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Testing the acoustic adaptation hypothesis with vocalizations from three mongoose species

Aitana Garcia Arasco [a, b, c], Marta Manser [a, b, d], Stuart K. Watson [a, d, e], Solomon Kyabulima [f], Andrew N. Radford [g], Michael A. Cant [f, h], Maxime Garcia [a, b, d, *]

[a] Animal Behaviour, Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland
[b] Kalahari Meerkat Project, Kuruman River Reserve, Van Zylsrus, Northern Cape, South Africa
[c] Université de Rennes 1, UFR SVE, France
[d] Center for the Interdisciplinary Study of Language Evolution, University of Zurich, Zurich, Switzerland
[e] Department of Comparative Language Science, University of Zurich, Zurich-Oerlikon, Switzerland
[f] Banded Mongoose Research Project, Mweya, Queen Elizabeth National Park, Uganda
[g] School of Biological Sciences, University of Bristol, Bristol, U.K.
[h] Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Cornwall, U.K.

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Acoustic signals degrade and attenuate as they propagate through the environment, thus transmitting information with lower efficiency. The acoustic adaptation hypothesis (AAH) states that selection should shape the vocalizations of a species to maximize transmission through their habitat. A specific prediction of the AAH is that vocalizations will transmit better when emitted in their native habitat versus nonnative habitats. We tested this prediction using vocalizations of three mongoose species that dwell in structurally different habitats: banded mongooses, *Mungos mungo*, dwarf mongooses, *Helogale parvula*, and meerkats, *Suricata suricatta*. Representative vocalizations of the three species were broadcast and rerecorded in each habitat at six distances from the source. Rerecorded vocalizations were compared to nondegraded calls through spectrogram correlation. Using generalized linear mixed models, we then quantified the differences in transmission fidelity of each species' vocalizations. Overall, we found partial support for the AAH within the mongoose family: habitat type strongly affected sound transmission, but depending on the species, vocalizations did not always transmit best in their native habitat, suggesting various degrees of acoustic adaptation. Vegetation cover within habitat type was also found to have a significant influence on the transmission properties of vocalizations. In addition, we found evidence that by changing their behaviour, either by producing vocalizations at different amplitudes or by choosing a specific calling location, mongooses can reduce sound degradation and attenuation over distance, thereby enhancing their communication efficiency. Our work highlights how habitat features may be key determinants of vocalization structure in mongooses, and is generalizable to other species living in similar conditions. It also suggests that, given a species and habitat, other selective pressures might prevail and limit acoustic adaptation in animal communication systems. Finally, our study provides insights into how mammals can adjust their vocal behaviour to compensate for environmental constraints on the transmission of their vocalizations.

Acoustic communication plays a crucial role in the coordination of animal activities (Bradbury & Vehrencamp, 2011). Diverse species rely on acoustic signals to find mating partners (Ellis et al., 2011), coordinate activities within social groups (Gall & Manser, 2017), defend a territory (Naguib & Wiley, 2001) or avoid predation (Daniel & Blumstein, 1998). In these contexts, the successful transmission and reception of information is crucial (Adami, 2016). Nevertheless, the physical and biotic characteristics of a signaller's environment (e.g. jungle, Eyring, 1946; forest, Slabbekoorn, 2004), as well as the typical ambient noise levels (Slabbekoorn, 2004; Waser & Brown, 1986), impose a number of constraints which directly affect the transmission of acoustic signals. The impairment of signal quality caused by these

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* Corresponding author.
E-mail address: maxime.garcia@ymail.com (M. Garcia).

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characteristics can subsequently hinder the ability of receivers to decode the important information conveyed therein (Wiley & Richards, 1978). Therefore, acoustic signals that efficiently transfer information and resist degradation in the natural environment in which they are used should be favoured to ensure optimal communication (Marten & Marler, 1977; Morton, 1975). Shedding light on these environmental pressures acting on signal evolution is critical to a comprehensive understanding of how signals evolve and diversify more broadly.

The acoustic adaptation hypothesis (hereafter AAH; Morton, 1975) predicts that the acoustic properties of a given species' vocalizations will have been selected for optimal transmission to overcome the constraints imposed by the features of their native environment. Studies focusing on disentangling the physical phenomena associated with sound transmission (Ingård, 1953; Wiley & Richards, 1978) have identified two broad processes: sound attenuation (i.e. amplitude loss) and degradation (i.e. changes in acoustic structure). Attenuation results from several physical factors, such as spherical spreading, ground reflection and temperature- and humidity-dependent molecular absorption (Harris, 1966; Wiley & Richards, 1978). As an example, spherical spreading entails a decrease of 6 dB of the signal per doubling of distance from an origin point (Jacobsen & Juhl, 2013; Wiley & Richards, 1978). Vocalizations can also be affected by frequency-dependent attenuation (i.e. greater attenuation for specific frequencies; Morton, 1975). Other phenomena like reflection and diffraction can both cause attenuation and degradation of acoustic signals by deflecting acoustic waves (Wiley & Richards, 1978). Finally, the accumulation of irregular amplitude fluctuations (i.e. atmospheric turbulence), as well as acoustic reverberation and scattering (multiple reflections due to rough surfaces), can also bring about the degradation of the signal (Ingård, 1953; Wiley & Richards, 1978). Similarly, vegetation and background noise may reduce sound quality (Aylor, 1971; Luther & Gentry, 2013; Martens & Michelsen, 1981). Vegetation is an effective sound barrier, notably at high frequencies, while ambient noise hinders receiver ability to resolve differences among signals or to discriminate signals from background perturbations (Aylor, 1971; Luther & Gentry, 2013; Martens & Michelsen, 1981). Given the great diversity of habitat structures and daily noise distribution, each environment is likely to have its own acoustic limitations for sound transmission (e.g. Aylor, 1971; Lemon & Date, 1993). Broadcasting vocalizations in different environments is key to assessing the effect of these limitations and increasing our knowledge on how species optimize their acoustic communication systems.

For several decades, researchers have been addressing how the environment influences vocal communication. Overall, in closed habitats (e.g. forest, jungle) where vegetation density is high, reverberation and absorption are ubiquitous, leading to a stronger selective pressure on the acoustic parameters of vocalizations (Waser & Brown, 1986). This results in stereotyped signals with lower dominant frequencies, narrower frequency ranges, longer durations and lower amplitudes or frequency modulation. By contrast, in open spaces, short and frequency-modulated signals should provide a selective advantage (Marten & Marler, 1977; Morton, 1975; Richards & Wiley, 1980; Wiley & Richards, 1978). To date, studies on several animal clades fulfil the predictions and therefore support the AAH (e.g. birds, Hunter & Krebs, 1979; primates, Brown et al., 1995; frogs, Goutte et al., 2018). However, more recent studies have found mixed evidence or failed to demonstrate this tendency (reviewed in Hardt & Benedict, 2021). These contradictory results could be explained by: (1) a very broad categorization of habitats such as 'open' versus 'closed', which oversimplifies complex habitat conditions; (2) a focus on a single species (Holzmann & Areta, 2020) or a single call type (Daniel & Blumstein, 1998); and/or (3) acoustic analyses that do not necessarily rely on similar parameters across studies (e.g. focusing on either frequency- or time-related parameters (Graham, Sandoval, Dabelsteen, & Mennill, 2017; Mikula et al., 2021; Zimmerman, 1983)). In addition, isolating the specific effect of habitat on the structure of an acoustic signal might be further complicated by potentially confounding factors, such as phylogenetic relatedness, physiology, morphology, social system, interspecific acoustic competition, context of calling or internal state of the caller (Cardoso & Price, 2009; Forrest, 2015; Manser, 2001; Taylor & Reby, 2010). Limiting the possible interaction of these factors is key to pinpointing the effect of habitat on the evolution of acoustic signals' structure. Therefore, we expect to gain valuable insights into acoustic adaptation by examining sound transmission of multiple call types (in both native and non-native habitats) from closely related species with similar social structures but living in different habitats.

