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Can you hear me now? A review of signal transmission and experimental evidence for the acoustic adaptation hypothesis

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ABSTRACT

The Acoustic Adaptation Hypothesis (AAH) posits that animal acoustic signals used in long-range communication should be adapted to transmit well within the habitats in which they evolved. However, comparative studies of signal form indicate mixed support for predictions of the AAH. Several studies have employed experimental playback approaches to testing signal transmission which can complement comparative studies. Here, we summarise these experimental playback tests of the AAH in birds, mammals, insects, and anurans, we describe the methodologies used in these tests, and we assess the evidence for habitat-specific signal degradation and species-specific acoustic fidelity (i.e. whether signals propagate best in native versus foreign habitats). Experimental evidence, like comparative evidence, varies across habitats and taxa. Although transmission properties consistently differed by habitat, with closed habitats degrading signals more than open habitats, animal signals were not always adapted to propagate best within their native habitats. Researchers felt they had convincing evidence for species-specific acoustic fidelity in less than half of the 67 reviewed studies, with the most support found for birds and the least for anurans. We discuss potential explanations for differences within and between habitats and taxa and conclude with suggestions for standardised methodology and areas of future research.

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Active space; acoustic adaptation hypothesis; animal communication; bioacoustics; signal degradation; signal transmission

Introduction

Animals across a diverse set of taxa produce long-range acoustics signals for the purpose of communication. These signals can provide information about the signaler's identity, sexual status, size, aggression, or other information (Kroodsma and Miller 1982; Searcy and Andersson 1986; Ryan 2001; Bradbury and Vehrencamp 2011) and are therefore important factors in the daily lives of social animals. However, acoustic signals degrade during transmission through media such as air or water, and these signals degrade faster than expected given the media alone (Wiley and Richards 1978). This excess reduction in signal quality can lead to information loss or misinterpretation by receivers (Wiley and Richards 1978; Bradbury and

Vehrencamp 2011) and resulting failed communication may have consequences for successful resource defence, mate attraction, or other behaviours important to survival and reproductive success (Welch et al. 1998; Reby and McComb 2003). Consequently, assessment of acoustic signal transmission fidelity and the factors which contribute to signal degradation have gained much attention, especially in taxa where acoustic communication is pervasive, including insects, birds, anurans, and mammals.

Because different habitats have unique structures and therefore vary in acoustic environment, it is not difficult to imagine that habitat structure contributes to differences in signal degradation. Environmental attenuation of sound is well documented and caused by a combination of factors, including atmospheric absorption, ground attenuation, beam scattering, and deflection of sound by vegetation (Aylor 1972; Harris 1966; Price et al. 1988; Huisman and Attenborough 1991). Further, experimental playbacks of synthesised signals clearly show that physical acoustics vary between open and closed natural habitats (reviewed in Wiley and Richards 1978; Boncoraglio and Saino 2007), where interference due to reverberation and waveguides causes serious distortion of sounds in closed habitats, especially sounds in higher frequency ranges (Bradbury and Vehrencamp 2011). The sensory drive hypothesis suggests that variations in environment that lead to differences in sensory perception such as this can influence a species' preference and signalling traits (Endler 1992; Schaefer and Ruxton 2015); for example, a songbird species living in a habitat with excessive acoustic distortion may prefer low-frequency songs that best counteract that distortion. Along this line, the acoustic adaptation hypothesis (AAH) posits that due to this context-dependent preference, animals should use long-range acoustic signals which are adapted to propagate well within the environment in which they are found (Morton 1975; Hansen 1979). Specifically, species living in closed, forested habitats should use long-distance signals with a pure tone-like sound and low-frequency range, while those in open habitats may use signals with highly modulated, repetitive sounds (Morton 1975; Wiley and Richards 1978). These predictions originate from a series of experiments which suggested that forest habitat acoustics produce selective forces on bird songs that reduce signal degradation caused by the above factors, while open habitats may select for repeated phrases which reduce the probability of information loss due to the instability of the acoustic environment (i.e. wind and temperature fluctuations; Morton 1975).

Since its conception, extensive comparative observational research on signal form has been done to test the predictions of the AAH (reviewed in Boncoraglio and Saino 2007; Ey and Fischer 2009). Observational studies typically correlate features of acoustic signals with the habitats in which they are used and assess whether the measured acoustic features fit the habitat-specific predictions of the AAH. Comparative studies generally show support for some but not all of the AAH's predictions (Boncoraglio and Saino 2007); in general, acoustic signals do tend to vary in ways predicted by the AAH across highly dissimilar habitats (birds: Slabbekoorn 2002; Tobias et al. 2010; mammals: le Roux et al. 2002, Peters and Peters 2010; anurans: Velásquez et al. 2018). Further, acoustic signal divergence is more correlated with the sound transmission properties of habitats than with genetic distance, ambient noise, or pleiotropic effects in Amazonian birds, suggesting that habitat influences signal form in some taxa (Tobias et al. 2010). However,

observational evidence in support of the AAH does not appear to be as ubiquitous as initially expected (Ey and Fischer 2009).

Although studies correlating signal structure with habitat are often extensive and provide a good test of the signal structure predictions of the acoustic adaptation hypothesis, they do not directly test signal propagation. An underlying prediction of the acoustic adaptation hypothesis is that selection should favour the use of sound that minimises degradation in a specific environment (Morton 1975); experimental research which directly tests transmission quality of signals, therefore, offers a powerful test of the AAH.

This review aims to assess the evidence for the AAH among birds, mammals, anurans, and insects based on experimental tests of signal transmission and degradation. We include all studies that measure sound transmission via playback and re-recording, but do not include comparative studies of signal form, as those have been previously reviewed elsewhere (Boncoraglio and Saino 2007; Ey and Fischer 2009). Because signal 'degradation' can be measured in many ways, we first determine which measures of signal quality are most often used in the literature and discuss the benefits and drawbacks of each. Secondly, we examine the evidence for whether habitat structure has the potential to act as an evolutionary pressure shaping acoustic signal transmission, and present evidence for whether animals show 'acoustic fidelity' – that is, whether their signals have adapted to maximise transmission quality in the habitats in which they evolved. We expect to see trends in signal degradation that parallel the findings of previously reviewed observational studies, such that degradation is generally minimised in a species' native environments when compared to non-native environments, though perhaps to different degrees in each taxon (Boncoraglio and Saino 2007). Throughout, we discuss gaps in the literature. Finally, we lay out some ideas for future research in this field.

Methods

We searched available literature using the Web of Knowledge database, using combinations of the following keywords: "acoustic adaptation", 'environmental selection', 'acoustic communication', 'vocal communication', and 'sensory drive'. We restricted searches to the years after the conception of the acoustic adaptation hypothesis (1975–2020) and included experiments investigating acoustic signal degradation in insects, anurans, birds, and mammals. We also explored relevant literature cited by these studies. We recognise that the field of acoustic adaptation is extensive and that we may have missed some studies in our search; however, we attempted to include all relevant studies.

We located 67 studies that used playback to experimentally test sound propagation in an animal communication context. For each, we noted how many and which species and habitats were assessed, whether the study included intra- or inter-species analyses, at which distances signals were recorded, whether the experiment included natural or synthesised sounds, and how sound degradation was measured. The specific details of each included study can be found in Table 1. Finally, we noted whether the study supported the prediction of the AAH – that animal acoustic signals adapt to native habitats, using the authors' conclusions whenever possible. The variable and unstandardised methodologies of the assessed papers precluded comprehensive statistical meta-analysis; therefore, we focus on basic descriptive quantification of patterns in the field.

