

Review

Animal Calling Behaviours and What This Can Tell Us about the Effects of Changing Soundscapes

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Abstract: The behavioural, physiological, and energetic repercussions for wildlife that result from changes in their soundscapes are increasingly being realized. To understand the effects of changing acoustic landscapes, we first must establish the importance of the acoustic sense for species to transfer information between the environment, con- and heterospecifics, and a receiver, and the functional role of calling in behaviours such as foraging, navigation, mate attraction, and weaning. This review begins with a discussion of the use of calling and the acquisition of the vocal repertoire, before providing examples from multiple taxa on the functional applications of signals and communication. The acoustic sensory mode adds to, if not being inherent in, many critical life history stages over a range of species. The potential effects on an animal resulting from a change in its perceived soundscape and disturbance on its acoustics use is outlined. This can then be used to consider the implications of an altered acoustic niche or active space in the success and survival of an individual or species. Furthermore, we discuss briefly metrics that could be used to understand the implications of these changes, or could be used to guide mitigation action to lessen the impact.

Keywords: acoustic ecology; soundscape; vocal repertoire; call acquisition; active space; learning; culture; niche space definitions



Citation: Burnham, R. Animal Calling Behaviours and What This Can Tell Us about the Effects of Changing Soundscapes. *Acoustics* **2023**, *5*, 631–652. <https://doi.org/10.3390/acoustics5030039>

Academic Editor: Jian Kang

Received: 6 March 2023

Revised: 27 April 2023

Accepted: 28 April 2023

Published: 4 July 2023



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1. The Use of Sound and the Acoustic Modality

The acoustic sense is used by many taxa in a wide range of social and behavioural contexts to send and receive information. The soundscape is the acoustic environment that an individual perceives and responds to. Acoustic cues from this sonic landscape aid navigation, prey detection and capture, and conspecific identification and localization. They also help to identify threats or the intrusion of another species, and are used in territory defense. The acoustic sense can be used to maintain social hierarchies and group cohesion, and aid in mate selection. Sound production shows similarity across taxa; it can engage the larynx to manipulate air flow, or use muscle-driven vibrations or drumming [1,2]. Signal modification is invoked via the vocal tract, tongue, beak, trunk, or alternative sound production spaces (e.g., [3,4]). The morphology of the animal can dictate the energy level of the sound, whereby larger individuals are typically thought to invoke longer, deeper, or louder signals. Indeed, an inverse relationship between the animal's size and the peak frequency of the calls in their repertoire has been established for many taxa (see [5–7]). These morphological adaptations can, therefore, also influence mating signals, and give an indication of fitness or the prominence of a trait to potential mates (e.g., the morphological adaptation hypothesis (MAH) in birds [8,9] and insects [10]). Vocalizations and calling behaviours can also respond to changes in the acoustic environment. Altered ambient noise levels from natural or anthropogenic noise, or altered propagating conditions, can initiate adaptations to how, when, or where an individual calls. The process of sound reception is adapted to each species, and reflects both the medium in which they receive sound and the frequencies they are most sensitive to.

An animal's vocal repertoire is adapted to maximize conspecific communication, or the exchange of information through acoustic means with others of its own species, sub-species,

or group. An individual may utilize a spectrum of calls to retain this contact within a group or between individuals. Calls can be modified by the social, behavioural, or environmental context of the caller, as well as indicating an individual's group membership, internal state, or the setting under which the call is being made. Courtship calls or song can, for example, play a role in species recognition and help define the acoustic niche definition of a group, predominantly arising from the male vocalizations (see for e.g., [11]). The call structure and diversity of the repertoire could also be an indicator of the size and social structuring of the population. The linguistic niche hypothesis [12] suggests that language complexity in humans reflects the socio-demographic variables of the population or sub-group. It proposes that the complexity of the inflections and lexical constructs used are a reflection of population size [12]. This hypothesis could also possibly have similar applicability to non-human animal communications.

Acoustic signal use can also be informed by the environment that the sounds are emitted into. Pure tone signals, with narrow frequency bandwidths, show greater reverberation. This allows longer, louder transmission—for example, by birds in dense forests [4,13,14]. This differs from frequency-modulated notes or tones that rapidly sweep through a range of frequencies—for instance, in bats' probing 'chirps', which return as a single pulse echo after a time delay [1]. This is in accordance with the Acoustic Adaptation Hypothesis (AAH), whereby the acoustic properties of the environment in which the calls are produced influence the use of call types and the structure of these calls. Signals are selected to maximize efficacy in calling and minimize degradation of the call content as it is transmitted (see for e.g., the meta-analysis by [15] and review in [16]). This hypothesis suggests that species in environments where call propagation might be more dampened or obstructed, or habitats described as 'closed', use calls that differ in their frequency extents and peak frequency than those in more 'open' areas. Typically, calls in closed habitats are adapted for longer-range propagation [17,18]. Similar to this hypothesis, the sensory drive hypothesis also suggests how perceived differences in the acoustic environment, or the individual's soundscape, can change their signaling traits and behaviours [19,20]. This hypothesis furthers the AAH by suggesting that calling behaviours are adapted to overcome a distortion or a source of acoustic masking. However, the strength of the relationship between the habitat or soundscape structure and call structure may be obscured by the influence of morphological, physiological, or social variables acting on the caller, also shaping the signals used (e.g., [21] and references therein).