Mongooses are small carnivores (Order: Carnivora; Family: Herpestidae; Bothma, 1998) that provide an excellent opportunity to address questions relating to the transmission of vocalizations. In this study, we tested the AAH by specifically focusing on three closely related species of mongooses that natively occupy different habitats: banded mongooses, *Mungos mungo*, dwarf mongooses, *Helogale parvula*, and meerkats, *Suricata suricatta*. These species differ in the habitats they occupy: while meerkats dwell in more open, dry areas, banded mongooses and dwarf mongooses occur in more vegetated sites, partly overlapping in their geographical distribution (Manser et al., 2014). In addition, despite their phylogenetic proximity and the fact that they all are highly social (Veron, Colyn, Dunham, Taylor, & Gaubert, 2004) and produce a wide variety of calls, their vocal repertoires differ significantly (Manser et al., 2014). This vocal diversity can be quantified both in terms of: (1) acoustic structure, with large variation found in call types that have a similar function in different species (e.g. antipredator alarm calls or 'close' calls produced while foraging cohesively); and (2) function, with for example shifts in amplitude (i.e. in call loudness) matching group dynamics, or with context-specific call types found in some but not all of the three species (e.g. meerkat barks, or sentinel calls in dwarf mongooses and meerkats). These differences in vocalizations may be driven by differences in habitats and/or the behaviours associated with species-specific life contexts (note that, in all three species, between-group vocal communication barely ever occurs and is thus unlikely to drive acoustic differences in their vocal repertoires). For instance, sentinel calls are produced in dwarf mongooses and meerkats by individuals that seek an elevated position (e.g. by climbing on a bush) to scan for predators and warn groupmates of danger (Kern & Radford, 2013; Rauber & Manser, 2017). This behaviour may be adaptive to more efficient signal transmission (although this could be an evolutionary by-product resulting from an improved vigilance strategy), by avoiding ground attenuation (Kern & Radford, 2013; Wiley & Richards, 1978).

To investigate how habitat may have shaped vocalization properties in social mongooses, we broadcast a set of representative call types from these species in each of the three habitats and rerecorded them at six different ranges to evaluate signal degradation. Based on the AAH, we predicted that the vocalizations of each species would overall transmit with less degradation within their native habitat relative to those of the other two species. We also predicted that, as vegetation cover increases, this should significantly reduce sound transmission. Finally, in line with the context-specific production of vocalizations highlighted above, we explored whether these species can overcome the acoustic constraints (in particular signal attenuation) imposed by their environment through adjustments of their

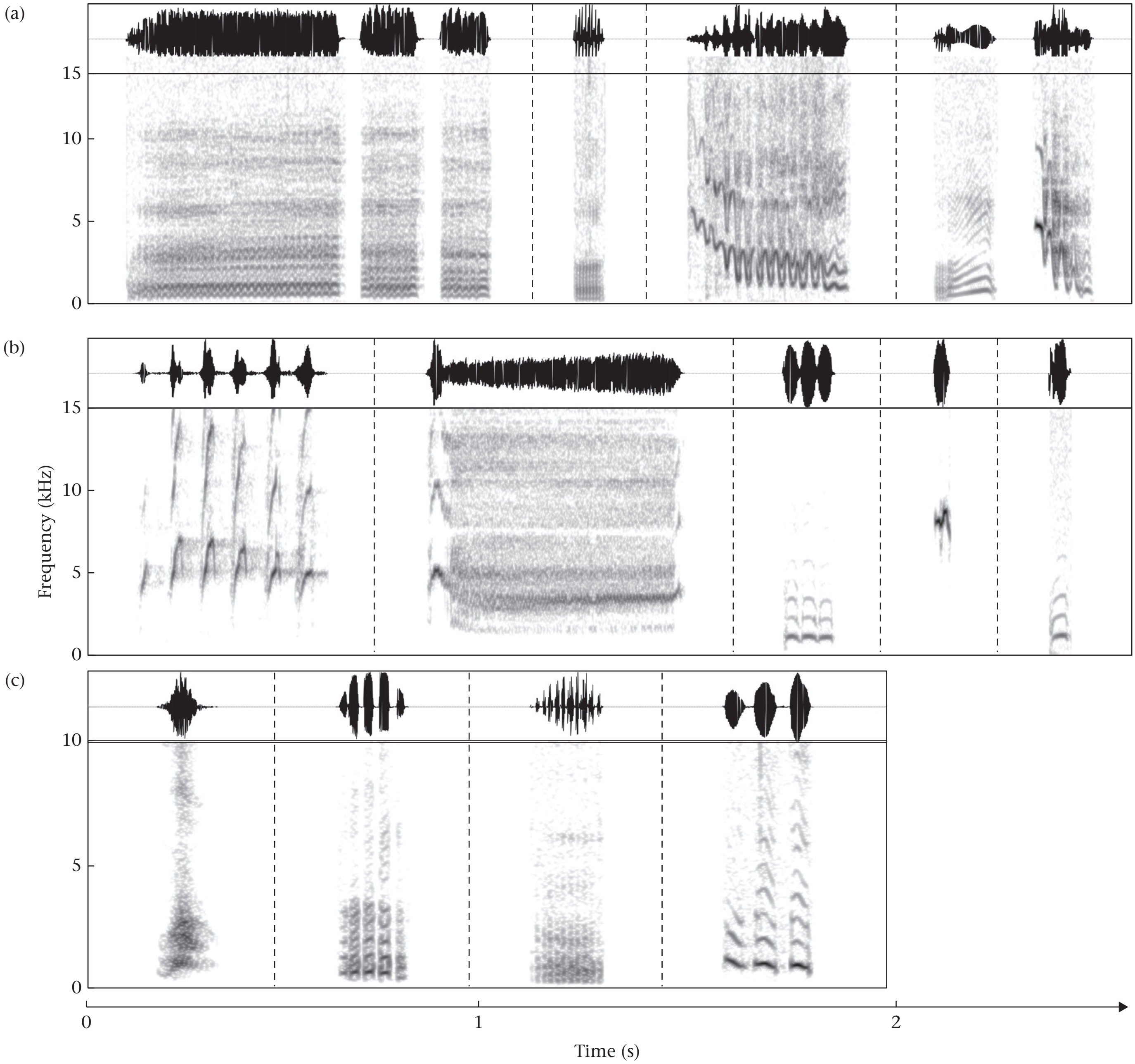

Figure 1. Spectrograms of the call types used in our propagation experiments. (a) Banded mongoose vocalizations (from left to right: alarm call, close-forage call, mobbing/recruitment call and moving call). (b) Dwarf mongoose vocalizations (from left to right: aerial alarm call, terrestrial alarm call, contact call, mobbing/recruitment call and sentinel call). (c) Meerkat vocalizations (from left to right: bark, contact call, mobbing/recruitment call and sentinel call).

vocal behaviour such as amplitude shifts or call-specific spatial positioning.

METHODS

Study Sites and Species

Data were collected from habituated but wild populations of the three study species: banded mongooses, dwarf mongooses and meerkats. These three mongoose species dwell in Africa and partly overlap in their geographical distribution, although meerkats typically occupy arid environments (Clutton-Brock et al., 1998) while dwarf and banded mongooses are found in more vegetated habitats such as woodlands and wooded savannas (Collier, 2017; Jansen, 2013). Given their small body size and similar foraging behaviour, they are all exposed to a suite of predators (raptors, medium-sized terrestrial carnivores and snakes). Although they are all group living and forage cohesively, they differ in group size (maximum group size in dwarf mongooses: <30; meerkats: <50; banded mongooses: <70). Both meerkats and dwarf mongooses show a despotic reproductive system with the dominant pair monopolizing breeding, while reproduction in banded mongoose groups is more egalitarian (Manser et al., 2014). All group members help rear offspring in each species.