Table 1. Summary of reviewed articles. For the 'Degradation Measures' column, EA = excess attenuation, SNR = signal-to-noise ratio, MAD = mean/max amplitude difference, BR = blur ratio, TSR = tail to signal ratio, A = simple attenuation, MCC = max correlation coefficient, DD = discrimination distance, RMS = root mean squared, and CD = communication distance. General descriptions of these methods can be found in Table 2.

Authors	Year	Sound type	Inter- or intra-specific	# Species/Signals	Species Name	# Habitats	Habitat Designation	Distances (m)	Acoustic Measures	Supports AAH?
Birds										
Morton, E.	1975	Synthesised Pure Tones	NA	1	NA	3	forest, edge, grassland	7.5, 30, 60, 90	EA	Partial
Hunter, M., Krebs, J.	1979	Recorded Song, Synthesised Song,	Intra	1	Great Tit (<i>Parus major</i>)	2	dense forest, open woodland	40	Average Power Ratio	Yes
Gish, S., Morton, E.	1981	Synthesised Pure Tones	Intra	1	Carolina Wren (<i>Thyothorus ludovicianus</i>)	1	native, foreign	50	EA	Yes
Brenowitz, E.	1982	Recorded Song	Intra	1	Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	1	open field	5, 10	EA	Yes
Cosens, S. Falls, J.	1984	Recorded Song, Synthesised Pure Tones	Intra	1	Song Sparrow (<i>Melospiza melodia</i>)	2	open field and river island	27, 54	MAD	Yes
Shy, E., Morton, E.	1986	Recorded Song	Intra	1	Blackbird (<i>Turdus merula</i>)	1	deciduous forest	25, 50, 100, 150, 200	EA, SNR, BR	Yes
Date, E., Lemon, R.	1993	Synthesised Song	Intra	3	American Redstart (<i>Setophaga ruticilla</i>)	3	deciduous forest, coniferous forest, open forest	2.5, 10, 25, 50	EA, differential attenuation, decay time	No
Fotheringham, J., Martin, P., Ratcliffe, L.	1997	Recorded Song	Inter	4	4 warblers and ovenbird species	1	open field	1-, 100	MAD	No
Holland, J., Dabelsteen, T., Pedersen, S., Larsen, O.	1998	Recorded Song	Intra	1	Eurasian Wren (<i>Troglodytes troglodytes</i>)	1	mixed primeval forest	25, 50, 75, 100	EA, SNR, BR	Yes
Nemeth, E., Winkler, H., Dabelsteen, T.	2001	Recorded Song	Inter	5	5 Antshrike Species	5	4 forest heights	Various	EA, SNR, BR	Partial
Slabbekoorn, H. Smith, T.	2002	Synthesised Pure Tones	Intra	2	Little Greenbul (<i>Eurillas virens</i>)	2	rainforest, ecotone forest	4, 16	BR	No

(Continued)



Table 1. (Continued).

Authors	Year	Sound type	Inter- or intra-specific	# Species/Signals	Species Name	# Habitats	Habitat Designation	Distances (m)	Acoustic Measures	Supports AAH?
Balsby, T., Dabelsteen, T., and Pedersen, S.	2003	Recorded Song	Intra	5	Whitethroat (<i>Sylvia communis</i>)	2	hedgerow, open meadow	12.5, 25, 50	SNR, EA, TSR, BR	Partial
Brown, T. and Handford, P.	2003	Recorded Song	Inter	2	Swamp Sparrow (<i>Melospiza georgiana</i>), White-throated Sparrow (<i>Zonotrichia albicollis</i>)	4	open field (day and night), forest (day and night)	25, 50, 75, 100	MCC	Partial
Blumenrath, S., and Dabelsteen, T.	2004	Recorded Song	Intra	1	Great Tit (<i>Parus major</i>)	2	mixed deciduous forest (before/after foliation)	15, 30, 60	TSR, EA, SNR, BR	Yes
Hansen, J. et al.	2005	Recorded Song	Intra	3	Black-capped Chickadee (<i>Parus atricapillus</i>)	2	undisturbed and disturbed forest	50	Change in entropy	No
Leader, N., Wright, J., Yom-Yov, Y.	2005	Recorded Song	Intra	2	Orange-tufted Sunbird (<i>Nectarinia osea</i>)	2	open and closed urban habitats	5, 10, 25, 50, 75, 100	SNR, A	No
Mathevon, N., Dabelsteen, T., Blumenrath, S.	2005	Recorded Song	Intra	1	Eurasian Blackcap (<i>Eurasian Blackcap</i>)	3	2, 4, and 9 m height in a forest	12.5, 25, 50	EA, SNR, BR, TSR	No
Kroon, F., Westcott, D.	2006	Recorded Song	Intra	4	Golden Bowerbird (<i>Prionodura newtoniana</i>)	4	local, foreign	2, 50	MCC	No
Nicholls, J., Goldizen, A.	2006	Recorded Song, Synthesised Pure Tones, White Noise	Intra	5	Satin Bowerbird (<i>Ptilonorhynchus violaceus</i>)	6	6 forest types	5, 40	BR, MCC	Partial
Slabbekoorn, H., Yeh, P., Hunt, K.	2007	Synthesised Song	Intra	1	Dark-eyed Junco (<i>Junco hyemalis</i>)	2	montane pine forest, urban	25	TSR, SNR	Yes
Dingle, C., Halfwerk, H., Slabbekoorn, H.	2008	Synthesised Sweeps	Intra	1	Grey-breasted Wood-wren (<i>Henicorhina leucophrys</i>)	2	Subspecies populations	10	Reverberation	Partial
Jensen, K., Larsen, O., Attenborough, K.	2008	Synthesised and Recorded Song	Intra	1	Hooded Crow (<i>Corvus corone cornix</i>)	1	open field	300, 600, 900, 1200	EA	Yes
Barker, N., Dabelsteen, T., Menzies, D.	2009	Recorded Song	Intra	2	Rufous-and-white Wren (<i>Troglodytes rufoalbus</i>)	3	mature and regenerating forest, open field	5, 10, 20, 40	EA, TSR, BR, SNR	Yes
Nemeth, E. and Brumm, H.	2010	Recorded Song	Intra	2	Great Tit (<i>Parus major</i>), Blackbird (<i>Turdus merula</i>)	2	urban, deciduous forest	NA	DD	Yes

(Continued)

Table 1. (Continued).