Acoustic environments are dynamic; individuals may use compensatory responses in signal production to overcome noise additions to the ambient sound field. This adaptation in calling in response to the perceived soundscape is in accordance with the Lombard Effect [22], which is typically described as an involuntary increase in vocal amplitude. Lombard-like responses have also been seen to alter the frequency, duration, and repetition rate of calls (see for e.g., [23]), but animal responses to changing acoustic environments are not limited to these adaptations. The Lombard Effect is physiological [24]; changes in humans' speech due to the Lombard Effect have been noted to differ from 'loud speech', when a person simply speaks louder, but the mechanisms in non-human animal taxa are mostly unknown [25]. To understand the impact of noise on wildlife, a description of vocal repertoire acquisition, functional use, and complexity is presented here. There is a provisional discussion of the implications of noise. However, this review is not intended to be a detailed review of animals' reactions to noise, nor is it an in-depth look at recent bio- or eco-acoustic studies that add to the understanding of behavioural changes in calling as acoustic environments are modified. It is a more general presentation of our current knowledge of animals' acoustic use, and the reliance on this modality by some taxa. Suggestions of areas for further analysis—for example, in the level of disturbance or cost to animals as a result of altered soundscapes—will be made. This is with the aim to better understand how changes in noise levels and the transmission of sound might initiate behavioural reactions and change call repertoires. The hope is to highlight the integral nature of acoustics use to many species, drawing on specific examples. These examples

are not focused on a particular taxa or group and are not fully exhaustive, but are purely used to illustrate where the concept or behaviour has been observed. Much of this type of research has been conducted on mammal or bird species, but, where possible, exemplar cases are given from other taxa. First, aspects of repertoire acquisition including social learning are considered. This is followed by an examination of the functional facets of acoustic signaling, including its social, behavioural, and cultural aspects, and finishing with a discussion of the potential impacts of altered soundscapes.

2. Acoustic Information Exchange

Although, for many species, call structure and application may seem simple, there can be great complexity in the call parameters and use. Vocal behaviours have innate components, but have aspects that are shaped by the experience of the individual. Repertoires are constrained by phylogeny and morphology (MAH), but call use is reinforced through learning and social interaction. Evidence of this social strengthening of call use and repertoire development arises from individuals that have been removed from their mothers or natal group, whereby call types appear present initially and then are lost (e.g., from gray whales (*Eschrichtius robustus*) [26]). Periods of ‘babbling’ have been noted in several species across taxa. This occurs during an individual’s first few months of life, when vocal learning occurs, and the adult vocalizations are being acquired (e.g., [27–30]). Signal units within calls, and their sequence, form, and syntax, may also be a product of learning [31,32]. Characteristics such as frequency sweeps, the onset of calling, and temporal variations in call pattern, amplitude, frequency, length, and repetition are rehearsed. This period of ‘babbling’ may also be marked by the use of adaptive mother–calf calls (‘motherese’ in gray whales [33,34] and bats [35]) as learning occurs.

Species with the capacity for vocal learning acquire their acoustic repertoire by imitation and mimicry [36], with phases of practice and refinement [37–41]. Species capable of this type of call acquisition include songbirds, parrots, hummingbirds, bats, elephants, pinnipeds, and cetaceans [36]. Vocal learning is the acquiring of calls and vocal patterns via a social channel, where a conspecific teacher monitors progress and provides feedback. Following this socially directed learning, the behaviours should persist in the absence of the demonstrator or teacher [42]. Learning could be vertical, whereby the information flows from a parent or more experienced elder to the individual (downwards transmission). It can also be horizontal, which represents peer-directed social learning, which occurs between individuals in the same population group or generation [43]. This can pass on group-specific social traditions in calling as well as the repertoire itself. Learning occurs predominantly during the weaning phase, especially for species with more limited parental investment, whereby the young acquire adult calls and stimulate vocal development. However, it can continue throughout the individual’s lifetime. It can aid the spread of novel behaviours in a population or group (e.g., humpback whales (*Megaptera novaeangliae*) [44]). Imitation can help with the recognition of individuals and reinforces group cohesion. This then aids in the identification and sharing of resources, mate finding, or within-group recognition. This is especially beneficial in the adaptation to elevated ambient noise [31] or increasing the complexity of sounds and signals used by a group [45].

