich and Langemann, 2011). From the cochlea’s distal to proximal end, the length of the stereocilia decreases, while their number and width increase; correspondingly, higher frequencies are sensed proximally. Nocturnal auditory specialists, such as the barn owl or the kiwi, deviate from this tonotopic pattern by over-representing areas that correspond to biologically important frequency bands.

Birds can detect frequencies from 100 Hz to 10 kHz, but are most sensitive to frequencies of 1–5 kHz. The barn owl is sensitive to high-frequency sounds exceeding 10 kHz, and it may also be sensitive to rather low frequencies; the homing pigeon *Columba*

*livia* seems to be sensitive to infrasound and can use it for navigation. Songbirds (e.g. sparrows, tits, starlings and crows), a suborder of Passeriformes comprising approximately half of extant bird species, show better detection of higher frequencies than nonpasserines such as chickens (Galliformes), ducks and geese (Anseriformes), doves and pigeons (Columbidae), and hawks (Accipitridae). Consequently, the high-frequency 8 kHz alarm calls of great tits (Paridae) and related songbirds are barely audible to their avian predators. Nonetheless, nocturnal predators such as owls have hearing that is superior to that of all other groups over the entire frequency range. The main energy of avian long-range vocalizations generally falls within the frequency region of their best hearing, in contrast to calls for more intimate communication (Dooling et al., 2000; Gleich and Langemann, 2011).

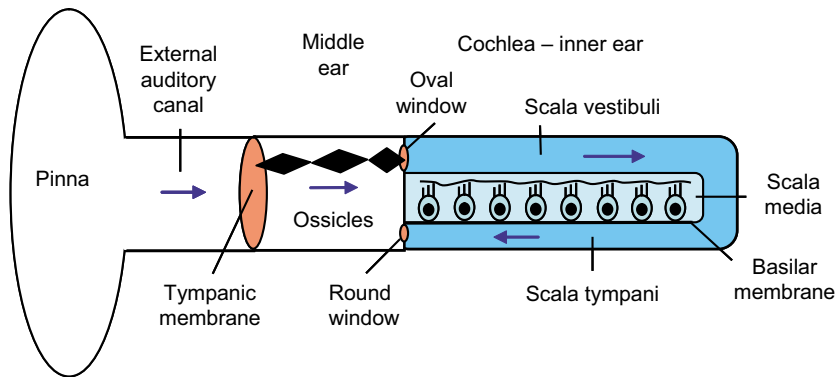
### Terrestrial and aquatic mammals

Mammals differ from all other vertebrate classes in ear morphology and in their audible frequency range, which is significantly broader than that of other vertebrates owing to the ability of most mammals to detect ultrasound (but see Narins et al., 2014). The mammalian outer ear consists of a pinna, which is often moveable and which enhances sound transmission to the inner ear (Fig. 6A). The middle ear bears three auditory ossicles (malleus/hammer, incus/anvil and stapes/stirrup), in contrast to frogs, reptiles and birds. This contributes to the whole system’s sensitivity to higher frequencies. There is an interesting functional analogy between the auditory ossicles in otophysine fish (discussed above) and in higher vertebrates, especially mammals, despite the different phylogenetic origins of these structures. The mammalian inner ear cochlea is longer and narrower than that of birds and is coiled. Mammals have a sensory structure known as the ‘organ of Corti’, which possesses two types of hair cells: one row of inner hair cells and three to five rows of outer hair cells. Only the latter are attached to the tectorial membrane, and they control the sensitivity of inner hair cells (Yost, 1994).