Authors	Year	Sound type	Inter- or intra-specific	# Species/ Signals	Species Name	# Habitats	Habitat Designation	Distances (m)	Acoustic Measures	Supports AAH?
Mockford, E., Marshall, R., Dabelsteen, T.	2011	Recorded Song	Intra	2	Great Tit (<i>Parus major</i>)	2	urban, rural woodland	12, 48	TSR, EA, SNR, BR	Partial
Mouterde, S., Theunissen, F., Elie, J., Vignal, C., Mathevon, N.	2014	Recorded Song	Intra	2	Zebra Finch (<i>Taeniopygia guttata</i>)	2	open dirt, subarid desert	2, 16, 64, 128, 256	EA, SNR, BR, DD	Yes
Sandoval, L., Dabelsteen, T., Mennill, D.	2015	Recorded Song	Intra	2	White-eared Ground Sparrow (<i>Melospiza leucotis</i>)	1	natural and artificial thickets	4, 8, 16, 32	SNR, TSR, BR, EA	Yes
Piza, P and Sandoval, L.	2016	Recorded Song	Intra	2	White-eared Ground Sparrow (<i>Melospiza leucotis</i>)	1	natural thicket	4, 8, 16, 32	SNR, TSR, BR, EA	Yes
Rek, P., and Kwiatkowska, K.	2016	Recorded Song	Inter	3	3 Crakes and Rails	1	grassy marsh	5, 10, 20, 40, 80, 160, 320	EA, SNR	Yes
Graham, B., Sandoval, L., Dabelsteen, T., Mennill, D.	2017	Recorded Song	Intra	3	Rufous-and-white Wren (<i>Parus major</i>)	3	dry forest, wet forest, montane forest	5, 10, 20, 40	TSR, EA, SNR, BR	No
Priyadarshani, N., Castro, L., Marsland, S.	2018	Recorded Song	Inter	20	New Zealand Native Birds	2	forest, rugby field	20, 25, 50, 100	SNR	No
Phillips N., Rochefort C., Lipshutz S. Derryberry GE, Luther D, Derryberry EP	2020	Synthetic Pure Tones	Intra	6	White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	2	urban, coastal scrub, pasture	5, 30	SNR, A, TSR	Partial
Anurans										
Ryan, M., Coccoft, W., Wilczynski, W.	1990	Recorded Calls	Inter	2	Crickets (<i>Acris crepitans</i>)	2	pine forest, open habitat	1, 4, 8, 16	MCC	No
Penna, M. Solis, R.	1998	Recorded Calls, Synthesised Pure Tones and Noise	Inter	5	5 South American Frogs	2	marsh, bog	1, 2, 4, 8	EA	No
Boatright-Horowitz, S., Cheney, C., Simmons, A.	1999	Recorded Calls, Synthesised Pure Tones and Noise	Intra	1	American Bullfrog (<i>Lithobates catesbeianus</i>)	2	above and below pond water	1, 2, 4, 8	RMS Amplitude	Yes

(Continued)



Table 1. (Continued).

Authors	Year	Sound type	Inter- or intra-specific	# Species/ Signals	Species Name	# Habitats	Habitat Designation	Distances (m)	Acoustic Measures	Supports AAH?
Kime, N.	2000	Recorded Calls	Inter	22	22 Central American frog species	2	tall grass field, forest	1, 2, 3, 10, 20	MCC	No
Castellano, S., Giacomina, C., Ryan, M.	2003	Recorded Calls	Inter	3	12 frog species	1	open grassland	2, 4, 6, 8, 16, 32	Calibrated MAD	No
Penna, M., Márquez, R., Bosch, J., Crespo, E.	2006	Recorded Calls, Pure Tones	Inter	2	Midwife Toads (<i>Alytes cisternasii</i> , <i>A. obstetricans</i>)	2	oak forest, pine forest	0.5, 1, 2, 4, 8	EA	No
Llusia, D., Gómez, M., Penna, M., Márquez, R.	2013	Recorded Calls, Synthesised Pure Tones and Noise	Inter	2	American Bullfrog (<i>Lithobates catesbeianus</i>), Perez's Frog (<i>Pelophylax perezii</i>)	2	native, foreign	0.5, 1, 2, 4, 8	EA	No
Penna, M., Plaza, F., Moreno-Gómez, F.	2013	Recorded Calls	Intra	1	Ground Frog (<i>Eupsophus calcaratus</i>)	1	volcanic bog	0.25, 0.5, 1, 2, 4	MAD	No
Penna, M., Moreno-Gómez, F.	2014	Recorded Calls	Intra	1	Ground Frog (<i>Eupsophus emiliopugini</i>)	1	volcanic bog	0.25, 0.5, 1, 2, 4	MAD	No
Penna, M., Moreno-Gómez, F.	2015	Recorded Calls	Inter	2	Ground Frogs (<i>Eupsophus calcaratus</i> , <i>E. emiliopugini</i>)	1	volcanic bog	0.5, 1, 2, 4, 8	BR	No
Velásquez et al.	2018	Synthetic Calls	Intra	3	3 populations of South American Frog	3	breeding pools	0.5, 2, 4, 8, 16	MCC	No
Mammals										
Brown, C.	1989	Recorded Calls	Inter	2	Blue/Grey-cheeked Monkey (<i>Cercopithecus mitis</i> , <i>Cercocebus albigena</i>)	1	rainforest	Up to 2000	DD	Yes
Brown, C., Gomez, R., Waser, P.	1995	Recorded Calls	Inter	4	4 primate species	2	savanna, rainforest	12.5, 100	MCC	Yes
Daniel, J., Blumstein, D.	1998	Recorded Calls	Inter	4	4 marmots and woodchucks	1	dry grass meadow	10, 20, 30, 40	MCC	No
De La Torre, S. and Snowdon, C.	2002	Recorded Calls	Intra	3	Pygmy Marmoset (<i>Cebuella pygmaea</i>)	2	flooded and non-flooded rainforest	1, 10, 20, 40, 80	Modulation depth	Partial
Perla, B.	2002	Recorded Calls, Pure Tones	Intra	1	Gunnison's prairie dogs (<i>Cynomys gunnisoni</i>)	2	alpine meadow	1, 5, 20, 40, 60, 80, 100	EA	Partial
Sugjura, H., Tanaka, T., Masataka, N.	2006	Recorded Calls, Pure Tones	Intra	2	Japanese Macaque (<i>Macaca fuscata yakui</i>)	2	sparse forest, secondary growth forest	1, 16, 32	EA	Partial

(Continued)

Table 1. (Continued).

Authors	Year	Sound type	Inter- or intra-specific	# Species/Signals	Species Name	# Habitats	Habitat Designation	Distances (m)	Acoustic Measures	Supports AAH?
Morrill, R., Thomas, N., Schiel, N. et al.	2013	Pure Tones, Recorded Calls, and Clicks	Intra	3	Common Marmoset (<i>Callithrix jacchus</i>)	1	semi-deciduous forest	10, 20, 40, 80	MCC	No
Hedwig, D., DeBellis, M., Wrege, R.	2018	Recorded Rumbles	Intra	1	African Forest Elephant (<i>Loxodonta cyclotis</i>)	1	tropical Forest	Variable	MAD	Partial
Holzmann, I., Areta, J.	2019	Synthesised Howls	Intra	1	Black-and-gold Howler Monkey (<i>Alouatta caraya</i>)	4	gradient from open to closed in winter and spring	10, 50, 100	MAD	No
Insects										
Van Staaden, M., Römer, H.	1997	Recorded Song	Intra	1	Bladder Grasshopper (<i>Bullacris unicolor</i>)	2	grassland (day and night)	1–450	CD	Yes
Lang, F.	2000	Recorded Song	Intra	1	Gomphocerine Grasshopper (<i>Chorthippus biguttulus</i>)	2	short grass, long grass	0.1–10	EA, CD	Yes
Sueur, J., Aubin, T.	2003	Synthetic Calls	Inter	2	Cicadas (<i>Tibicina haematodes</i> , <i>Cicada orni</i>)	2	vine foliage, vine trunks	1, 2, 4, 8, 6	RMS Amplitude	No
Couldridge, V., Van Staaden, M.	2004	Recorded Song	Inter	7	Bladder Grasshopper Spp. (Orthoptera; Pneumoridae)	4	succulent karoo, fynbos, savanna, forest	1, 5, 10, 25, 50, 100	MAD, MCC	Partial
Couldridge, V., Gordon, M.	2015	Recorded Song	Intra	1	Bladder Grasshopper (<i>Bullacris unicolor</i>)	2	forest (day and night)	1, 5, 10, 35, 50, 100	MCC	Partial
Other										
Richards, D., Wiley, R.	1980	Synthesised Pure Tones	NA	5	NA	2	mixed deciduous forest (before and after foliation), open field simulated open and closed habitats	5, 10, 20, 40, 60, 80	Variation in amplitude, index of reverberation	Partial
Brown, T., Handford, P.	1996	Synthesised Pure Tones	NA	2	NA	2	three maturities of tropical monsoon forest	NA	MCC	Partial
Marten, K., Quine, D., Marler, P.	1977	Synthesised Pure Tones	NA	24	NA	3	mature broadleaf forest, woodland, scrubland, marsh, grassland	2.5, 100	EA	Partial
Brown, T. J., Handford, P.	2000	Synthesised Pure Tones	NA	4	NA	5	broadleaf sapling	50	MCC	Partial

(Continued)



Table 1. (Continued).