Deciphering the information coded into calls has been a central area for study in animal communication [46–48]. Vocalizations can relay information on the internal and external environment of the caller. The stability of the call structures and their use, and the way in which notes can be formed into patterns, forms the basis of categorizing each species’ repertoire by function. This can begin to be interpreted from the temporal aspects of calling—for example, the season—as well as the social context or behavioural, emotional, or physiological state of the signaler when calling [49].

Signalling and Communicating

In animal communications, a sender produces a signal to be perceived and understood, and elicit a response in a receiver [50]. If the signal is an auto-communication [51],

such as echolocation in bats and toothed whales, or electrolocation by some fish, it is the interpretation of the echo of the caller's own signal that carries the information.

Signals project information, without expectation of an acoustic response, although the information conveyed could influence the behaviour of the receiver. Signals also share information about the presence of the signaler or their state of arousal, motivation, or emotion (e.g., [52–54]), or could be a display of physical characteristics (e.g., [55,56]). They can convey information about age, group membership, individuality, and fitness (e.g., elephants [3]; bats [57,58]), or the context in which the call is being made. It may be possible, for example, for the receiver to determine whether the caller is in an antagonistic or threatening situation, alone or isolated, or feeling playful/affiliative or aggressive (e.g., mammals [59–63]; birds [64,65]). In addition, the ordering and emphasis of the call components may represent the urgency of the response or priority of actions needed from the receivers. This might range from a warning from a signaler to listeners (e.g., Richardson's ground squirrel (*Spermophilus richardsonii*) [66]) to mobbing behaviours (e.g., Carolina chickadees (*Poecile carolinensis*) [67]). Affiliative calls could be used to aggregate conspecifics or direct social behaviours, such as flight calls in migrating birds (e.g., [68]). They could also direct conspecifics to prey resources (e.g., [69]). These signals may be used to propagate information over great distances, and are structured to be minimally influenced or degraded by the acoustic environment [48].

Communicative calls come with the expectation of an acoustic response from the receiver, as well as possibly modifying behaviour. Calling has been described as 'maintaining the social life' of birds [70], with this likely to also be true for other taxa. If vocalizations are part of an interactive exchange or chorus, it is rare for calls to be unanswered [71–73]. The initial signaler elicits a response from a receiver, with the context of the sender and receiver, and the interaction between the two, being core to the communication. Modification to calls, such as the amplitude and speed, may be made based on the intended target and their distance from the sender (e.g., zebra finches (*Taeniopygia guttata*) [70,74]). Vocal communication takes the form of a back-and-forth, give-and-take exchange of information between conspecifics through acoustic means, even from early infancy. Contact calls between conspecifics combine patterns of frequency modulations, rhythmic call series, and amplitude parameters to confirm species, group, or colony membership or encode individual identity [74–76].

3. Functional Uses of Calling

The behavioural significance and function of a call can be determined by observing interactions with conspecifics during and following the vocalizations [77], and may take into account the geographic or social context, correlated with the call's structural syntax. Experimental manipulation of the acoustic environment and playback studies have also been used to estimate the information content of animal calls. Moreover, temporal patterning and periodicity in calling may indicate call application—for example, the seasonal feeding–breeding dichotomy in calling noted for some baleen whale species (e.g., [78–81]).

3.1. Group Membership and Definition

Acoustic projections confirm species, group, or colony membership [74–76]. The ability to identify a caller as a herd or flock-mate can limit time and energy that would be used for defense. Furthermore, the recognition of a caller as a male or female helps the courting process. Species markers may be inherent to the frequencies in which the calls are made, or the modulation over a frequency range over the duration of the call. Krause [82] suggested that each species has their own sonic niche, also described as their acoustic channel, defined by the range of frequencies that their repertoire covers. This is the acoustic niche hypothesis (ANH). Call traits such as absolute pitch and pitch ratio are also consistent within and among species (e.g., birds [83–88]). Birds are able to use call features and syntax to distinguish calls of conspecifics and intruder species, which dictates their response (e.g., shearwaters *Procellariidae*, [49,89,90] songbirds [46,49,91–94]). Flock- or group-specific traits

in calls and call patterns have also been described, with the structure and inter-note interval distinguishing groups within a species (e.g., killer whales (*Orcinus orca*) [95–98]; sperm whales (*Physeter macrocephalus*) [99,100]). Group/herd calls show stability over time, but the vocal signatures may be modified for each interaction [101,102]. The species recognition hypothesis suggests that, although the influences of context and environment might alter calls, closely related species would show greater divergence in their call or song structure than those species separated geographically [8].