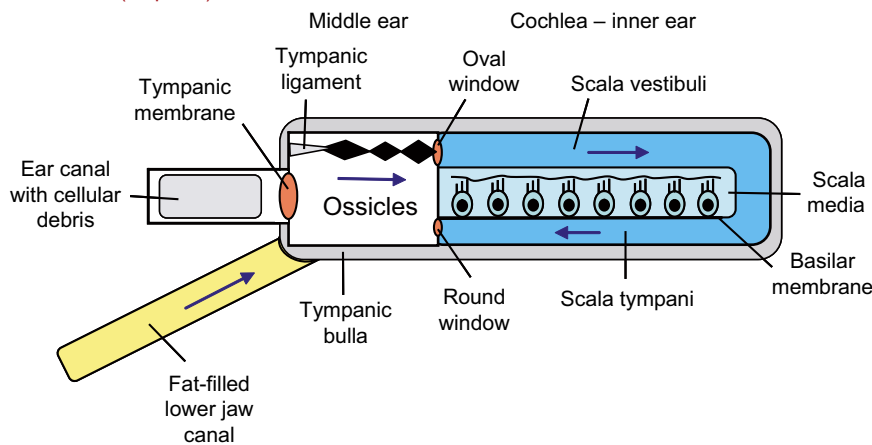
The audible frequency range in mammals is highly diverse (Fay, 1988; Ladich, 2017). Some species, such as the largest terrestrial and aquatic species, are able to detect infrasound. Elephants can detect low-frequency sounds up to a few kilometres away, and mysticetes such as blue or fin whales can hear low-frequency sounds over dozens (perhaps hundreds) of kilometres (Langbauer et al., 1991; Tyack and Clark, 2000). Most mammals, such as cats, horses and rodents, hear ultrasound, either for intraspecific communication or for detecting predators or prey. High-frequency hearing is linked to the predatory lifestyle of bats and dolphins: they need to detect echolocating clicks reflected from obstacles and prey. Accordingly, bats detect sounds up to 130 kHz to hunt moths, and dolphins can detect even higher frequencies (see below) (Fay, 1988; Au and Simmons, 2007).

The cetacean ear differs from that of terrestrial mammals in several ways. The outer ear has neither a pinna nor a functional air-filled auditory canal. The ear canal is narrow, filled with cellular debris and most likely non-functional. Middle and inner ears are encased in a bony structure (the tympanic bulla), which is connected only by cartilage and connective tissue to the skull (Au and Hastings, 2008; Mooney et al., 2012). It is currently assumed that in toothed whales, acoustic energy is conducted through the fatty canal of the lower jaw directly to the tympanic bulla. The malleus is not connected directly to the tympanic membrane, but instead is connected via a ligament to the tympanic bulla (Fig. 6B). It remains unclear how ossicles are acoustically coupled to the bulla. Removal experiments have revealed that the malleus is less important for hearing than the incus and stapes (Ketten, 1997; Au and Hastings,

## A Land mammals



## B Whales (dolphins)



**Fig. 6. Schematic drawing of ears in land mammals and cetaceans.** (A) Most mammals have pinnae and all have three auditory ossicles. The inner ear (cochlea) is coiled in all mammals and consists of three fluid-filled canals. (B) In toothed whales, the external auditory canal is filled with cellular debris and does not conduct sound to the tympanum; both the external auditory canal and the tympanum are non-functional. Instead, sound is transmitted via a fat-filled canal in the lower jaw to the bony tympanic bulla, which encases the middle and inner ear and in some way vibrates the hearing ossicles. Arrows indicate movement of ossicles and inner ear fluids. Drawings modified from Bradbury and Vehrencamp (1998) and Ladich (2017).

2008). The odontocete sound conduction pathway is not applicable to mysticetes because their lower jaw is not connected to the temporal (ear) bones.

The auditory sensitivities of both suborders of whales differ considerably because of their different lifestyles. Physiological and behavioural experiments have shown that toothed whales can hear up to 200 kHz, while no such data exist for baleen whales (Richardson et al., 1995; Au, 2000b). Ketten (1997, 2000) concluded that the ear of baleen whales is adapted to low-frequency hearing, based on comparative cochlear morphometry.