Authors	Year	Sound type	Inter- or intra- specific	# Species/ Signals	Species Name	# Habitats	Habitat Designation	Distances (m)	Acoustic Measures	Supports AAH?
Ellinger, N., Hödl, W.	2003	Synthesised Pure Tones	NA	13	NA	1	neotropical lowland rainforest	28, 52, 92	EA, MCC	Yes
Naguib, M.	2003	Synthesised Trills	NA	3	NA	3	mixed deciduous forest (before and after foliation), open field	20, 40, 80, 120	Reverberation index	Yes
Nelson, B.	2003	Synthesised Noise	NA	1	NA	1	Florida scrub habitat	15, 30, 45, 60	Attenuation, EA, Variation (SD) in Attenuation	Yes
Padgham, M.	2004	Balloon Burst	NA	1	NA	2	dry forest, moist forest	20, 40, 60, 80, 100	Reverberative Decay Rate, Max Power Range	No
Boycott, T., Gao, J., and Gall, M.	2019	Synthesised Pure Tones, White Noise, and Trills	NA	20	NA	2	undisturbed mixed deciduous forest, deer- browsed forest	1, 3, 5, 7, 9, 11	MCC	Partial

Table 2. Common measurements of acoustic signal distance and quality related to the acoustic adaptation hypothesis, along with their benefits and limitations.

Signal Measurement	Description	Benefits	Limitations
Measures of Signal Transmission Distance			
Communication Distance (CD)	How far a signal can travel	Easily calculated	Ignores biological relevance of information decoding
Discrimination Distance (DD)	How far a signal can be interpreted	Biologically relevant	Difficult or impossible to calculate depending on species information
Measures of Signal Transmission Quality			
Mean/Max Amplitude Difference (MAD)	Difference in relative amplitude	Easily calculated	Requires model sound; ignores acoustic interference
Blur Ratio (BR)	Loss of loudness across distance	Easily calculated	Highly dependent on background noise; requires model sound
Signal-to-Noise Ratio (SNR)	Separation from background noise	Easily calculated	Mostly uninformative on its own
Attenuation (A)	Clarity relative to non-degraded signal	Measures differences across entire signal	Requires model sound; structural influences cannot be compared across habitats
Excess Attenuation (EA)	Attenuation in excess of that expected from meteorological processes	Measures differences across entire signal; measures differences due to structure only	Requires model sound; ignores biological relevance of some abiotic factors
Tail-to-Signal Ratio (TSR)	Reverberation	Easily calculated	Highly dependent on background noise; subject to observer bias
Other Measures of Signal Degradation			
Variation in Signal Quality	Measures consistency of quality	Can answer different questions than standard measures of quality	Specific technique is not standardised
Other Measures	Varies	Answers specific questions	Not comparable to other studies

Results and discussion

Experimental approaches

Transmission experiments in the reviewed literature were always set up such that animal signals or synthesised sounds were played through a speaker and recorded at various distances in particular habitats, though the specific equipment and set-up varied. Each recording was digitised and analysed for some measure(s) of signal degradation, or in some cases, perceptual abilities of the receiver (discrimination distance; see below). Below, we describe the most common and notable measurements used under this approach (summarised in Table 2), and research outcomes relevant to the AAH.

Quantifying signal transmission and degradation

Measures of signal transmission distance

Communication Distance (CD) attempts to resolve how far a signal travels through the environment, usually by calculating the distance at which a signal's sound pressure falls below the average sound pressure of a temporally adjacent noise sample. Theoretically, signals that travel far are most advantageous for long-range communication because they

allow the signaller to communicate to a broader range of potential receivers (Gish and Morton 1981). This measure, however, does not consider signal clarity or the ability of the receiver to interpret the signal at a given distance. Under this measure, it is possible for a receiver to hear an acoustic signal without receiving clear enough information to recognise and decode it. This method appeared only in two studies published before 2000, and its use appears to have diminished in favour of more complicated measures. This is likely because the more modern methods listed below better capture biologically relevant interpretations of signal degradation in the context of animal communication.

Discrimination Distance (DD), also known as ‘active space’, is similar to communication distance but has the advantage of taking into account whether the receiver can discriminate a signal at a given distance (Brown 1989; Ellinger and Hödl 2003; Hedwig et al. 2018). If an individual can discriminate a signal, one may assume that communication is occurring. However, discrimination distance is often difficult to calculate because it requires information on how the signal receiver perceives sound, which can be impractical or challenging to obtain. Due to these difficulties, discrimination distance was found only twice in the context of the acoustic adaptation hypothesis (Nemeth and Brumm 2010; Mouterde et al. 2014), though it holds great potential for exploring the AAH in well-studied organisms in the future.

Measures of signal transmission quality

Mean/Max Amplitude Difference (MAD) is a measure that takes the mean/max amplitude of a non-degraded signal and compares it to the mean or max amplitude of a degraded signal. Calculation of MAD requires a model sound, which is either the original recording or the signal recorded at a short distance from the speaker (0.5–2.5 m). Because this recording distance is so small, it captures the signal before significant degradation can occur (Dabelsteen et al. 1993). To calculate MAD, the mean or max amplitude of the non-degraded sound (A_x) and the amplitude of the noise floor (A_n) is subtracted from the amplitude of the degraded test sound (A_y) such that $MAD = A_y - A_x - A_n$. This measure is perhaps the easiest transmission quality measure to acquire, but it fails to consider several aspects of physical acoustic interference captured by other measures outlined below. Further, unless recorded signals are properly calibrated using sounds of known amplitude, absolute values of amplitude measurements cannot be compared across studies unless the studies use identical recording setups due to variation in gain between recording equipment (Center for Conservation Bioacoustics 2019). Mean/max amplitude difference appeared most often in mammalian (Hedwig et al. 2018; Holzmann and Areta 2019) and anuran (Penna et al. 2013; Penna and Moreno-Gómez 2014; Velásquez et al. 2018) studies, and was used in 9 of 67 reviewed articles.

Blur Ratio (BR), sometimes called distortion, measures the ratio of energy of an attenuated model sound (E_x) to the energy of the test sound (E_y) (described by Dabelsteen et al. 1993). Simplified, this can be interpreted as a measure of ‘loudness lost’ relative to a non-degraded version of a signal. Blur ratio is a basic but informative measure. Unfortunately, its calculation can be heavily influenced by the amount of background noise in the test sound, so the energy of the background noise (E_n) is often measured alongside blur ratio and factored into analyses such that $BR = E_x / (E_y - E_n)$ (Dabelsteen et al. 1993; Holland et al. 1998; Sandoval et al. 2015; Piza and Sandoval 2016; Graham et al. 2017) though this is not always the case. Background noise for this

purpose is generally measured from a 1–5 second slice of recorded ambient noise immediately preceding signal playback (Balsby et al. 2003; Leader et al. 2005; Priyadarshani et al. 2018). Blur ratio was primarily used in avian studies and appeared in 15 out of 67 reviewed studies.