It is during the first few months of life that the young acquire species-specific calls [86] and signature calls or whistles that confirm the individual's identity. These calls reflect group membership, lineage, or social affiliation (e.g., [103,104]). Bloomfield et al. [86] suggest that the discrimination of individuals is through a 'constellation of features' of calls, with individuality in calling recognized for many mammal species [105–109], including bats (e.g., [102,110,111]); primates (e.g., [112–118]); rodents (e.g., [119,120]); carnivores (e.g., [121–128]); proboscideans (e.g., [129]); perissodactyls (e.g., [130–132]); artiodactyls (e.g., [133–135]); and pinnipeds (e.g., [136]). Sixty years of research have been dedicated to describing signature whistles in dolphin species [137]. This learnt referential call type has been documented in common dolphins (*Delphinus delphis*) [138], Atlantic spotted dolphins (*Stenella frontalis*) [139], Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) [140], and Indo-Pacific humpback dolphins (*Sousa chinensis*) [141]. These calls are used by conspecifics to identify the caller [138]. Individual identification through acoustic means is especially important in habitats where the caller's identity may be obscured visually—for example, when individuals are out of view or remote to each other and their identity may be hidden by aspects of the environment (e.g., trees and foliage for songbirds, or turbid water for river dolphins) or distance. They also demonstrate the complexity and nuanced nature of call use in animals [137]. Signature calls can comprise a high proportion of the calls used by an individual and, once developed in the early stages of life, are stable throughout the individual's lifetime [142].

It was Darwin [143] who first suggested a link between communication and complexity in vocal repertoires with the social structure and dynamics of a species. Studies in birds (e.g., chickadees (*Poecile* spp.) [144,145]) and rodents [146] have confirmed this hypothesis. Hierarchical classification of individuals can be established from determining an individual's identity, and establishing if they represent an opponent [86]. Songbirds have been seen to type match their song or call repertoire as part of a threat display or an aggressive response to the close approach of a neighbour, as well as a means to set boundaries [147,148]. Similar displays to confer territory and hierarchy have been observed for bats at roosting sites (e.g., [149]); between alpha male hippopotami (*Hippopotamus amphibius*), (e.g., [150]); in ring-tail lemurs (*Lemur catta*) competing for rank [151], and in frogs to maintain spacing between competing conspecifics (e.g., [152–155]). Acoustic projections can be made to threaten or intimidate. Examples here include far-reaching seismic ground transmissions of mock charges and trunk banging by elephants [156], foot thumping in kangaroos [157], and body slamming in seals [158]. Vocalizations and song projections have been used by baleen whales to establish male-based hierarchies and territorial spacing [159–162], but no aggressive components of these call types have been noted. Calling may also be a means to protect others during disputes of territory—for example, to guard pinniped harems (e.g., [163–165]), or as mediation for calling site fights in frogs (e.g., [166,167]).

3.2. Contact Calling

Contact calls retain group cohesion, and are defined as calls between separated conspecifics that result in an approach or acoustic interaction. Contact calling is also a mechanism used during migration/travelling to maintain herd cohesion (e.g., [168–170]). Social linkages and the maintenance of contact between individuals with means to identify the caller and its group affiliation have been noted in sperm whales and their use of overlapping, duet-like sequences of coda calls [100,171] and the whistles of dolphins [142,172]. Contact calls to facilitate group aggregation and reunion have been noted in walrus

(e.g., [101]); bats (e.g., [173–175]), and elephants (e.g., [176–179]). Group or pack calls described as ‘rallying calls’ have been noted for primates, wolves, hyenas, coyotes, and lions [180]. Rumbles thought to represent a ‘let’s go’ rallying call in elephants [177], and trill calls in white-faced capuchin (*Cebus capucinus*), have been associated with the initiation and reinforcement of movement [181]. Calls aiding group cohesion and the transference of information to guide navigation when visual cues are obscured have been described in baboons (*Papio* spp.), who use ‘bark’ calls when moving through thick forests [182], and in migrating cetaceans and their use of low-frequency ‘moans’ (e.g., in gray whales [170,183]).

Calling to facilitate the reunion of a mother with her offspring represents a special case in contact calling. Here, individual recognition also prevents misdirected parental care. Typically, the vocal structures are more aligned, with calls between mother and young showing more similarity in their parameters than those directed to other group members. These calls can develop in the first few hours to days of life. For instance, vocalizations between lambs and kids and their mothers are almost acoustically indistinguishable [184–187]. Long-distance call recognition has been seen in seal species to aid reunion [124], and the unique calls used by penguins to reunite with their chicks and mates [168,187–189]. Lingle and Riede [189] suggest that stress calls in young have similarities in attributes and structure across taxa. Calls emitted following separation, termed ‘isolation calls’, prompt reunion, with comforting ‘caregiver calls’ also used by primates (e.g., [190–192]), for example. The young also model their calls on sounds they hear, including their mothers’ vocalizations. Moreover, the use of a ‘motherese’, or a set of calls used only between mothers and their young, has been noted in some species, preceding and perhaps guiding the development of the adult repertoire of calls (e.g., bowhead whales (*Balaena mysticetus*) [168]; gray whales [34,183]).