### Comparison between aquatic and terrestrial hearing

The main difference between hearing in air and water relates to the mismatch in acoustic impedance (see Glossary) between the sound receptor and the medium. In air, sound pressure fluctuations directly oscillate a thin membrane (tympanum) on the outside of the body, whereas in water, such a membrane could not pick up sound directly because the animal moves in phase with the medium (see above). On land, sound is transmitted from this tympanum to the auditory ossicles, and from the perilymphatic labyrinth to the auditory end organs of the inner ear. Fishes, cetaceans and amphibious tetrapods have to rely on different pathways for conducting the sound underwater to the inner ear (Hetherington and Lombard, 1982).

Interestingly, numerous fishes have evolved the ‘tetrapod way’ of sound pressure detection via a vibrating ‘tympanic’ membrane within the body (e.g. anterior wall of swim bladder) and even auditory ossicles (Chardon and Vandewalle, 1997; Clack and Allin, 2004). In such cases, sound pressure detection has widened their

detectable frequency range, which is thus comparable to that of frogs (Fay and Megela-Simmons, 1999; Ladich and Schulz-Mirbach, 2016).

### Life histories, ecology and communication in aquatic, amphibious and terrestrial vertebrates

Here, we wish to address the question of whether the differences between the two media discussed above are reflected in the role that acoustic communication plays in the life history of terrestrial versus aquatic animals. This and other aspects are discussed below.

### Aquatic vertebrates

Fully aquatic vertebrates, namely, fishes and cetaceans, differ considerably in the way they generate and detect sounds. The difference between fishes and cetaceans can be explained phylogenetically. Fishes had no terrestrial ancestors, in contrast to whales, which evolved from terrestrial mammals and had to adapt the mammalian acoustic mechanisms for underwater communication. This difference between the two main groups of aquatic vertebrates raises several questions. Do these two taxa resemble each other in terms of their acoustical behaviour because of the physical constraints imposed by underwater sound propagation (see Introduction) on both groups? Are there similarities among aquatic vertebrates that separate them from terrestrial ones in terms of acoustic communication? Do closely related amphibian taxa that communicate as adults acoustically entirely in water (pipid frogs) or on land follow these rules? Let us initially focus on the first question.



The life histories of fishes and cetaceans differ in numerous ways. Fishes comprise approximately half of all vertebrate species (>30,000). They cover a large body size range, from a few centimetres up to several metres, which enables them to inhabit a large diversity of aquatic habitats, from shallow creeks down to the deep sea. In contrast, cetaceans comprise fewer than 100 species, cover a size range from 1 to 30 m and mainly inhabit the open ocean, with a few species living in rivers. These differences in size, species numbers, habitat use, the necessity to breathe air at the water surface and their phylogeny result in major differences in behaviour and, consequently, acoustic communication between these two groups.

First, note that acoustic communication is not a unique characteristic of all fish species: numerous taxa such as cartilaginous fishes and many bony fishes do not produce acoustic signals. For instance, particular sound-generating mechanisms may evolve in a single genus of a family only. The tendon-plucking mechanism is known only in the genus *Trichopsis* (croaking gouramis, three species) but not in any other genus within the family Osphronemidae or fishes in general (Kratovich, 1985). Other mechanisms, such as the intrinsic drumming muscles, are (most likely) a characteristic of the entire order Batrachoidiformes (toadfishes). Besides acoustic and visual signals, fish can also communicate via chemical (pheromones), electric organ discharge (see Glossary) and vibrational (lateral line) signals, channels that are either not present or unimportant (pheromones) in cetaceans (Kremers et al., 2016). However, cetaceans, especially toothed whales, live in permanent and highly complex social systems. They very much rely on acoustic signals that can cover large distances, and some possess an impressive repertoire of vocalizations, that may aid in group coherence and group coordination. Beluga whales (sea canaries) and killer whales are known to produce dozens of different call types, whose functional significance is widely unknown. Ford (1989) and others argue that distinctive repertoires of calls have potential recognition functions, including individual, group and regional identification. Beyond large numbers of call types, cetaceans may produce complex vocal displays, with the songs of humpback whales, *Megaptera novaeangliae*, being the most spectacular, rivalling those of songbirds (Payne and McVay, 1971).