Signal-to-Noise Ratio (SNR) measures the ratio of the energy of the test sound (E_y) to the energy of the background noise (E_n) (Dabelsteen et al. 1993). SNR is calculated as $10\log [(E_y - E_n)/E_n]$. Simplified, SNR can be thought of as a measure of ‘signal separation’ which can inform us about how well the animal’s signal stands out from ambient background noise at various distances. This is an important addition to calculation of blur ratio because a signal may retain relatively high amounts of energy but still be ineffective if it is not separate from competing noise. However, SNR is generally uninformative on its own and almost always appears as a supplement to other measures of signal quality, most typically blur ratio and excess attenuation (see below). In the reviewed literature, signal-to-noise ratio appeared in over half of all avian studies but has not been used for other taxa.

Attenuation (A) measures retention of a signal’s form over distance and can be interpreted as a measure of ‘clarity’. Clarity is important because even if a signal is loud and separate from noise, communication does not happen effectively when the signal is slurred so badly that information cannot be decoded correctly. There is some variation in how researchers obtained a measure of attenuation in transmission studies, but it is generally extracted by finding a maximum cross-correlation coefficient (MCC) between Hilbert-transformed amplitude envelopes of the test and model sounds (see Dabelsteen and Pedersen 1985). Such measures of attenuation are helpful for within-habitat comparisons of signal degradation but can be problematic when comparing between habitats because attenuation is heavily influenced by atmospheric pressure, temperature, and humidity (Harris 1966). Attenuation differences between habitats could be due to these factors instead of the physical structure of the environment itself. Measures of simple attenuation appeared in 20 of the reviewed studies, not including those measuring excess attenuation (see below).

Excess Attenuation (EA) is similar to attenuation, but measures attenuation in excess of that expected by atmospheric absorption and spherical spreading that occurs due to normal physical processes (Dabelsteen et al. 1993). Traditionally, EA has been calculated as $EA = -(20\log k - A)$, where k is the minimum energy (E_x) of the blurring of the test signal’s amplitude function and $A = 6$ dB per doubling of the distance between sound source and receiver (Dabelsteen et al. 1993). A modern version, which also accounts for atmospheric absorption, is as follows:

$$EA = L_s - 20\log_{10}(r) + K - A$$

For this equation, L_s is the source sound in decibels, r is the distance in metres, K is a constant equal to $-10\log_{10}(4\pi)$ for spherical spreading and A is the atmospheric absorption (Mouterde et al. 2014). Atmospheric absorption depends on frequency, temperature, humidity, and atmospheric pressure, and can be calculated with an equation published by the International Organisation for Standardisation (IOS 9613–1:1993). Excess attenuation was one of the most commonly used measures of signal degradation in reviewed studies, especially in more recent publications investigating avian taxa (Piza and Sandoval 2016; Ręk and Kwiatkowska 2016; Graham et al. 2017); it was used in nearly

40% of all reviewed studies. It is possibly one of the best metrics for comparison across habitats when asking questions about differences in signal quality due to habitat structure specifically. However, by integrating temperature, humidity, and atmospheric pressure into its calculation, EA fails to consider any possible potential signal adaptations to abiotic environmental conditions such as heat and elevation, which may contribute to signal degradation just as much or more than physical structure itself (Harris 1966).

Tail-to-Signal Ratio (TSR) measures reverberation, or the relative amount of acoustic energy that persists in the environment for a set time after the signal has ended (Balsby et al. 2003). This can be expressed as the energy of the tail (E_{tail}) over the energy of the signal (E_s) over the same time frame (Holland et al. 2001). This can be informative because tail reverberations take up acoustic space and may interfere with an individual's own communication. A drawback of this measure is that, like blur ratio, it is highly dependent on the energy of the background noise which occupies the same space as the measured tail. Further, determining the true 'tail' of an acoustic signal can be difficult and potentially subjective. Calculation of TSR is not as common as EA, BR, and SNR, and has only been used in avian studies, but adds another potentially useful measure of signal energy degradation. It may be worth investigating TSR in taxa outside of birds.

Other measures of signal degradation

Measures of variation in signal quality were far less common than other measures. Generally, these were used to test the idea that overall transmission quality may not be as important as consistency in quality (see below). Variation has been measured as the standard deviation of signal amplitude (Richards and Wiley 1980) or attenuation (Nelson 2003), or as variation of cross-correlation across a signal (Brown and Handford 1996, 2003). Measures of variation appear only in studies investigating open habitats (Brown and Handford 1996; Nelson 2003) due to the predictions of the AAH, but little has been done to test its response to structurally diverse habitats, including dense forests.

Other measures included reverberation index (Naguib 2003), decay rate (Padgham 2004), change in modulation depth (De La Torre and Snowdon 2002), and change in entropy (Hansen et al. 2005). These novel measures can be useful depending on the questions being asked, but make comparison to other studies difficult.

Evidence for the acoustic adaptation hypothesis

Methodological approaches

The reviewed studies generally tested the acoustic adaptation hypothesis by comparing transmission of multiple signal types in one habitat or by comparing the transmission of the same signal in different habitats. While most experiments used previously recorded vocalisations of target species, especially in recent years, some used synthesised sounds which mimic animal vocalisations to control for variation in recording quality (Hunter and Krebs 1979; Jensen et al. 2008; Velásquez et al. 2018) and others exerted more control by using entirely synthesised pure tones, trills, or white noise (see Table 1: Other). Synthetic sounds can be informative for testing the theory behind the AAH. For example, Naguib (2003) played low, medium, and highly modulated synthesised avian trills in a deciduous forest and found that fast trills degrade more than slow trills. Because observations showed that forest-dwelling birds tend to have slower trills, the author

concluded that those species may have adapted trill rates to minimise signal degradation in forests during the breeding season (Naguib 2003). Experiments using real recorded signals can theoretically provide more evidence for the AAH than experiments using synthesised sounds because they directly test signals which have been exposed to adaptive pressures. However, recent work suggests that broadcasting recorded animal signals may simplify the conditions in which animals communicate naturally (Penna et al. 2012). In any case, the form of broadcasted acoustic stimuli must be considered carefully when designing playback experiments targeting specific components of the AAH.

Among experiments that used recorded signals, the majority investigated intra-specific transmission differences, especially outside of anurans (Table 1). These studies tested specific hypotheses about the adaptation of acoustic signalling in one species, attempting to explain variation within (Holland et al. 1998) or between (Dabelsteen et al. 1993; Balsby et al. 2003; Jensen et al. 2008; Sandoval et al. 2015; Piza and Sandoval 2016) signal types. Studies that tested the signals of multiple species usually did so in a single habitat type or in one ‘open’ and one ‘closed’ habitat type. Few reviewed studies for each taxa (birds: Brown and Handford 2003; Priyadarshani et al. 2018; anurans: Ryan et al. 1990; Brown et al. 1995; Penna and Solís 1998; Kime 2000; Penna et al. 2006; mammals: Brown et al. 1995; insects: Couldridge and Van Staaden 2004; Sueur and Aubin 2003) conducted reciprocal playback experiments where multiple species’ signals were played in multiple habitats.

Effects of habitat structure on signal propagation

In a following section we examine acoustic fidelity and whether signals have adapted to habitat structure; here we focus on reviewing whether habitats affect signal propagation. Acoustic signal transmission experiments have primarily been conducted in forested habitats across taxa, but tested habitats in the literature include forests, open meadows, scrub, sub-arid deserts, grassy marshes and bogs, urban areas, and more (Table 1).