Banded mongooses

The study population was located on the Mweya Peninsula (hereafter ‘Mweya’), in the Queen Elizabeth National Park, western

Table 1
Natural peak SPL values of call types used in propagation experiments

Banded mongoose		Dwarf mongoose		Meerkat	
Call type	Average peak amplitude (dB)	Call type	Average peak amplitude (dB)	Call type	Average peak amplitude (dB)
Alarm (*N* = 8)	78	Aerial alarm (*N* = 9)	86.5	Bark (*N* = 56)	98.5
Close forage (*N* = 33)	66.5	Contact (*N* = 45)	64.5	Contact (*N* = 22)	72.5
Mobbing/recruitment (*N* = 9)	85	Mobbing/ recruitment (*N* = 34)	88.5	Mobbing/recruitment (*N* = 22)	75–80[a]
Moving (*N* = 17)	74	Sentinel (*N* = 17)	61.5	Sentinel (*N* = 40)	71.5
		Terrestrial alarm (*N* = 14)	83		

Call types selected are indicated together with their natural peak SPL (in dB SPL). The number of recordings used for SPL calibration is given in parentheses.

[a] For reasons inherent to field work logistics, the meerkat mobbing/recruitment vocalizations were initially broadcast with a peak amplitude of 80 dB SPL and later calibrated with a peak SPL of 75 dB SPL. This does not impact 'high' and 'low' amplitude conditions (since amplitude is then normalized; see section below for details on experimental conditions) and allows comparative investigation across field sites.

Uganda (0°12′S, 27°54′E). Annual rainfall is typically 800–900 mm, with two dry periods in January–February and June–July (Cant, Nichols, Thompson, & Vitikainen, 2016). Individuals were clearly identified by unique fur-shave patterns, and groups were found by radiotracking a few individuals equipped with a radiocollar within each group (Marshall et al., 2016). All research work was carried out under licence from the Uganda National Council for Science and Technology, and all procedures were approved by the Uganda Wildlife Authority (research permit Ref. COD/96/05). All procedures were approved by the Ethical Review Committee of the University of Exeter.

Dwarf mongooses

The study population was located on Sorabi Rock Lodge (hereafter 'Sorabi'), a private game reserve in the Limpopo Province, South Africa (24°11′S, 30°46′E). The climate is characterized by two distinct seasons: cold, dry winters (May–August) and hot, wet summers (September–April), with a mean annual rainfall around 467 mm, occurring mostly between October and April (Kern & Radford, 2013). Individuals were clearly identified by distinctive physical features or blonde dye marks (Wella UK Ltd, London, U.K.) applied to their fur (Kern & Radford, 2013), and groups were found and followed based on daily hikes through the reserve. All research work was conducted under permission from the Department of Environmental Affairs and Tourism, Limpopo Province (permit number: 001- CPM403-00013), the Ethical Review Group, University of Bristol (University Investigator Number: UIN/17/074) and the Ethical Committee of Pretoria University, South Africa (permit number: EC049-16).

Meerkats

The study population was located at the Kuruman River Reserve in the southern Kalahari Desert (hereafter 'Kalahari'), Northern Cape Province, South Africa (26°58′S, 21°49′E). Annual rainfall in this area averages around 250 mm, mostly occurring between December and March (Clutton-Brock et al., 1999). All group members were uniquely dye-marked (Garnier Nutrisse, L'oréal, Paris, France) to allow individual identification, and one or two individuals of each group were fitted with a radiocollar to facilitate localization of the group (Jordan, Cherry, & Manser, 2007). All research work was carried out under a permit issued by the Northern Cape Conservation Service, South Africa, and was approved by the University of Pretoria Ethics Committee (Permit Number: EC031-13).

For all three species and projects, all procedures adhere to the ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research and Teaching (ASAB Ethical Committee/ABS Animal Care Committee, 2012).

Acoustic Recordings

For each of the three study species, we selected call types for use in propagation experiments to be as representative as possible of the acoustic structure variability (in terms of frequency range and tonal/nontonal quality) found in their full vocal repertoire. When possible, we also aimed to include call types carrying out a similar function across species. This resulted in four call types for banded mongooses and meerkats and five call types for dwarf mongooses (Fig. 1, Table 1). Study populations were habituated to human presence, which allowed audio recordings to be made 0.5–2.5 m from focal individuals. Recordings used in this study either came from existing files collected as part of the long-term projects or from fieldwork carried out by M.G. (November 2018–December 2019) when a better sampling/representation of the chosen call types was necessary. For each call type, we collected 10 different exemplars to capture natural acoustic variation within each call type. Whenever possible, each of these 10 calls came from a different individual (number of individuals per call type: mean ± SE = 8.7 ± 0.4; range 6–10). Recordings were made using a Sennheiser ME66 microphone (frequency response: 40–20 000 Hz ± 2.5 dB; Sennheiser Electronic GmbH & Co. KG, Wedemark, Germany) powered through a K6 module, connected to a Marantz PMD 661 MK II (48 kHz sampling frequency and 16-bit quantization), and mounted on a Rycote Modular Windshield (Stroud, U.K.) WS 7 Kit to reduce shock- and wind-induced noise. All recordings were saved as uncompressed WAV files. Similar or equivalent equipment was used to collect earlier recordings that were used in this study.

Sound Calibration

Prior to carrying out propagation experiments, we calibrated sound amplitude for each of the call types (i.e. 'how loud' the sounds produced by the animals were). This step involved measuring the sound pressure levels (SPL, expressed in decibels, dB) at which vocalizations were produced as well as documenting the distance (assessed visually, given that foraging individuals rarely remain still and thus prevent the use of e.g. laser measurement) between the microphone's membrane and the head of the vocalizing animal (range 10 cm–1.5 m; typically within 50 cm). Because vocalizations from the three species can be very short (<0.5 s), direct measurement of SPL was deemed more error-prone than measurements made during longer periods of steady silence. Therefore, we measured background noise level as a reference to later calculate the SPL of vocalizations. This was performed using a digital sound level meter (Voltcraft SL-100; Hirschau, Germany; accuracy: ±2 dB, frequency measurement range 31.5 Hz–8 kHz) using the following acquisition settings: 'dB C', 'fast' acquisition and

Table 2
Summary table of the experimental design

Field site [species]	Vegetation cover			Amplitude				Time of day		
	Open	Intermediate	Dense	High	Low	Natural ground	Natural perch	AM	NOON	PM
Kalahari [meerkats]	4	4	4	41	40	40	39	4	4	4
Mweya [banded mongooses]	4	4	4	36	37	36	36	4	4	4
Sorabi [dwarf mongooses]	4	4	4	38	38	40	37	4	4	4

Counts correspond to the number of times that the full propagation sequence (composed of 130 vocalizations) was played and rerecorded, depending on experimental conditions (Vegetation cover, Amplitude and Time of day). Species are indicated in brackets together with their native habitat.

‘Lo’ dB range given the low amplitude of background noise recorded. Following a recording session, we could derive the signal's natural amplitude relative to that of the background noise, extracting the peak amplitude for each vocalization using Praat acoustic software (function ‘Get maximum intensity’; pitch settings: min = 75 Hz & max = 2000 Hz; averaging method = ‘mean energy’; Boersma & Weenink, 2020). Eventually, this process produced average peak SPL values for each call type (see Table 1), based on recordings from multiple vocalizations and multiples distances (number of vocalizations: 8–56; recording distance: 0.15–2.5 m). Because the number of vocalizations for each call type was not equal, a median peak SPL value was obtained for each call type (and preferred over a mean peak SPL to reduce potential effect of outlier values). Because the Praat software absolute amplitude values are meaningless without a reference, these peak SPL values were adjusted based on the background noise amplitude for which we had ‘true’ measurement (i.e. actual readings from the digital sound level meter). Finally, the resulting final SPL values (corresponding to true amplitudes but measured at different distances) were scaled to provide the natural amplitude for call types produced at 1 m, using the following equation:

$$\mathrm{SPL_{d1}} = \mathrm{SPL_d} - \left|20 \times \log_{10}\left(\frac{\mathrm{d}}{\mathrm{d1}}\right)\right|$$

where $\mathrm{SPL_d}$ is the SPL value measured at a given distance (‘d’) between the microphone membrane and the animal's head, and d1 is the distance of 1 m (i.e. is equal to 1). Hence, $\mathrm{SPL_{d1}}$ is the SPL value at 1 m from the loudspeaker.