3.3. Alarm Signalling

Alarm calls may be used to indicate danger or territorial conflict. The type, level, and immediacy of the threat can be inherent to the call used (e.g., bird species [116,193–195]). The alarm vocalizations are designed to elicit and manipulate a listener’s attention and response to the threat by affecting their neural, sensory, and learning systems [194–198]. The basic alarm call structure is designed to arouse conspecifics and activate a change in behaviour. The production of these alarm calls is more likely when animals are in proximity to conspecifics rather than alone, and if the company is kin or preferred companions [199].

Species with multiple predators, and those that employ several predator-specific defense strategies, may use differentiated alarm calls to elicit the most appropriate response in the receiver. Alarm calls may vary based on the predator and the direction of the attack—for example, if the threat was from the ground or the air (e.g., in primates [198–206]). Signals may be paired or altered to change the specificity of the alarm call (e.g., pairing and adding suffixes in Campbell’s monkeys (*Cercopithecus campbelli*) [200,201]).

3.4. Foraging

A number of bird and mammal species vocalize to locate and capture prey [202–208]. Bats, for example, adjust their echolocation call to target prey. The signals show characteristic changes in the call time–frequency structure as they progress through the search, to the approach and terminal (buzz) phases, with projections becoming increasingly repetitious and shorter as the hunt progresses [209]. A similar mechanism is found in odontocetes, whereby the returning echo also determines features such as the size and density of the prey [210–213]. Foraging calls may also synchronize prey capture by conspecifics (e.g., humpback whale ‘feeding cries’ [1,213,214], or prey sharing, e.g., killer whales [215,216]).

Social transmission of specialization in prey capture and handling has been noted in several species of primates, rodents, mustelids, birds, and cetaceans, and is reinforced through vocalizations. Primate calls, for example, are thought to be a physiological response triggered by finding a desirable food item [217–219], and may also express the caller’s personal food preference (e.g., ‘rough grunts’ of chimpanzees (*Pan troglodytes*) [206]). Calls

can also carry information on the food's quality or quantity [220–225], and may encourage the approach of conspecifics to the caller to share (e.g., spider monkeys (*Ateles* spp.) [226]).

3.5. Acoustic Signaling for Wayfinding and Navigation

Sonically derived impressions of the surrounding environment can be formulated as a result of the passive reception of signals from conspecifics or cues from environmental features. Fish, for example, use a form of acoustic orientation, relying on sonic information received from biotic or abiotic sources [4]. Water turbulence, wind-driven waves and surf noise, geothermal noise, the diversity of marine life present, bathymetry, and the seafloor and shoreline composition create unique, location-based sound fields [82]. Wladichuk et al. [225] suggest, for example, that gray whales utilize these sound additions for navigational cues during migration, with a similar suggestion also made for humpback whales [226]. Conversely, bats actively use echolocation for navigation, localization, and identification in complete darkness. They dynamically control the direction, timing, and frequency of their 'biosonar' projections with respect to objects in the environment and the task at hand [149]. Similarly, returns from low-frequency infrasonic calls are used by baleen whales during migration or travel under ice [227–237], complemented by frequency-modulated and patterned counter-calling to maintain group unity (e.g., fin (*Balaenoptera physalus*) and blue whales (*Balaenoptera musculus*) [233,236,238]; right whales (*Balaenoptera glacialis*) [237]).

3.6. Social Interactions and Mating Displays

The use of vocal displays to transfer information and influence the receiver in the context of sexual selection and courtship typically consists of males projecting information regarding their health, vigor, arousal, or genetic make-up to females to influence mate choice [196,239–249]. The complexity of an animal's vocal repertoire may be driven evolutionarily by mate preferences if the mating scheme is acoustically mediated (e.g., cetaceans [7,240], songbirds [92], and insects (*Drosophila montana*) [11]). Courtship calls may also initiate a state of sexual receptivity in females (e.g., anurans [241,242,245]; birds [242,249]; mammals [243,244,246–248]).

Mate choice may be initiated from pairing calls, used to display the relative suitability of potential partners. Call frequency, complexity, duration, or rate may be used as acoustic advertisements, representing the fitness and/or size of the caller. This type of display of physical fitness has been described as 'honest communication', and is produced potentially at a cost to the signaler. Additionally, hormone levels can influence the quality of courtship signals (e.g., anurans [245]; elephants [72,156,246–248]).

Some pairing calls have been described as 'song', as they are highly patterned and consist of repetitions of 'syllables' and 'phrases'. Song has been described for birds, anurans, primates, and cetaceans [4,249,250]. Song quality is fundamental to sexual selection and mating success, with modifications in timing and counter-singing with other males undertaken to advertise territory and sexual prowess. Social synchrony in song performance, such as chorusing in arthropods, anurans, aves, mammals, and sciaenids [4,167,245,250–266] or duetting between passerine bird partners [252,253], maximizes the effectiveness of the vocalizations. However, although seemingly unified, ultimately, every individual wants to out-signal their competitors, which may drive modification or increased call complexity (e.g., anurans [166,167,254–256]). Calls may be modified or reorganized over time to convey a different or 'more attractive' message [92,257,258,261]. Studies from birds [259–261], bats [262], primates [263], and whales [232,264–268] suggest that song complexity and production is influenced by female choice. Song may also function to repel rival males, acting as a social sorting mechanism [158]. Evolution and revolutions in song structure occur between male singers synchronously and result from cultural influences incorporated by vocal learning (e.g., humpback whales [31,36,44,264–272]). Indeed, the plasticity in the song calls demonstrates the rapid cultural transmission of acoustic information by conspecifics in a specific breeding area.