The most research has been done in deciduous forests, perhaps due to ubiquity and ease of access, though other tested forest habitats include coniferous forests, tropical forests, rainforests, and montane forests (Table 1). We report habitat types as designated by the authors in cited papers. Although we catalogued the use of over 40 different habitats, the true breadth of study remains ambiguous. Several authors reported different names for habitat types (i.e. grassland, open field, meadow) which, without detailed quantitative description, may be structurally identical. Inversely, subjective habitat determination may have led some authors to, for example, deem a habitat ‘forest’ when others would name it ‘woodland’. Clearly, some form of naming standardisation is needed.

The majority of studies that tested multiple habitats found significant differences in transmission quality between habitats (though this is not always the case; see Holzmann and Areta 2019). This indicates that different habitats should provide different selective pressures on long-range animal acoustic signals. As predicted by Morton (1975), signal propagation differences are most prominent between what are considered ‘open’ and ‘closed’ environments, but differences were often measurable between many classes of habitat within these distinctions, including within different types of temperate forests (Penna et al. 2006), tropical forests (Barker et al. 2009), and open spaces (Couldridge and Van Staaden 2004). Further, transmission properties can differ between even extremely

similar habitats that diverge mainly in climate profiles rather than physical structure (Mouterde et al. 2014), indicating that meteorological habitat may play an important role in adaptation. In general, it appears that forested or otherwise dense environments consistently attenuate signals more so than other, more open habitats (Ryan et al. 1990; Barker et al. 2009; Maciej et al. 2011), while those with no canopy (grasslands, fynbos, marshes, etc.) tend to cause large variability in signalling quality (Couldridge and Van Staaden 2004; Priyadarshani et al. 2018). Only 20% of studies investigating degradation differences in open versus closed habitats did not find any evidence for this trend.

Most studies that did not find differences in signal transmission between habitats generally tested habitats that were, in theory, structurally similar. For example, Padgham (2004) did not find differences in reverberative decay of signals between moist and dry Australian forests, suggesting that they may be too physically similar to have measurably different acoustic environments. Similarly, Hansen et al. (2005) found no difference in the signal entropy of Black-capped Chickadee (*Poecile atricapillus*) songs played in disturbed vs. undisturbed forest habitats.

Interestingly, few studies characterised habitats quantitatively. Some measured habitat characteristics to verify that their playback locations were representative of typical or different habitat (Perla 2002; Castellano et al. 2003; Sandoval et al. 2015), but few studies (Hunter and Krebs 1979; Richards and Wiley 1980; Hansen et al. 2005; Sebastián-González et al. 2018; Phillips et al. 2020) attempted to correlate transmission properties with specific, quantifiable habitat measures, such as wind speed or tree density. This trend, however, appears to be changing with increasingly easy access to relevant tools such as LiDAR (light detection and ranging) scanners (see Priyadarshani et al. 2018; Sebastián-González et al. 2018; Phillips et al. 2020), although none have yet assessed multiple quantitative variables at once. Qualitatively assigning environments to pre-determined habitat types can be problematic for two reasons: 1) By not using some quantitative measure, researchers may introduce bias by subjectively determining which environments belong to which categories (i.e. 'open' vs. 'closed'), and 2) assigning broadly-defined habitat types may cause researchers to miss important differences in micro-habitat. For example, both a rocky high desert and a sandy low desert could be considered 'open' or 'arid deserts', even though one may have more reflective surfaces, higher temperature, less vegetation, and other features that may influence signal propagation. Future studies should strive to determine habitats quantitatively, or at least to provide statistical evidence that pre-determined habitats are indeed structurally different.

Temporal influences on signal propagation

A small subset of reviewed studies investigated whether temporal shifts in habitat structure might influence signal evolution, a question that is especially important for taxa that continue to produce long-range calls throughout the year. Two avian studies (Naguib 2003; Blumenrath and Dabelsteen 2004) narrowed a single geographical forest habitat into two temporal habitats – deciduous forest before and after foliation. Both studies found significant differences in signal transmission quality before and after foliation, suggesting that ephemeral habitat structure may serve as an additional evolutionary pressure on signal form. Although deciduous forests may have the most obvious seasonal differences in structure because of foliation events, it is possible and probable that other habitats do as well, particularly when considering potential effects of

meteorological processes in areas with seasonal fluctuations in temperature and humidity. In concordance with this, one study investigating differences in acoustic habitat by season found that prairie dog alarm calls transmit differently in the early summer versus the end of summer in temperate grasslands (Perla 2002). Contrarily, similar experiments found no difference in transmission quality of Black-and-gold Howler Monkey (*Alouatta caraya*) howls between spring and summer (Holzmann and Areta 2019) or between common marmoset (*Callithrix jacchus*) calls broadcast in the wet and dry seasons (Morrill et al. 2013) in subtropical forests. Combined, these results indicate that acoustic environment seasonality may be habitat dependent, or that some taxa have long range calls adapted to transmit equally well throughout the year.

An interesting test of temporal influences in the future might involve reciprocal playback of signals produced by migratory animals in both their breeding and overwintering habitat. For this, we might predict that signals transmit equally well in each location, that they transmit best in breeding season habitats where they may be most important to reproductive success (Bradbury and Vehrencamp 2011), or that animals use temporally specific signals which propagate best in each associated habitat. Regardless of the prediction, the signals of migratory animals provide an untouched and promising area of research for those interested in the AAH.

More study on extremely fine-scale temporal differences in transmission quality would also be beneficial, as studies on daily fluctuations in acoustic environment are relatively rare. Two studies show that katydid (Coultridge and Gordon 2015) and bladder grasshopper (Van Staaden and Römer 1997) signals propagate differently in the same location when played during the day and at night. Similar studies in birds imply that dawn chorusing might be explained by the findings that signals propagate with reduced amplitude loss (Brenowitz 1982), better signal-to-noise ratio (Priyadarshani et al. 2018), and more consistency (Brown and Handford 2003) at dawn versus other times of the day. Together, these studies suggest that acoustic space can vary on a daily cycle, and this merits further experimental investigation.

Evidence for acoustic fidelity across species

Although 80% of studies found differences in transmission quality between different habitats, evidence for organisms adapting their signals to accommodate those differences is far rarer. If habitats provide meaningful adaptive pressures, we should expect to see ‘acoustic fidelity’ in a species – that is, a species should produce signals that propagate best in native habitats as opposed to foreign habitats. However, in concordance with previous reviews of observational studies by Ey and Fischer (2009) and Erdtmann and Lima (2013), the studies reviewed here indicate that experimental evidence for the AAH is not as widespread as previously thought. Authors felt that they had found convincing evidence for the acoustic adaptation hypothesis in only 35% of reviewed studies, and approximately 28% of studies concluded that their experiments provided partial or species-dependent support for predictions posed by the AAH (Table 1). The authors of the remaining 34% of studies did not feel they found evidence for the AAH (Table 1). As suggested by Ey and Fischer (2009), this may indicate that the AAH only works under certain specific circumstances; potentially for only some taxa.