Propagation Playback Experiments

Propagation experiments were carried out in April–May 2019 (Sorabi and Mweya) and November–December 2019 (Kalahari). These experiments consisted of broadcasting the previously recorded vocalizations from a portable loudspeaker (Behringer Europort MPA30BT; frequency response: 70–18 000 Hz ± 3 dB) connected to a MacBook Pro (Retina, 15-inch, Mid 2015) and rerecording the sequences using an array of six microphones (all Sennheiser ME66; same model specifications as for acoustic recordings). The microphones were placed horizontally on the ground (thereby mimicking the head height of foraging mongooses) on a straight line, 1, 3, 6, 12, 24 and 48 m from the loudspeaker and angled directly facing it (see Supplementary material, Fig. S1 for pictures) and connected to a Zoom F8 multichannel digital audio recorder (Zoom Corporation, Tokyo, Japan). This choice covers ecologically relevant distances since most behaviours in these three species occur while individuals are within this range. This set-up allowed simultaneous sound acquisition from the six distances, and gain settings were all set to the same value of +34, which allowed optimal signal-to-noise ratios and enabled comparability of sound amplitude from the rerecorded vocalizations.

Propagation playback sequences were composed of 130 vocalizations (10 calls per call type). Vocalizations were separated by 0.6 s silence intervals and concatenated following a random order. In each of the three habitats, sequences were played back with the following conditions.

For amplitude, three conditions, ‘low’, ‘high’ and ‘natural’, were assessed. All vocalizations were scaled to 67.5 ± 3 dB SPL at 1 m and 92.5 ± 3 dB SPL at 1 m for ‘low’ and ‘high’ amplitude, respectively. The aim of standardizing amplitude was to investigate the effect of the acoustic structure of vocalizations independently from the natural variation in the amplitude at which they are naturally produced, yet within a natural range (the low and high values chosen are within the natural amplitude range found across the call types of the three species: 61.5–98.5 dB, Table 1). In the ‘natural’ condition, all vocalizations were scaled to their natural amplitudes (Table 1), allowing investigation of their natural degradation properties.

The experimental set-up was always installed on flat ground, and trials were carried out in three different vegetation cover conditions. These were ‘open’ (no obstacle between the loudspeaker and the microphone array), ‘dense’ (as much vegetation as possible, including grass, shrubs and/or rocks, and trees, between the loudspeaker and the microphone array) and ‘intermediate’ (a compromise between ‘open’ and ‘dense’) vegetation cover (see Supplementary material Fig. S2 for pictures). Because we established these three categories of vegetation cover based on a relative assessment within a given habitat, we could not compare similar vegetation cover levels across habitats. Instead, we addressed this issue by looking at the effect of vegetation cover within each habitat separately.

To investigate behavioural vocal adjustments in relation to height, sequences were played by placing the loudspeaker either on the ‘ground’ or on a ‘perch’ at a height of 1 m, simulating the natural foraging behaviour and the natural elevation adopted by meerkats and dwarf mongooses when producing sentinel calls, respectively. ‘Low’ and ‘high’ amplitude sequences were systematically played from the loudspeaker located at ground level, while ‘natural’ amplitude sequences were played both from the ground and from a perch.

Experiments were carried out in the morning (‘AM’, from 0630 to 1130), around noon (‘NOON’, 1100–1400) and in the afternoon (‘PM’, 1530–1905). In all experimental trials, wind speed and temperature were documented to account for possible variation in environmental conditions. The variable ‘Time of day’ is used in place of temperature and wind values in statistical models (see Statistics section below), after preliminary inspection revealed significant temperature and wind differences between AM, NOON and PM conditions (Kruskal–Wallis tests followed by pairwise Wilcoxon rank sum comparisons with Bonferroni corrections for multiple testing; Table A1).

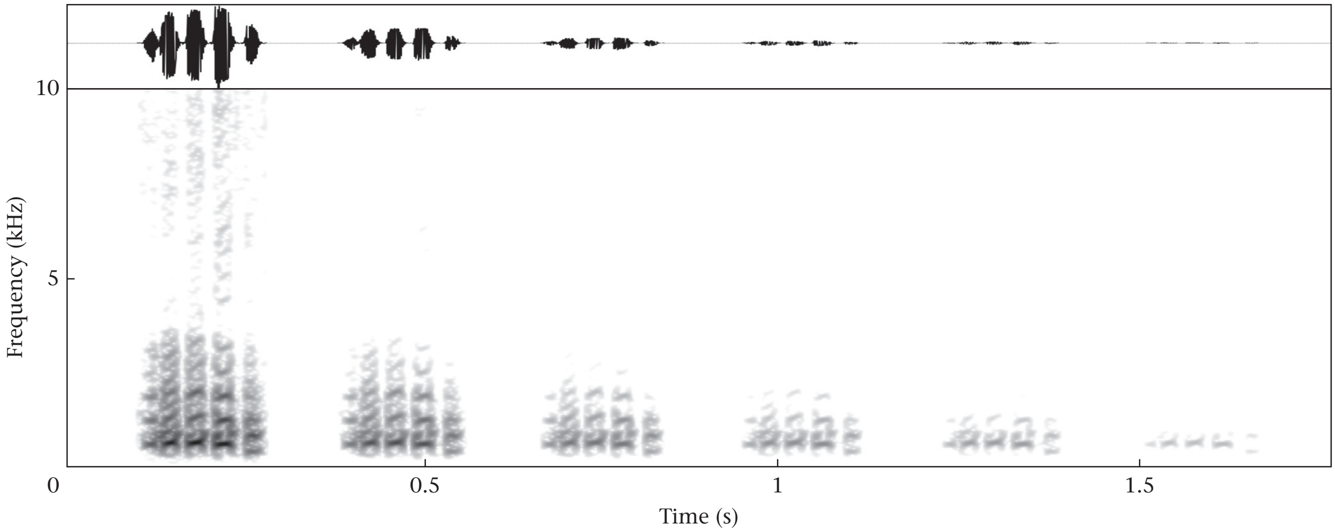

Figure 2. Spectrograms of a meerkat contact call recorded at 1, 3, 6, 12, 24 and 48 m (from left to right). The digital spectrogram of the recording made at 1 m was used as a reference for spectrogram correlations with recordings collected from all other distances.

For each amplitude condition within a given habitat, the playback sequence was repeated several times to provide sufficient replicated data, with the aim of minimizing the potential effect of background noise (such as overlapping bird calls) in the analyses. A crossed experimental design was used, which ensures a balanced combination of the various conditions (detail on the number of times that the sequence was played in each condition is provided in Table 2).

Postprocessing and Analyses

Postprocessing of the rerecorded sequences involved time synchronization of the various channels (six in total, corresponding to one microphone per distance), as well as extraction and annotation of each rerecorded call. This was done using a custom-made Praat script (authorship: M.G.). After call extraction, clipped signals (i.e. those for which the maximum amplitude could not be captured due to the microphone's membrane being overridden, occasionally found for some meerkat barks rerecorded at 1 m) were removed, together with their corresponding rerecordings (i.e. the same call recorded at other distances). The aim of this procedure was to remove calls unsuitable for further acoustical analyses. Following this step, we carried out spectrogram correlation analyses. For each of the 130 vocalizations, the spectrogram of the recording obtained at 1 m was used as a reference for correlation with spectrograms of recordings obtained at the five other distances (see Fig. 2 for illustration). This was performed by digital spectrographic cross-correlation (using the 'xcorr' function from the R package 'WarbleR'; Araya-Salas & Smith-Vidaurre, 2017). This approach involves digital spectrograms, i.e. the comparisons are made using matrices that include the time, frequency and amplitude values of the spectrogram. Because this method is a cross-correlation with a sliding window, the output is a cross-correlation function, with a correlation value for each sliding step. The final cross-correlation value provided is then the peak value from the cross-correlation function. Therefore, each call recorded at 3, 6, 12, 24 and 48 m has a specific spectrogram correlation value, allowing, for each of the conditions considered, quantification of acoustic degradation over distance. Prior to computing spectrogram correlations and because call types differed in their frequency range, a band-pass filtering was applied ranging from 50 Hz (a conservative lower boundary due to the frequency response of the microphones used for recordings) to the 95th quantile of the vocalization rerecorded at 1 m (using the function 'acoustat' from the R package 'Seewave'; Sueur, Aubin, & Simonis, 2008). In other words, this is the frequency value below which we find 95% of the acoustic energy of the signal rerecorded at 1 m, and it is used as an upper frequency boundary for spectrogram correlations carried out with the rerecorded vocalizations at 3, 6, 12, 24 and 48 m.