4. Language and Culture

The consideration of language starts with the communication of encoded information. This exchange of calls with a referential context, function, and perhaps meaning may be a first step in assigning cultural utility to acoustics use in animals. By using acoustics as a means to determine ‘friend or foe’, animals use markers to form a cultural identity and describe group membership and/or rank. This is used to determine the behavioural response to an individual, and whether it will be cooperative or hostile. Calls could be likened to symbols and seen to form a ‘system of meaning’ [272]. The process of social learning and reinforcement from conspecifics could form a vocal tradition or acoustic culture too. The first few months of life when acoustic repertoires are being learned is crucial to development and may define the individual’s survival or mating success in the future. The acquisition of these vocal cultures and traditions, however, is dependent on social bonds and conspecific interactions in many taxa.

The definition of language typically relies on the ability to discern meaning. Our understanding of the meaning, and not only the function, of vocalizations is limited to what can be inferred from observations. We see that animals are able to combine discrete units or notes to produce sequences that influence receiver behaviour. Field studies with mammals and birds have shown, for example, that the order of the same or similar calls can mean the difference between a sequence of calling for group cohesion and calls of warning and danger (e.g., [273]). Subtle nuances or additions of prefixes or suffixes can change the structure but, more importantly, the meaning of the vocal projections. Being able to understand how this variation generates meaningful acoustic variation in an animal’s repertoire brings us one step closer to describing the calls as part of a language. This is in addition to aspects of animal acoustics use such as babbling, call rehearsal, audience effects, conversation-like contact calling, and geographically or socially distinct dialects that are traditionally considered part of language. The cultural process of vocal learning, mother-offspring cultural transmission through ‘motherese’, and hierarchical and demographical structure maintained by acoustics is evident in several animal species. An appreciation of all of these processes adds to our understanding of the complexity of the use of acoustics by animals and how, for some, it is integral to their success and survival.

5. Implications of Changes in Soundscapes

Numerous bird and mammal species demonstrate calling and the integration of vocal cultures into key behaviours [270–281]. Increasingly, the complexity of animal call repertoires is being realized. The vocal production of primates and terrestrial mammals is now known to be greater and more flexible than had been previously appreciated [274]. Moreover, the emotional underpinning of vocal mechanisms is increasingly being recognized [270–274]. The abilities to project affective states as vocal signals and threat-associated alarm calls are only two examples of the flexible use of acoustics to portray a caller’s state. As discussed above, calling is not simply a means to keep in contact with conspecifics, but can permeate aspects of foraging, migration, and reproduction. A better starting point would be to consider that all vocal signals have a function. The function of both signals and communication is to produce an effect and drive behavioural change in a receiver, and so the acoustic modality influences, rather than simply shares, information.

The distance over which a call can be detected, interpreted, and enacted upon forms part of an animal’s active space. This can be the distance over which an acoustic signal or cue from a calling individual can elicit a response in a receiver. It equally can be the distance over which an individual can interpret the echoes of its own signals via echolocation, electrosensory, and electrolocation mechanisms. This gives an acoustic aspect to the concept of the ecological niche [275], and surpasses the idea of ‘active sensing’ [276]. An acoustically derived active space is the area over which sonic information can be sent, received, and processed to form the perceptual concept of an individual’s soundscape. Changes in the acoustic environment, in the sound sources, and/or in the sound transmission properties can modify the calls and call structures used and so may re-shape the active space. Fore-

shortening of the active space could hinder contact calling, as well as an animal's ability to navigate, find, and capture prey, and locate and aggregate with conspecifics. Essentially, the efficacy of any process that is aided or sustained by acoustic information would be reduced. Additional noise sources in the acoustic environment, natural or man-made, can instigate a reduction in active space through the acoustic masking of the relevant signals. Signals that are masked by noise become less discernable from the background acoustic landscape and so may not be received as intended, and not provide all or some of the information inherent in the signal [277,278]. The zone of masking around a sound source [277,278] represents the area in which the individual's soundscape and signal perception might be impacted by noise, and is specific to a time, place, and frequency. Active space and acoustic behaviours can also vary as the propagative properties of an area are altered, changing the way and distance over which a call or sound of interest is transmitted.