Support for the AAH indeed varied across taxa, with mostly positive results in birds, but less evidence in mammalian, insect, and anuran systems. In fact, only one of eleven

reviewed anuran studies claimed support for the AAH (Boatright-Horowitz et al. 1999); it concluded that American Bullfrogs (*Lithobates catesbeianus*) have signals adapted for in-air as well as in-water communication, but not that the species shows evidence for habitat-specific acoustic fidelity. More frequent habitat-specific acoustic fidelity in birds might occur because birds have an advantage over other taxa in that they have quick escape methods (i.e. flight) which may release their long-range acoustic signal evolution from the counter-selective force of eavesdropper/predator avoidance. Indeed, there appears to be some relationship between support for the AAH and how mobile a taxon is (mobility in this case increasing from anurans, to mammals, to flighted insects, to birds). Alternatively, it may be that because passerine avian songs are learned rather than innate, their long-range acoustic signals have more plasticity with which to adapt to local habitat. In support of this idea, many of the mammalian studies showing support for the AAH investigated primate signals, which can also be influenced by cultural selection (Briseño-Jaramillo et al. 2015), and recent work suggests that avian species with learned song have higher rates of diversification than those with innate signals (Mason et al. 2017). However, it is important to note that only two of the 32 avian studies reviewed (Slabbekoorn 2002; Ręk and Kwiatkowska 2016) included non-passerine species that do not learn their vocalisations, and this bias may skew the relative importance of the AAH to avian taxa as a whole. More research is needed in non-vocal-learning avian species to clarify larger patterns. Finally, it may be that on average, birds, insects, and mammals make signals that on principal must travel farther than those produced by smaller, less itinerant anurans, which tend to congregate in spatially clumped groups during long-range communication bouts used for mate attraction.

Inconsistencies in evidence for the acoustic adaptation hypothesis both between and within taxa may be in part due to methodology. As described above, measures of signal quality varied substantially across studies – though the suite of measures used does not appear to be related to whether the study supported the AAH or not (Table 1). Experiments also varied in the distances at which test signals were recorded. Researchers often justified recording distances by considering biological relevance; for example, territory size is regularly used to determine recording distances in avian studies because territory edges are often where acoustic interactions take place during resource competition (Catchpole and Slater 2008). However, this approach disregards the fact that communication can also happen within a territory, often between mates. To solve this, it has become well-established practice to record playback sounds at multiple distances which could simulate communication within and across animal territories (Table 1). Studies that did not give specific justification for recording distances tended to choose increasing distance increments of 5–25 m (Brenowitz 1982; De La Torre and Snowdon 2002; Brown and Handford 2003; Padgham 2004; Leader et al. 2005) or increased distances at a logarithmic scale (Castellano et al. 2003; Barker et al. 2009; Mouterde et al. 2014; Sandoval et al. 2015; Piza and Sandoval 2016; Velásquez et al. 2018). Concern has been raised in the past over how well experiments can be compared when recording distances are so different (Barker 2008). While it is true that absolute values of degradation cannot be compared between species/habitats when recorders are not placed at identical distances, it may be more important to consider biologically relevant signal transmission distances while designing playback studies (Hunter and Krebs 1979; Holland et al. 1998). In the future, it may be beneficial to standardise recording distances

at a set percentage of known average long-range interaction distances – perhaps at 50, 100, 150, and 200% of territory size or expected communication distance when relevant – though this method may not be plausible for every question or study system.

Differences in evidence for acoustic fidelity to habitat could also be species-specific due to differences in the way species respond to physical evolutionary pressures on signal transmission. In support of this, we see consistency in transmission properties for species' signals that have been tested in multiple habitats. Great Tits (*Parus major*) consistently show support for the AAH; their songs propagate better in native dense deciduous forest habitats when compared to foreign open woodlands (Hunter and Krebs 1979), unfoliated deciduous forests (Blumenrath and Dabelsteen 2004), and urban habitats (Nemeth and Brumm 2010; Mockford et al. 2011). Acoustic fidelity also appears to exist for Carolina Wrens (*Thryothorus ludovicianus*; Gish and Morton 1981), Yellow-headed Blackbirds (*Xanthocephalus*; Cosens and Falls 1984), Spot-backed Antwrens (*Herpsilochmus dorsimaculatus*; Nemeth et al. 2001), Dark-eyed Juncos (*Junco hyemalis*; Slabbekoorn et al. 2007), Rufous-and-White Wrens (*Thryophilus rufalbus*; Barker et al. 2009), Zebra Finches (*Taeniopygia guttata*; Mouterde et al. 2014), Blue Monkeys (*copithecus mitis*; Brown et al. 1995) and some bladder grasshoppers (Orthoptera, Pneumoridae; Van Staaden and Römer 1997; Couldridge and Van Staaden 2004), though these species' signals have not been tested in more than two habitat types. There does not appear to be any relationship between genetic relatedness and whether a species adapts its signal to the environment (Table 1). For example, a study by Nemeth et al. (2001) tested five species of closely related Antwrens and found partial evidence for the AAH in only three of them, and convincing evidence in only one. Similarly, forest-dwelling old-world monkeys appear to have acoustic fidelity while closely related savannah-dwelling species do not (Brown et al. 1995). Instead, adaptation may be more habitat-dependent, or the signals of some species may be subject to other selective pressures that outweigh the effects of habitat structure. However, inclusion of relatedness data in AAH experiments is rare and evolutionary history needs further, targeted study in the context of signal adaptation.

Remarkably, all species which showed acoustic fidelity and support for the AAH live in woodland, forest, or dense marsh habitats. This suggests that forest or marsh-dwelling species are more likely to adapt their signals to the acoustic environment. This may be an artefact of study bias or it may be that, as originally proposed by Morton (1975), open habitats do not have the capacity to select for signal characteristics which counter degradation because the acoustic environment is too unstable (temperature, humidity, wind, etc.; see Richards and Wiley 1980). Open habitats could instead select for simple signals with repeated elements which code for the same information, increasing the chance of effectively transferring that information at some point during the signal's transmission (Brown and Handford 2000). Indeed, those few studies which included some measure of variability in transmission quality found that signals produced by open-habitat passerine species transmit with less variability in open habitats when compared to closed habitats (Brown and Handford 1996, 2000) and that signal consistency may be more important than signal quality for the temporal spacing of singing bouts in birds (Brown and Handford 2003). In future studies, we suggest including some measure of transmission variability to account for different selective pressures between open and closed habitats regardless of habitat type. It is plausible that open habitat-dwelling species

adapt their signals to the environment in ways that are different from, but just as important as, adaptations seen in forest-dwelling species.

Not all studies in dense or forested habitat showed support for acoustic habitat fidelity. However, it is important to note that most studies which did not find support compared transmission quality between very similar habitat types. These comparisons include rainforests vs. ecotone forests (Slabekoorn and Smith 2002), dry vs. moist forests (Padgham 2004), open vs. closed urban habitat (Leader et al. 2005), and different populations within the same forested habitat (Kroon and Westcott 2006; Velásquez et al. 2018). It may be that the AAH does not operate on that fine a scale, as such specific acoustic environmental tuning could be maladaptive by essentially reducing the amount of 'suitable' acoustic habitat available for the species. In support of this idea, Barker et al. (2009) and Graham et al. (2017) both found that Rufous-and-white Wren songs were adapted to transmit better in forest vs. open habitats, but not within specific forest types. It may be helpful to characterise these habitats with quantitative variables as discussed above in an effort to elucidate any potential differences between relatively similar habitats. It may also be interesting to test hypotheses about whether habitat generalists and specialists show divergent patterns of acoustic adaptability, as it appears that known invasive species (American Bullfrog: Boatright-Horowitz et al. 1999; Llusia et al. 2013; Hawaiian birds: Sebastián-González et al. 2018) tend to be less influenced by environmental acoustics and show less acoustic fidelity than native species.

Tests of transmission and acoustic fidelity within species

Many of the studies reviewed here investigated whether transmission quality varied within (Holland et al. 1998; Couldridge and Gordon 2015) or between (Dabelsteen et al. 1993; Balsby et al. 2003; Jensen et al. 2008; Sandoval et al. 2015; Piza and Sandoval 2016; Graham et al. 2017) signal types of a single focal species, usually within a single habitat. Investigation of degradation in within-song elements (Holland et al. 1998) in Eurasian Wrens (*troglodytes troglodytes*) indicated that specific elements show differential transmission quality. This suggests that the AAH could theoretically work on such a fine scale, though the extent to which element-specific degradation is influenced by environment remains largely unknown.