In parallel, sound attenuation was estimated based on the decrease in amplitude of the vocalizations rerecorded at different distances. For this, we extracted the peak amplitude of each vocalization (again, using the function 'Get maximum intensity'; pitch settings: min = 75 Hz; max = 2000 Hz; averaging method = 'mean energy') and the mean amplitude value (function 'Get intensity'; pitch settings: min = 75 Hz; max = 2000 Hz; averaging method = 'mean energy') of both silent sections surrounding each vocalization. This allowed calculation of a single 'amplitude difference' value for each vocalization at each distance, corresponding to the vocalization peak amplitude minus the average background noise amplitude.

Finally, analyses were carried out to investigate whether the acoustic structure of vocalizations could help explain potential differences in sound transmission properties. In particular, we looked at the energy distribution within call types, measured via four parameters: the dominant frequency (peakF, extracted using the function 'specprop' from the R package 'seewave') and the Q25, Q50 and Q75 frequency quartiles (the frequency values below which we find 25%, 50% and 75% of the energy in the acoustic signal, respectively; extracted using the function 'acoustat' from the R package 'seewave'). These analyses were performed based on the raw audio files (i.e. the vocalizations used to create our propagation sequences, $N = 130$).

Statistics

To investigate differences in how vocalizations were adapted to the living conditions of the three study species, we performed various analyses of degradation patterns over distance. These tested for the effect of various predictors (species identity, living habitat location, vegetation cover, sound amplitude and behavioural adjustment) and their interaction with distance (note that

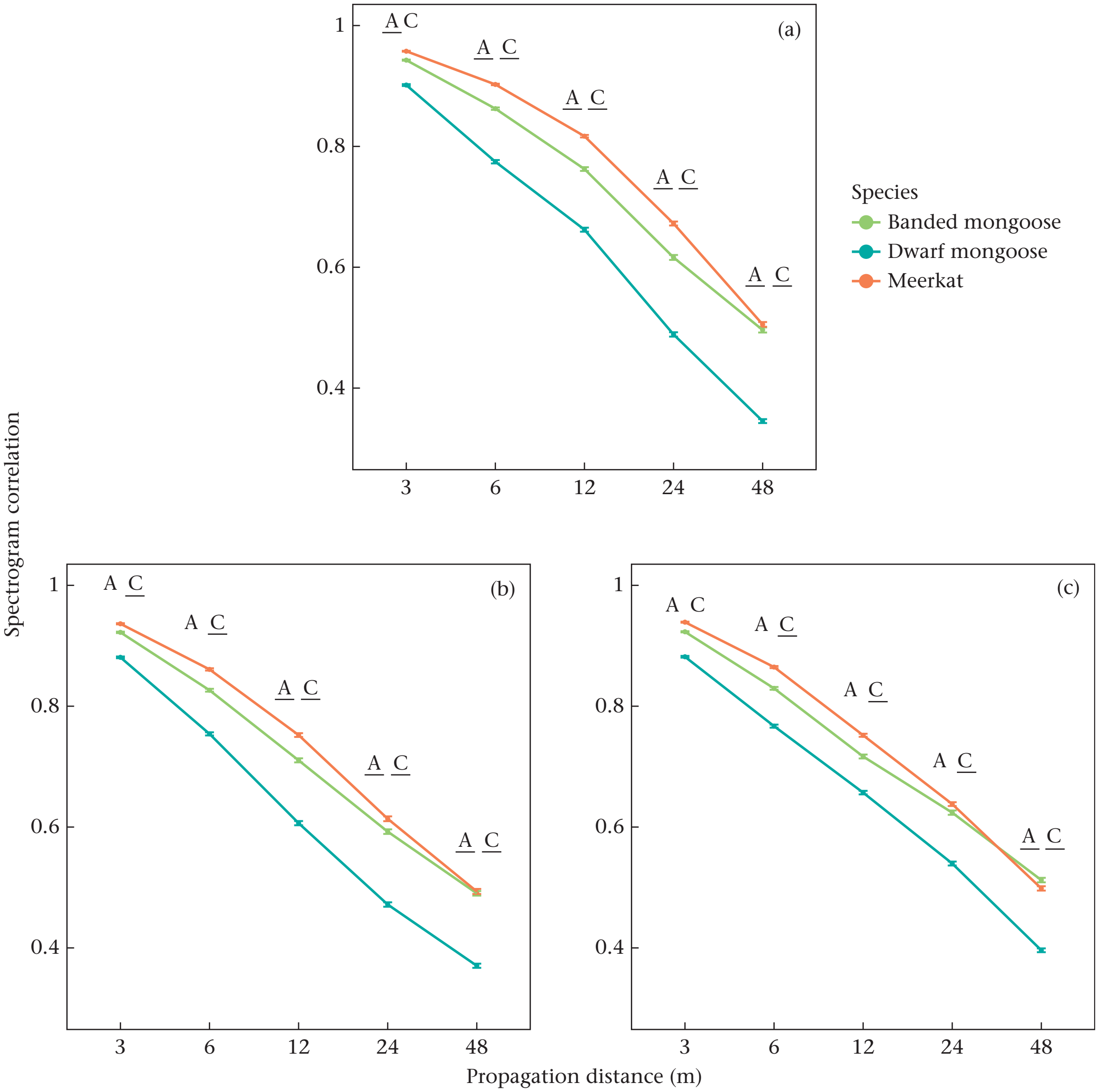

Figure 3. Within each habitat [(a) Kalahari: meerkat native; (b) Mweya: banded mongoose native; (c) Sorabi: dwarf mongoose native], spectrogram correlation values (mean ± SE) obtained from propagation experiments carried out using meerkat (MK), banded mongoose (BD) and dwarf mongoose (DW) vocalizations. All P values were adjusted with Bonferroni corrections. Tests and significance levels are indicated as follows: 'A' significant difference between BD and DW; 'C' significant difference between DW and MK; letters not underscored indicate $P < 0.01$; underscored letters indicate $P < 0.001$.

we avoided using too complicated models, i.e. multiple predictor variables at once, because (1) these models led to computation limits without reaching convergence, and (2) we were targeting analyses at different questions, each specifically addressed by a separate model). Because of the data distribution of the response variable (spectrogram correlation values), and after ruling out the use of linear mixed models (LMM) based on the distribution of the models' residuals, we performed these analyses by means of generalized linear mixed models (GLMM) fitted with a beta regression using the R package glmmTMB (Brooks et al., 2017). Typically, these models included the interaction between one of the predictor variables (those listed above) and Distance (included as an ordered factor with five levels: 3, 6, 12, 24 and 48 m) as a fixed effect. Random factors included the time of day (since this captures daily variation in temperature and wind conditions and can be included as a categorical variable in our models) and the call identity (ensuring control for repeated measurements of the same call; this identity is a composite of information on species, call type and call number). Finally, random slopes were also included for each of the predictor variables over distance since different degradation patterns can be expected for different levels of these predictors. Statistical significance was assessed by computing contrasts on the estimated marginal means resulting from the models (using the 'emmeans' function from the R package of the same name; Russell, 2021). Using a similar approach, we also investigated differences in how sounds attenuated over distance. This time the GLMMs included amplitude difference values instead of spectrogram correlation values as the response variable, and were fitted with a gamma distribution (note that prior to running GLMMs, the raw amplitude difference data were log transformed, after adding the 'absolute of the minimum amplitude difference value + 1' to the original values, so that their transformed value would fall within a positive interval, which is a prerequisite for the gamma distribution used in these models). Preparing our analyses