The vocal cultures and social learning of animals could be sensitive to soundscape changes. The addition of anthropogenic noise to sound fields is now a chronic and ubiquitous issue in both terrestrial and marine habitats. Similarly, additions of geophonic noise, such as wind and waves, and changing sound transmission properties from altered temperature, humidity, pH, or habitat composition are pervasive. Climate change and changes in ocean regimes will alter the structure of the acoustic environment. Although plasticity in calling may provide a route to adapt or modify vocalizations in the face of these changes, it likely will not provide complete resilience. Responses under the Lombard Effect (calling louder, longer, or more frequently, or with adapted frequencies), whilst used to try and retain effective conspecific communication, can be an energetic draw on the individual and also change the structure and meaning of the call. The interchange of information through the acoustic sensory mode is complex on a structural and social level; cognitive species with the capacity for social learning and individual variation in calling may show the greatest capacity for adaptation [279,280]. However, they may also feel the effects of soundscape changes most acutely.

Animals with rapidly evolving cultures may adapt to anthropogenic-derived habitat changes more readily [281]. Social connection and learning can be a buffer to changes in habitat suitability, or allow for individuals to respond to anthropogenic, abiotic, or biotic changes. Variation and novel behaviours can spread rapidly through populations (e.g., see [279–283]). In the case of soundscape alterations, the foreshortening of the area over which animals are able to send and receive information or effect imitation may impede this reform. The ability of animals to retain conspecific contact, find and capture prey, and defend themselves and their home-range territory is impacted by changes in active space driven by the acoustic environment. The imitation and emulation, teaching, and local enhancement of vocal behaviours may be lost, and modification of calls may be physiologically and energetically limited. The capacity for social learning and the transfer of information or behaviours between individuals of a community may also be hindered or lost. This interference by added noise is especially pertinent to the mother–young example, where the acquisition of the adult repertoire and acoustic cultures may be hampered by the intrusion of noise into the soundscape during a critical period. The lack of exchange of vocal repertoires is a loss in cultural inheritance and group sharing that reinforces culture and generational information transfer.

Vocal learning corresponds to changes and individualization in the duration and amplitude, pitch or frequency modulation, energy distribution, or timbre of signals [31,283]. Until recently, it was natural selection and the promotion of phenotypic traits that shaped communication and divergence in calling behaviours; however, it is changes in the sound field—more specifically, the elevation of ambient levels, and the introduction of human-derived noise—that now may be shaping vocalizations and call use. Selective pressures driven by mate preferences and individual success and convergent adaptations could be shaped themselves by genetic, morphological, or environmental constraints. Therefore, call or song production is affected by the mechanism of sound production and the features of the habitat that define sound transmission and propagation. Examples of variation in

calling range from short-term, Lombard-Effect-like responses to the acoustic habitat, to longer-term modifications in call frequency to mediate the changes in the soundscape and to use ‘acoustic windows’ where noise is absent (e.g., blue whales [282]. Modulation of calls in time or in structure can help to retain effective communication, although modification thresholds may exist due to morphological (MAH) or syntax restraints. Although useful, changes in the temporal aspects in calling are insufficient in birds for note and song discrimination between groups or individuals (e.g., [284,285]). Indeed, species have been seen to be much more sensitive to changes in call frequency than duration [286], suggesting that pitch cues are important to perceptual discriminations in the combination of cues that are used in individual recognition and group definition. Changes in the location and direction of the emission of call are also a strategy used to co-modulate a masking effect (e.g., habitat strata or tree height in birds [279–284]; direction of calls and echolocation signals in cetaceans [286]). This suggests, however, that the degradation of signals during transmission or because of noise interference is a problem (e.g., [286–289]).

Reductions in ambient noise are rare, but may occur as a result of a mitigation measure or a more wide-spread event that limits human activity. Many studies have commented on the changes in animal presence and use of habitats during the ‘Anthropause’ [290–293] during the COVID-19 pandemic, and the potential benefits to them from reductions in anthropogenic noise. A reverse Lombard Effect was seen for some species whereby birds, for example, reduced the amplitude of their song and were able to increase the frequency range of the repertoire as competition with noise sources was reduced (see, e.g., [292,293]). This increased their active space and, notably, the area over which courtship advertisement calls could be received [292,293]. Similar benefits might be expected for other equally acoustically sensitive and reliant species, such as cetaceans.