It has often been argued that, because of the advantages of sound propagation in water (see Introduction), such as low absorption and high sound velocity, acoustic signals should be the preferred means of animal communication underwater, where turbidity limits visual communication. But, do all aquatic vertebrates exploit this advantage similarly? And does their calling behaviour therefore contrast with that of terrestrial taxa?

The acoustic behaviour of the vocal fish species and cetaceans differs considerably. Vocal fish species are mainly substrate breeders in which males defend their nests vigorously against intruders and try to attract and court females acoustically (Ladich, 2014). Behavioural observations reveal that fish typically start to produce sounds after an opponent or mate has been detected visually (Amorim, 2006; Ladich and Myrberg, 2006; Myrberg and Lugli, 2006). Fishes may communicate over distances of just a few centimetres up to approximately 10 m when advertising nest sites (Myrberg et al., 1986). Potential communication distances of 30–100 m have been claimed for sciaenids (drums) but there is no experimental evidence (Locascio and Mann, 2011; Amorim et al., 2015). Fish vocalizations are typically not substitutes for visual signals, but serve to emphasize aggressive or courtship displays at short distances. This may explain why many shallow-water fish species (water depth ~1–2 m or less) paradoxically produce low-frequency sounds, although low frequencies do not propagate

beyond a few metres in shallow water (cut-off frequency phenomenon; see Introduction) (Fine and Lenhardt, 1983; Bass and Clark, 2003; Lugli, 2015).

In contrast to fish, dolphins and whales are not territorial but rather inhabit open ocean waters (coastal or pelagic), in which sound can travel hundreds of metres or even kilometres (Edds-Walton, 1997; Bass and Clark, 2003). Behavioural responses to sounds and thus communication distances of up to 10 km have been found in baleen whales during playback experiments (Clark and Clark, 1980; Mobley et al., 1988). The high-frequency echolocation system of dolphins, in contrast, appears to be limited to ranges of approximately 100 m (Tyack and Clark, 2000). Cetaceans, particularly baleen whales, therefore take advantage of the sound propagation characteristics in water and extend their communication distances far beyond those of visual signals and beyond acoustic communication distances on land.

Frogs may be the ideal group of vertebrates to demonstrate differences in sound communication owing to the different acoustic properties of sound propagation in air and water (Table 1). Completely aquatic pipid frogs communicate acoustically in shallow ponds using broadband clicks with main energies from 1 to 5 kHz. This seems to be an adaptation to shallow-water habitats, which facilitate the propagation of high-frequency sounds (see Introduction). Yager (1992b), however, pointed out that secondarily aquatic anurans largely retained the terrestrial anuran communication pattern. The frequency band used is not shifted upward, and coding of species specificity using temporal patterns has also been documented in tree frogs and toads. The largest difference occurs in sound generation, because pipid frogs do not vibrate membranes such as vocal folds (see above).

Even more interesting are those species floating and vocalizing at the water surface in shallow ponds (1–2 m) because, in these species, sound propagation can be studied in air and water simultaneously. Boatright-Horowitz et al. (1999) investigated the transmission of natural advertisement calls of bullfrogs chorusing at the air–water interface and showed severe attenuation of low frequencies and loss of spectral information underwater at meaningful distances (8–10 m). In contrast, the spectral shape and temporal patterns of calls are conserved at biologically relevant distances in air. Thus, bullfrog calls are well adapted for acoustic communication above the water surface, and it remains to be shown that the ‘aquatic’ acoustic energy is of any functional significance.