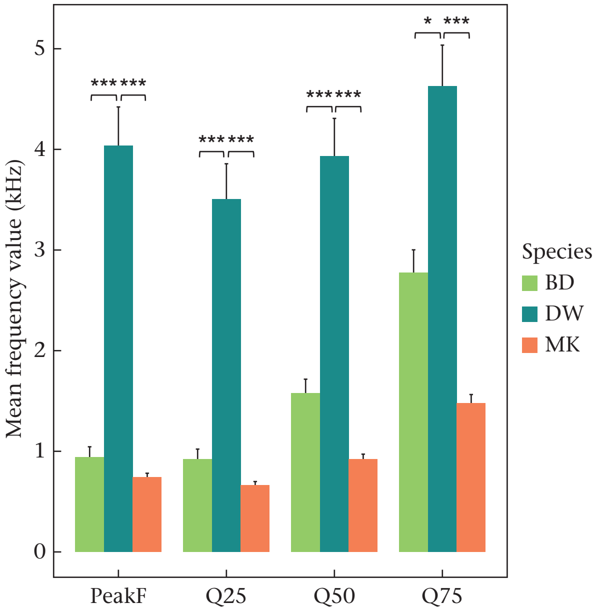

Figure 4. Mean + SE of the peak frequency (PeakF) and the 25th (Q25), 50th (Q50) and 75th (Q75) percentile frequencies of banded mongoose (BD), dwarf mongoose (DW) and meerkat (MK) vocalizations. All P values for pairwise species comparisons following linear mixed models were adjusted with Bonferroni corrections. $*P < 0.05$; $***P < 0.001$.

of acoustic attenuation, and because naturally occurring vocalizations vary considerably in their amplitude, we defined two categories of vocalizations, namely ‘loud’ and ‘soft’ (>75 dB SPL and <75 dB SPL, respectively; Table 1). These categories were used to assess whether vocal behaviour adjustments (of calling loudness in this case) could affect transmission properties of vocalizations.

In our analyses of sound degradation, the spectrogram correlations computed are an average of the ‘high' and ‘low’ amplitude conditions. For these analyses, standardizing the amplitude of the broadcast vocalizations allows us to quantify sound degradation while systematically ruling out the effect of different natural amplitudes. This eventually allows us to draw unambiguous conclusions on the role of acoustic structure in the transmission properties of vocalizations. By contrast, the ‘natural’ amplitude condition was used when investigating the effect of behavioural adjustments on vocalization degradation and attenuation, regardless of their acoustic structure.

We used LMMs to test whether frequency parameters differed between species' vocalizations (including ‘Call Type’ as a random effect; see Fig. 4 in the Results) and between ‘loud’ and ‘soft’ vocalizations (including ‘Species’ as a random effect with ‘Call Type’ nested within Species; see Fig. 9 in the Results). For all analyses, two-tailed statistics are reported, and significance levels are set to alpha = 0.05 (and follow adjustment of the P values for multiple testing using a Bonferroni correction when applicable).

RESULTS

Overall, the parameter extraction procedure performed for this study led to a data set comprising 346 362 vocalizations, distributed over six distances and various experimental conditions (three species, three habitats, three vegetation cover conditions within each habitat and three amplitude variants; see Table 2 for a quantitative summary of experimental trials).

Degradation and Environmental Tuning of Vocal Repertoires

Investigating the transmission properties of vocalizations from the three species through their native and non-native habitats, we found in all three habitats that dwarf mongoose vocalizations suffered significantly higher overall degradation than those of meerkats and banded mongooses (Fig. 3, Tables A2–A4). There was no significant difference in degradation between meerkat and banded mongoose vocalizations across all habitats. This suggests that some vocal repertoires are overall less affected by degradation than others, regardless of the habitat.

Examining further whether these degradation patterns were associated with the acoustic structure of vocalizations, we found that the peak frequency and the three frequency quartiles (Q25, Q50, and Q75) differed significantly between species (Fig. 4). In particular, dwarf mongoose vocalizations were overall found to have a higher peak frequency and frequency quartiles than vocalizations from the other two species (Table A5). By contrast, meerkat and banded mongoose vocalizations did not differ in their peak and quartile frequencies (Fig. 4).

When evaluating how vocalizations degraded in their own habitat versus the other two (non-native) habitats, for each species we found a significant difference in degradation depending on the habitat (Fig. 5). Meerkat vocalizations showed a significantly better transmission in the Kalahari (their native habitat) than in Mweya and Sorabi below 48 m ($P < 0.0001$; GLMM output Table A6), indicating that their repertoire is optimized to their own habitat. We found mixed results for dwarf mongooses. For short distances (below 6 m), their vocalizations seemed to suffer less overall degradation in the Kalahari, but for larger distances (12 m and above) the spectrogram correlation value was better in Sorabi, i.e. their native habitat (Fig. 5, Table A7). Finally, banded mongoose vocalizations showed a significantly better transmission in the Kalahari than in Mweya (their native habitat) or Sorabi until 12 m, then transmitted best in Sorabi for larger distances (Fig. 5, Table A8). Overall, we found no significant difference in the transmission of banded mongoose vocalizations between Mweya and Sorabi ($P = 1$).

Looking at the influence of vegetation cover on the transmission of vocalizations, we found that, for every species, vegetation cover had a significant effect on acoustic degradation. Yet, these differences are not statistically discriminable below 12 m for meerkat vocalizations propagated in the Kalahari (Fig. 6, Tables A9–A11). Moreover, meerkat vocalizations transmitted better through the intermediate than open vegetation cover. We further investigated this unexpected result by analysing two control conditions: we examined the transmission of meerkat vocalizations in Mweya and Sorabi, and the transmission of banded and dwarf mongoose vocalizations in the Kalahari. These analyses showed that meerkat vocalizations transmitted similarly to vocalizations from the other two species in Mweya and Sorabi (thus they transmitted best through open, then through intermediate, then through dense vegetation covers; Fig. A1, Tables A12–A13), and that banded and dwarf mongoose vocalizations transmitted better through intermediate than open vegetation covers in the Kalahari (Fig. A1, Tables A14–A15). These results overall suggest that the Kalahari habitat, rather than a meerkat-specific trait, is responsible for the increased degradation through open relative to intermediate vegetation cover.

Degradation and Species-specific Behavioural Adjustments

Testing whether adjustments of calling loudness affected sound transmission, we found a significant difference between degradation of loud and soft vocalizations for both banded