Climatic variability and geophonic noise additions initiate a Lombard Effect response or changes in acoustics use [294]. Acute additions of natural, non-biological noise such as rain or wind may increase the vocal activity of animals as a compensation mechanism (e.g., tawny owls (*Strix aluco*) [295]). Au et al. [209] demonstrated how the spatial extent of echolocation would be reduced substantially by rainfall without the use of a compensation mechanism, impacting their efficacy of use in foraging behaviours. Wind or air turbulence may result in calls with more pronounced frequency modulation being used [235]. Other variables, such as temperature, humidity, turbidity, or pH, could also correlate with changes in vocalization structuring and use. Indeed, modifications in calling in response to these variables may be noted before any visible changes in the habitat occur [294–296]. Changes in vocalizing behaviours, as previously mentioned, could impact the active space of the individual. If, for example, the number of days of intense rain or wind was to increase chronically, as is expected as climate change intensifies, it could have far-reaching consequences for animals that use acoustics to find a mate, establish territory, or avoid predators [294–300]. However, changes in environmental conditions due to climate change may cause modifications that also increase a vocal repertoire (e.g., [299–301]). Adaptation and learning may allow the remodulation of an acoustic niche [297–302], which would represent a change or adaptation to maintain the acoustic active space on a different scale to the Lombard-Effect-like responses. The most established example is the increase in ocean acidification due to climate change, whereby the absorption of low-frequency noise is reduced and therefore noise additions in this range propagate further. Animals that vocalize in these lower frequencies have adapted the frequency, duration, and intensity of vocalizations to avoid masking from the more prevalent anthropogenic noise [299–301]. Calling behaviours or structures also diversify as a result of morphology alterations to remain optimal to different foraging niches and influences from the acoustic environment. If vegetation density or food availability changes instigate an adaptation in bill size, for example, this variation in morphology in response to habitat could alter the properties and structure of birdsong (e.g., ant bird (*Thamnophilidae* spp.) [8]; white-crown sparrow (*Zonotrichia leucophrys*) [301]). Work by Seddon [8] suggests that, in accordance with MAH, body size correlates with the frequency of song, whereas morphological changes in bill

size alter the temporal patterning. However, they also suggest that the species recognition hypothesis would work in tandem with these ecological operations, to retain divergence in their song structure for closely related species to maintain acoustic identity [8].

The vocal learning capacity of species gives credence to the ubiquitous importance of conspecific learning. Species capable of vocal learning (songbirds, parrots, hummingbirds, bats, elephants, pinnipeds, and cetaceans) have been examined for culturally derived social behaviours in the acoustic modality in the wild, and even for these species, the information is still wanting. Thus, the implications of perceived soundscape changes by an individual are not widely applied to species in a broad cultural sense. Reactions to noise are considered predominantly in the short term, and from behavioural observations. This underestimates the complex and rich cultural underpinnings that the acoustic modality has. The social structure of acoustically sensitive populations reflects the opportunities for individuals to interact and for new traits to develop (e.g., [269,279–282]). However, by limiting acoustic behaviours through masking and altered soundscape properties, the repertoire of behavioural responses and social connectivity may become limited. Understanding the degree and extent of the masking effect, and thus changes in active space, can help to quantify the effect on an individual or group, with the calculation of masking metrics proposed as one means to develop effective noise mitigation strategies [302,303]. A species-specific mechanism to quantify the potential disturbance, even before behavioural responses are seen, advances our understanding of the effect of noise on wildlife, rather than purely describing changes in the acoustic environment relevant to that species. It considers the change in the soundscape as they perceive it, and the amount of acoustic data available to them to understand their surroundings.

Understanding a species ecology through the lens of their acoustic life may provide significant insight into their social structure and dynamics. Cultural evolution can instigate specialization, with the further narrowing of the niche through increasingly reduced active spaces, with consequences for both the individual and the species [304–308]. Understanding communication and the retention of contact between individuals gives a better comprehension of the social dynamics of animal societies [306–308].

Examining the functional use of calls moves research towards an understanding of the behavioural nature of vocalizing. Knowledge of call function and the use of different call types and their relationships with behaviour are important for interpreting autonomous acoustic recordings, and the significance of change for species. Modification of vocalizations has energetic, social, and behavioural implications for the calling individual, resulting from adjustments in call frequency, amplitude, and production rate (e.g., [308–311]). The emerging ecoacoustics discipline [294,312] aims to decipher the role of acoustics for individuals and species, and the role that call modification and acoustic niche adaptation can play in overcoming changes in acoustic environment [295–300,312]. Changes in the call use and rate among these calls that can be confidently categorized by function or context will aid in the identification of changes in behaviour or habitat use resulting from changes in acoustic environments. This is particularly true for human-derived additions, but also for altered transmission properties as a result of climate change. The study of acoustics use can be used alongside other ecological tools to advise managers as to the vulnerability of a species to altered ambient sound fields, and changing ecosystems more broadly. Altered vocalizing behaviours could become ecological indicators, using the vocal adaptation as a gauge for change. Changes in the calling behaviours, perhaps quantified through the use of acoustic indices, could represent a manifestation of acoustic habitat degradation or fragmentation. These indices may also be helpful to show changes in species diversity and ecosystem health, whereas masking metrics and an understanding of the role of active space, and the part that acoustics has in forming it for each species, demonstrates how the health and success of an individual or population may be impacted.

Funding: This research received no external funding.

Data Availability Statement: No new data were created or analyzed in this study. Data sharing is not applicable to this article.

Acknowledgments: Thanks to D. Duffus for the entertaining discussions on this topic to help find the message behind my musings.

Conflicts of Interest: The author declares no conflict of interest.

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