### Terrestrial vertebrates

Birds communicate over distances and with frequencies that are susceptible to environmental noise, atmospheric conditions, vegetation clutter and ground attenuation. The acoustic adaptation hypothesis posits that birds structure their long-distance signals to maximize their transmission fidelity (Morton, 1975). A meta-analysis supported this claim, but found little evidence for habitat-related effects (Boncoraglio and Saino, 2007). Noise generated by flowing water or urban traffic usually peaks at low frequencies, whereas insects produce high-frequency sounds that potentially disturb birds. The latter, however, seems to have a minor effect on bird song, whereas the former has profound influences (Wiley, 2015). Birds that sing in such noisy environments increase the pitch, and sing louder and slower (Slabbekoorn, 2013; Nemeth et al., 2013; Bueno-Enciso et al., 2015). Singing at a low pace and with longer syllables may also be a response to the reverberations that occur in urban environments with large buildings (Warren et al., 2006). In natural settings, reverberations could be exploited for enhanced sound transmission (Nemeth et al., 2006).



Signals that should carry far have frequency characteristics that permit, for instance, broadcasting in forests within a frequency band suitable for this kind of habitat. Sender positions high above potential receivers may enhance the broadcasting range, particularly in open habitats. Alternatively, birds may position themselves at high song posts to improve the reception of signals of competitors rather than enhance their own broadcasting (Mathevon et al., 2005).

To avoid interspecific and intraspecific eavesdroppers, avian signalers use low-amplitude vocalizations that may also be in a frequency band that does not enable long-distance transmission. This occurs during close-proximity interactions at the nest or for copulation, and also when serious fighting is underway or imminent (Winkler, 2001; Reek and Osiejuk, 2011). This type of short-distance low-amplitude aggressive signal has recently come into focus in research on the soft-song phenomenon in passerine birds (Reichard and Anderson, 2015) and in studies on mammalian communication (Gustison and Townsend, 2015).

Mammal (terrestrial and aquatic) vocalizations cover the largest frequency range among all vertebrates. They may communicate using infrasound as well as ultrasonic frequencies. The largest aquatic and terrestrial species (baleen whales and elephants) are able to use infrasound for long-distance communication, whereas the highest ultrasonic sounds are mainly used for echolocation to hunt prey and navigate. However, ultrasonic vocalizations are not limited to biosonar; they are also used for intraspecific acoustic communication in terrestrial mammals such as rodents and bats (Brudzynski, 2009; Musolf et al., 2010; Voigt-Heucke et al., 2010).

To communicate over long distances, animals can use loud low-frequency sounds down to infrasound. Low frequencies are an acoustic adaptation to increase propagation over distances of several hundred metres up to several kilometres. This may serve in creating spacing between groups or individuals (Clutton-Brock and Albon, 1979; Mitani and Stuht, 1998; McComb and Reby, 2009). In terrestrial mammals, low-frequency long-distance signalling occurs, among others, in elephants, nonhuman primates (e.g. howler monkeys), deer and wolves. A negative correlation seems to exist between call frequency and the distance over which mammals communicate. Mitani and Stuht (1998) demonstrated a significant negative relationship between call frequency (250–9500 Hz) and home range size (0.3–148 ha) among 29 species of nonhuman primates. Elephants use much lower infrasound frequencies and communicate at longer distances. They respond to recordings of conspecifics over distances up to 2 km by vocalizing, spreading the ears, orienting towards the sound source and finally walking towards the loudspeaker (Langbauer et al., 1991; Garstang, 2004).

#### Comparison between aquatic and terrestrial vertebrates

Why do fishes not communicate in open water similarly to cetaceans over large distances when producing low-frequency sounds? There may be several reasons for this difference between taxa. Vocal fishes are, on average, smaller than cetaceans and may not be able to produce sound loud and long enough to be detectable at distances beyond 10 m. Their acoustic communication is generally associated with reproductive behaviour, which is often linked to territoriality and parental care. This is mostly performed by males for a limited period of a few days or, as in the majority of species, does not exist at all (it should be noted that knowledge on pelagic fish is lacking). In contrast, cetaceans are surface-bound and females show parental care for months (baleen whales) or even years (dolphins) (Mann et al., 2000). Family members may stay together for years or even decades, and acoustic signalling helps in maintaining their social organization