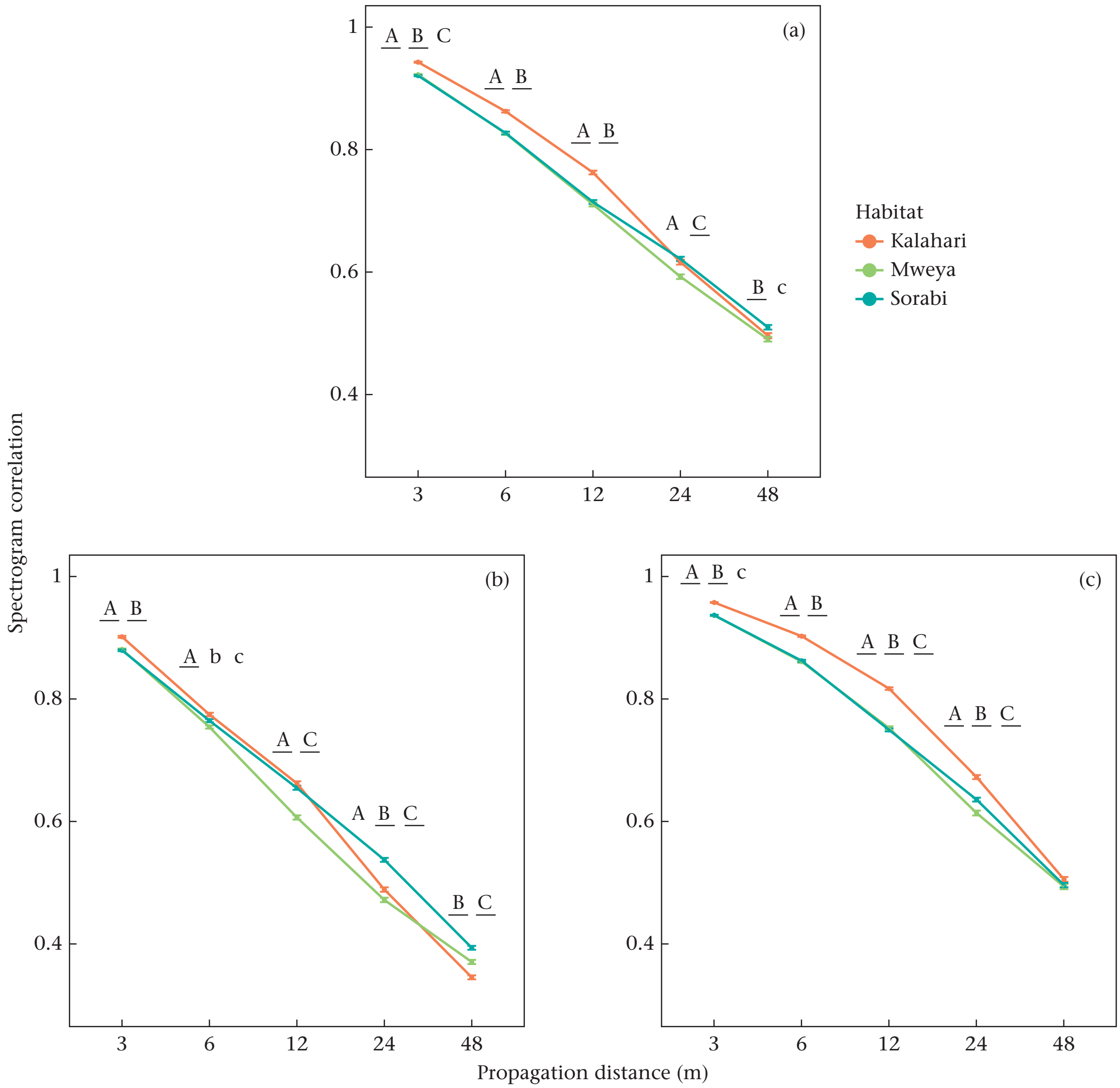

Figure 5. For each species [(a) banded mongooses; (b) dwarf mongooses; (c) meerkats], spectrogram correlation values (mean ± SE) obtained from propagation experiments carried out respectively in the Kalahari, Mweya and Sorabi. All *P* values were adjusted with Bonferroni corrections. Tests and significance levels are indicated as follows: ‘A’ significant difference between Kalahari and Mweya; ‘B’ significant difference between Kalahari and Sorabi; ‘C’ significant difference between Mweya and Sorabi; lowercase letters indicate $P < 0.05$; uppercase letters not underscored indicate $P < 0.01$; uppercase and underscored letters indicate $P < 0.001$.

mongooses and dwarf mongooses. For these two species, soft calls were overall less degraded (banded mongooses: $P < 0.01$; dwarf mongooses: $P < 0.0001$; Fig. 7, GLMM outputs Tables A17–A18). This difference was not present for meerkats ($P = 0.36$; Table A16), yet we identified a similar pattern for larger distances, once again with soft calls being better transmitted than loud calls (Fig. 7). Note that, in all these conditions, the vocalizations analysed were those for which amplitude had been standardized to ‘high’ and ‘low’ amplitude conditions. However, when we tested whether degradation differed between loud and soft calls propagated with their ‘natural’ amplitude, we found a different outcome (Fig. 8, Tables A19–A21). For both banded mongooses and dwarf mongooses, there was no significant difference between degradation of loud and soft vocalizations (banded mongooses: $P = 0.73$; GLMM output Table A20; dwarf mongooses: $P = 0.64$; GLMM output Table A21), while for meerkats, loud calls were significantly less degraded than soft calls ($P < 0.0001$; GLMM output Table A19). In addition, when considering sound attenuation, we observed that for all species and for every distance the amplitude values were (as expected) significantly higher for loud than for soft vocalizations (Fig. 8, Tables A22–A24). Accordingly, these results suggest that: (1) the acoustic structure inherent to loud vocalizations degrades faster over distance than the acoustic structure of soft vocalizations (based on propagations with standardized amplitude conditions); and (2) yet this effect disappears when loud and soft vocalizations are propagated at their natural amplitude.

In light of these results, we hypothesized that the acoustic structure of loud and soft vocalizations could overall explain the observed differences in degradation. Carrying out more in-depth acoustic analysis, we found a significant difference in the energy distribution between loud and soft calls: all parameters of frequency distribution, including peak frequency and frequency quartiles (Q25, Q50 and Q75), had significantly lower values for soft vocalizations (although only with marginal significance ($P = 0.052$) for Q25, see Fig. 9; LMM output Table A25).

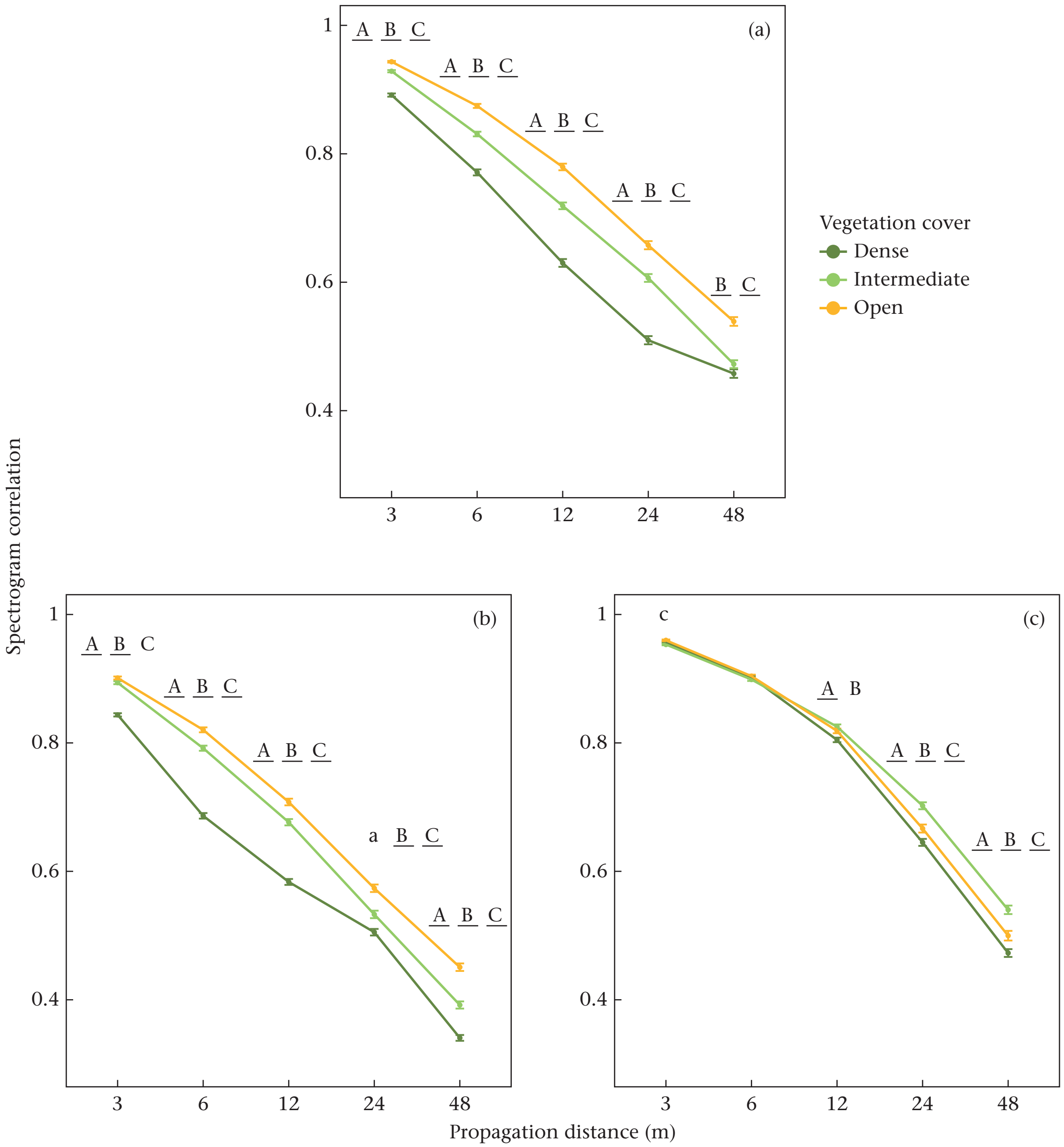

Figure 6. For each species in their native habitat [(a) banded mongooses in Mweya; (b) dwarf mongooses in Sorabi; (c) meerkats in Kalahari], spectrogram correlation values (mean ± SE) of their vocalizations in open, intermediate and dense vegetation covers (averaged from propagations made with 'high' and 'low' amplitude conditions). All P values were adjusted with Bonferroni corrections. Tests and significance levels are indicated as follows: 'A' significant difference between 'dense' and 'intermediate'; 'B' significant difference between 'dense' and 'open'; 'C' significant difference between 'intermediate' and 'open'; lowercase letters indicate $P < 0.05$; uppercase letters not underscored indicate $P < 0.01$; uppercase and underscored letters indicate $P < 0.001$.