Studies investigating transmission properties of different signals within a single species varied in their specific goals. Some studies investigated whether signals for a given species are specifically adapted to certain heights within a habitat. In general, call height is a well-known predictor of signal quality, where degradation is minimised when individuals call from high (Dabelsteen et al. 1993; Nemeth et al. 2001; Maciej et al. 2011) or moderate (Kime et al. 2000; Barker et al. 2009; Priyadarshani et al. 2018) locations compared to those near the ground, especially for anuran and insect species which spend the majority of signalling time near the ground (Lang 2000). This is likely because it allows the signaller to escape reverberative effects of vegetation and ground attenuation (Harris 1966). However, whether animal signals have adapted to this height effect remains unclear. Nemeth et al. (2001) tested the songs of five bird species living at five rainforest heights and found mixed support for signal adaptation in three of those species, and only solid evidence for one. In contrast, an intensive modelling study by Jensen et al. (2008) suggests that Hooded Crows (*Corvus corone cornix*) have adapted their calls to negate degradation caused by ground effects. Although perching high

during singing bouts is nearly ubiquitous in songbird species, this behaviour may not actually be an adaptation for improving signal quality in a less-than-ideal environment. In support of this, Mathevon et al. (2005) found that for Eurasian Blackcap (*Sylvia atricapilla*) songs, measures of degradation decreased considerably more with microphone height than for speaker height, indicating that perching high during communication may be for improved discrimination rather than for improved signal propagation.

Other studies tested differences in sex-specific signals. Barker et al. (2009) and Graham et al. (2017) found that female Rufous-and-White Wren songs degrade more quickly than male songs. Because these songs are transmitted in the same environment, it is likely they are not adapted to different habitats but for different purposes; in this system, the male song may be for long-distance male-male competition, while the female song may be for shorter-range mate contact (Barker et al. 2009). Mousterde et al. (2014) found that signal features providing the highest discrimination at a short distance are not the same as features providing the highest discrimination at a long distance, so sex-specific signals may be finely tuned to propagate well at different distances within a given habitat. For example, this study found that the segment of Zebra Finch songs that encodes for sex identification is remarkably resistant to degradation, and that male identifications can be discriminated further out in native arid habitats when compared to foreign habitats (Mousterde et al. 2014). The authors note that male songs are therefore likely to be more relied upon for contact calling at longer distances as opposed to female song. One study investigated differences in degradation between solo and duet songs rather than sex-specific differences (Sandoval et al. 2015) and found that duet song propagates no differently than solo song. Because both song types transmit well through the given environment, it is likely that both are used for long-range communication. Differences in sex-specific and duet signal propagation and their relations to habitat structure have not been examined fully, and offer a promising avenue of investigation into the acoustic adaptation hypothesis, especially in taxa outside of birds that have sex-specific acoustic signals.

Conclusions and future directions

Here we assess current evidence for the acoustic adaptation hypothesis as provided by experimental playback studies of animal signal transmission quality. These experiments provide direct tests of the AAH and are an essential complement to descriptive correlational tests of the same ideas. For example, Nicholls and Goldizen (2006) conducted a comparative analysis which showed that call structure in Satin Bowerbirds (*Ptilonorhynchus violaceus*) has converged by habitat regardless of geographic distance and genetic relatedness, but their transmission experiments showed that native songs were no less attenuated than foreign songs when played in a native habitat. These results highlight the importance of testing transmission itself and not relying solely on call structure as a proxy for transmission in acoustic studies.

As was found in previous reviews of comparative evidence for the AAH (Boncoraglio and Saino 2007; Ey and Fischer 2009), transmission experiments showed inconsistent support for the acoustic adaptation hypothesis. A lack of support for the AAH may arise because of other factors shaping acoustic signal structure, including anatomical limitations such as body size (in cats: Peters and Peters 2010; in frogs: Zimmerman 1983; in

birds: Ryan and Brenowitz 1985), cultural drift (in primates: De La Torre and Snowdon 2002 and Briseño-Jaramillo et al. 2015), or genetic drift (in frogs: Lee et al. 2016). Further, degradation patterns themselves may be under conflicting evolutionary pressures in species that use signal degradation for ranging purposes (in frogs: Ringler et al. 2017; in birds: Holland et al. 2001). Alternatively, inconsistencies in evidence may be due in part to widespread differences in methodology, as studies varied wildly in key experimental design factors such as recording distance and height, equipment, sound source, and computation of signal degradation (Table 1). Until methods are standardised within and across taxa, we expect that the large-scale mechanisms behind the AAH will remain elusive to researchers. We suggest that future tests of the acoustic adaptation hypothesis standardise approaches in several ways: 1) Measure multiple complimentary aspects of signal degradation. Promising or already widely used measures include excess attenuation, blur ratio, signal-to-noise ratio, and discrimination distance (Table 2). 2) Place microphones at distances that make sense for target species in terms of typical communication distances; further, several distances should be tested at relative increments. We propose 50, 100, 150, and 200% of known territory size or typical signal-receiver distance to help standardise across species, where applicable. 3) Use high-quality recordings of actual animal signals wherever possible, as these represent signals that have undergone selection. Further, normalise sound stimuli recording distances, as the degradation that occurs during recording cannot be otherwise accounted for during transmission experiments. This is especially important for studies investigating multiple species or sexes which may variably tolerate the proximity of a recordist. 4) Characterise habitat structure quantitatively rather than qualitatively or confirm that habitat designations are indeed significantly structurally different. Ideally, this includes habitat surveys of present vegetation, topology, and meteorology. We suggest using comparable forms of structural data such as percent canopy cover, average tree height, and average air pressure, as well as relative amounts of specific types of vegetation which distort signals differently (i.e. hardwood, leaves, thick moss, etc.). 3D LiDAR scanning has recently been used to tackle quantification (Priyadarshani et al. 2018; Sebastián-González et al. 2018; Phillips et al. 2020), though the precision and detail allowed by this technology has not yet been fully investigated in the context of acoustic space. The field could vastly benefit from investigation into the reliability of both traditional and 3D structural surveying of acoustic space.

Finally, although the AAH was proposed nearly 50 years ago, we have yet to effectively test several important aspects of the hypothesis (Morton 1975). Some potential areas of interest include: 1) Expanding tests of the AAH to novel environments with a focus on those outside of forests. Examples of untested or poorly tested habitats include riparian zones, canyons or cliffs, deserts, alpine tundra, and urban environments. 2) Including multiple taxa or signal types in reciprocal playback studies in multiple habitats and locations. Ultimately, this is the most efficient way to test the quality of a range of signals across habitats. 3) Designing tests that include a measure of variation in signal quality. Although originally proposed by Morton (1975), very little research has been done to test whether signals with repeated information transmit more consistently than more complex signals in environmentally variable habitats. 4) Further investigating whether the AAH extends to temporal variation in habitat. This is especially important for species which over-winter in a single, structurally variable environment or those that migrate to

distinct habitats over the year. Investigating these aspects of the acoustic adaptation hypothesis will help elucidate the nature of the relationship between habitat structure and long-range acoustic signalling.

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Ethical statement

All results reported here are based on available literature. As such, we did not use animal or human subjects.

Disclosure statement

The authors have not received any financial benefit from this research and have no conflicts of interest to disclose.

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Data availability statement

All results reported here are based on previously published studies; therefore, we have no new data to archive or make accessible. Data sources are detailed in [Table 1](#).

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