In contrast to the great differences in parental care between aquatic groups, the terrestrial groups (birds and mammals) often display well-developed biparental (birds) or female (most mammals) care that involves communication which, in many cases, is acoustic. The rich acoustic communication behaviour of birds and mammals reflects their highly developed cognitive and social capabilities. From an evolutionary point of view, both groups' sound production exploits the permanent flow of air associated with breathing. Together with the specific advantages of sound propagation in air, this opened the path for complex communication systems. The communication system of cetaceans can be understood based on their terrestrial ancestry and owing to their predominantly pelagic lifestyle, which allowed them to exploit the benefits of sound propagation in a dense, obstacle-free medium that provides fast and almost lossless signal transmission (Table 1).

#### Conclusions and perspectives

Comparing acoustic communication within and between aquatic and terrestrial vertebrates reveals that there is no 'aquatic way' of sound communication, as compared with a more uniform terrestrial one. While frogs, birds and land mammals utilize similar mechanisms for sound production, numerous fishes and cetaceans evolved sonic organs adapted to the higher acoustic impedance of water. Fishes evolved several mechanisms unrelated to breathing, whereas the cetaceans have a modified terrestrial breathing apparatus. Similarly, both fishes and cetaceans possess different mechanisms to transmit underwater sound to their auditory end organs (otolith in fishes versus lower jaws in dolphins), in contrast to a more uniform pattern in terrestrial tetrapods. These differences, together with differences in body size, social organisation and life history (often substrate breeding versus pelagic), seem to explain the fact that complex acoustic communication over large distances evolved in all cetaceans in contrast to fishes. Below, we consider some perspectives on future research questions on acoustic communication in different species.

Whereas the diversity of sonic and hearing mechanisms in fishes is well described, a major gap remains in our knowledge on the functional significance of sounds and on communication distances in fish (either those advertising nest sites acoustically or pelagic fish). This is due to a lack of appropriate equipment for underwater playback experiments in the field or the absence of long-distance communication signals in fish. This contrasts with the numerous field playback studies in frogs, birds and even mammals. Thus, any progress in this field will largely depend on the equipment that will be developed for these purposes.

In ornithology, the study of vocalizations remains a central pursuit, and it has produced insights that extend far beyond this taxon. Arguably, in no other group of vertebrates are we in a better position to integrate knowledge on sound production, vocal communication in its diverse behavioural and ecological aspects, and the underlying neuronal mechanisms. Bird studies are heavily biased towards the song of passerines and some functionally similar utterances in other groups, such as doves. However, there is a high diversity of other acoustic signals (usually termed 'calls') that arguably comprise most of the routine communication from early life stages on. Calls differ in behavioural, neurobiological and adaptive aspects from songs. Woodpeckers, for instance, have a repertoire of more than a dozen different calls, and many songbirds, too, command a diverse array of vocal signals. With a few exceptions, mainly begging and alarm calls, these signals have not caught the attention of behavioural ecologists or neurobiologists.

In cetaceans, further studies on sound-producing and -detecting mechanisms are necessary to support or perhaps falsify many hypotheses in this field of research. For example, it remains unknown whether baleen whales produce sounds with their larynx. Moreover, the hearing organs in both baleen and toothed whales need to be investigated in more detail. Like in fish, the functional significance of the large number of sound types in many species remains to be investigated, along with the behaviourally significant communication distances. Thus, there are many aspects of acoustic communication that remain to be investigated in both terrestrial and aquatic species, which we hope will provide many interesting advances in the future.

#### Acknowledgements

We thank three anonymous reviewers for numerous comments which improved the manuscript. Furthermore, we thank Michael Stachowitsch for scientific English proofreading an earlier version of the manuscript.

#### Competing interests

The authors declare no competing or financial interests.

#### Funding

This research received no specific grant from any funding agency in the public, commercial or not-for-profit sectors.

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