Finally, when studying the potential effect of behavioural adjustment on sound transmission, focusing specifically on sentinel behaviour, there was a significant effect of loudspeaker position for all three species (Fig. 10, Tables A26–A28). For every distance, there were significant differences in the propagation between ground and perch loudspeaker positions. At short distances (up to 3 m), sound transmission was better when the loudspeaker was placed at ground level. However, for distances of 6 m and above, this pattern changed and sound transmission with the loudspeaker placed on a perch was significantly better than from the ground. These results are based on all call types taken together for each species; yet, focusing specifically on sentinel calls in meerkats and dwarf mongooses led to equivalent results (Fig. A2, Tables A29–A30).

DISCUSSION

Degradation and Environmental Tuning of Vocal Repertoires

Testing the transmission properties of vocalizations from three mongoose species through their native and non-native habitats, we only found partial support for the acoustic adaptation hypothesis (AAH). First, considering differences between species within each habitat (Fig. 3), transmission of meerkat and banded mongoose vocalizations were not significantly different, but vocalizations of both these species transmitted with significantly less degradation than those of dwarf mongooses, including in Sorabi, the native habitat of dwarf mongooses. Second, considering transmission differences of species-specific vocalizations across all three habitats

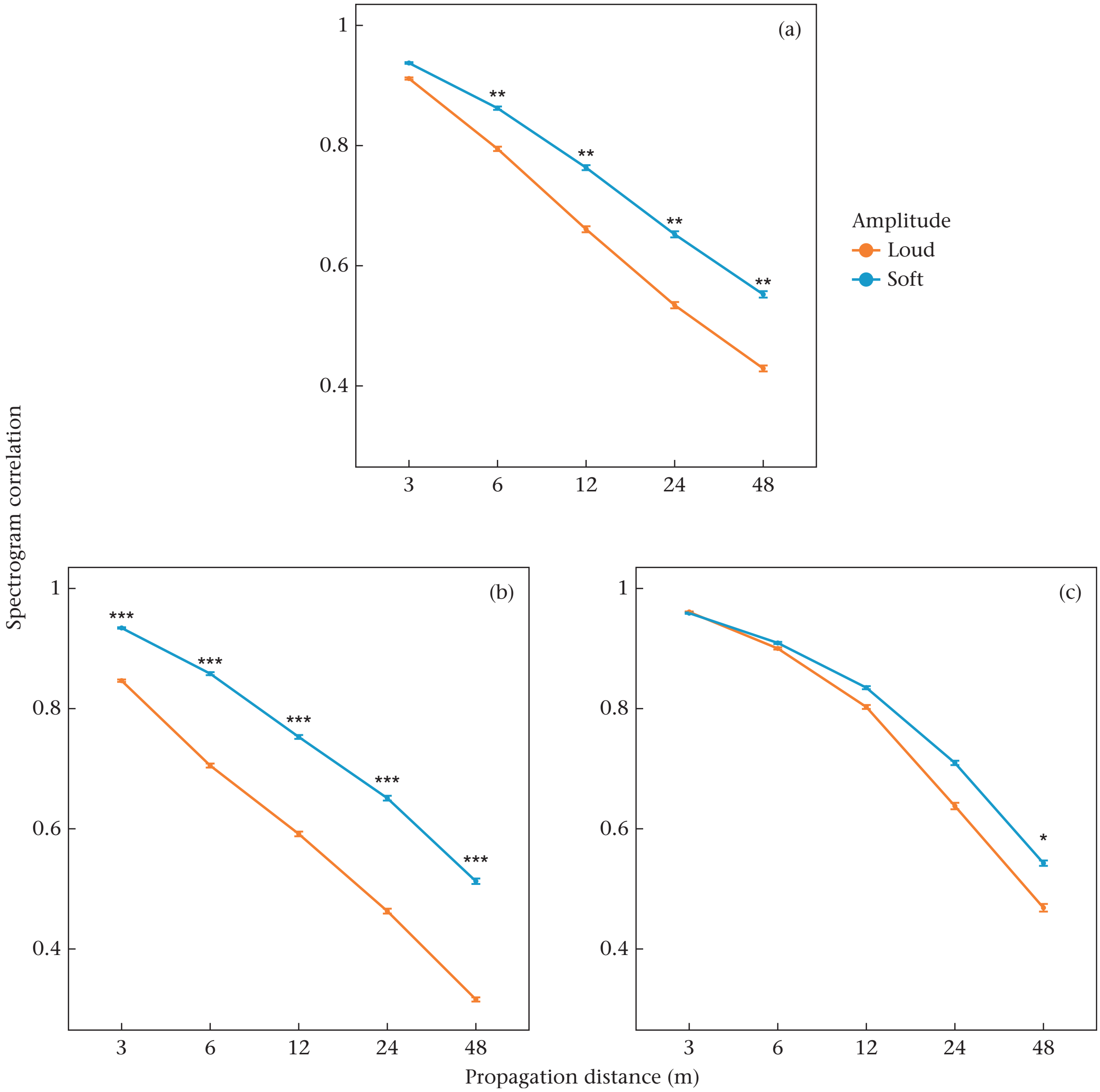

Figure 7. For each species in their native habitat [(a) banded mongooses in Mweya; (b) dwarf mongooses in Sorabi; (c) meerkats in Kalahari], spectrogram correlation values (mean ± SE) of their vocalizations categorized either as 'loud' or 'soft' (i.e. produced with a natural amplitude > or <75 dB SPL, respectively). Spectrogram correlation values are based on propagations carried out with standardized amplitude conditions to evaluate only the effect of acoustic structure on sound degradation. All *P* values were adjusted with Bonferroni corrections. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

(Fig. 5), meerkat vocalizations were best adjusted to the Kalahari (their native habitat), and dwarf mongoose vocalizations were best adjusted to Sorabi for distances above 12 m, therefore providing the partial support to the AAH mentioned above. By contrast, banded mongoose vocalizations were not found to transmit better in Mweya (their native habitat) than in the other two habitats (Fig. 5), despite their high overall transmission rates when compared with the other two species (Fig. 3). Together, these results provide partial support for the adaptation of vocalizations to general living habitat features across species: focusing on each species separately, our results are consistent with the AAH for meerkats only; they are partly consistent for dwarf mongooses and are not consistent at all in banded mongooses. Besides, considering the comparative approach applied in this study, our results rather indicate a lack of acoustic adaptation at the family level (i.e. in Herpestidae), and meerkat vocalizations may only show consistent findings with the AAH because of the more open habitat this species occupies relative to the other two species. The potentially very general features of these different habitats may thus not represent a selective pressure strong enough to shape vocal repertoires significantly, and other evolutionary drivers (e.g. social life and anatomy; Garcia & Manser, 2020) may have more influence on communication systems in this family.

A finer examination of sound transmission in different vegetation covers within each of the habitats revealed a pattern consistent with our predictions: vocalizations transmitted with least degradation in open, then in intermediate and then in densely vegetated areas (Fig. 6). Various mechanisms such as diffraction and absorption (both related to vegetation cover) could thus play an important role in sound degradation across habitats (Aylor, 1971). A striking counterexample occurred in the Kalahari, with an inversion of acoustic degradation levels between intermediate and open vegetation covers (vocalizations being better transmitted in the former than the latter) while dense vegetation cover remained the least

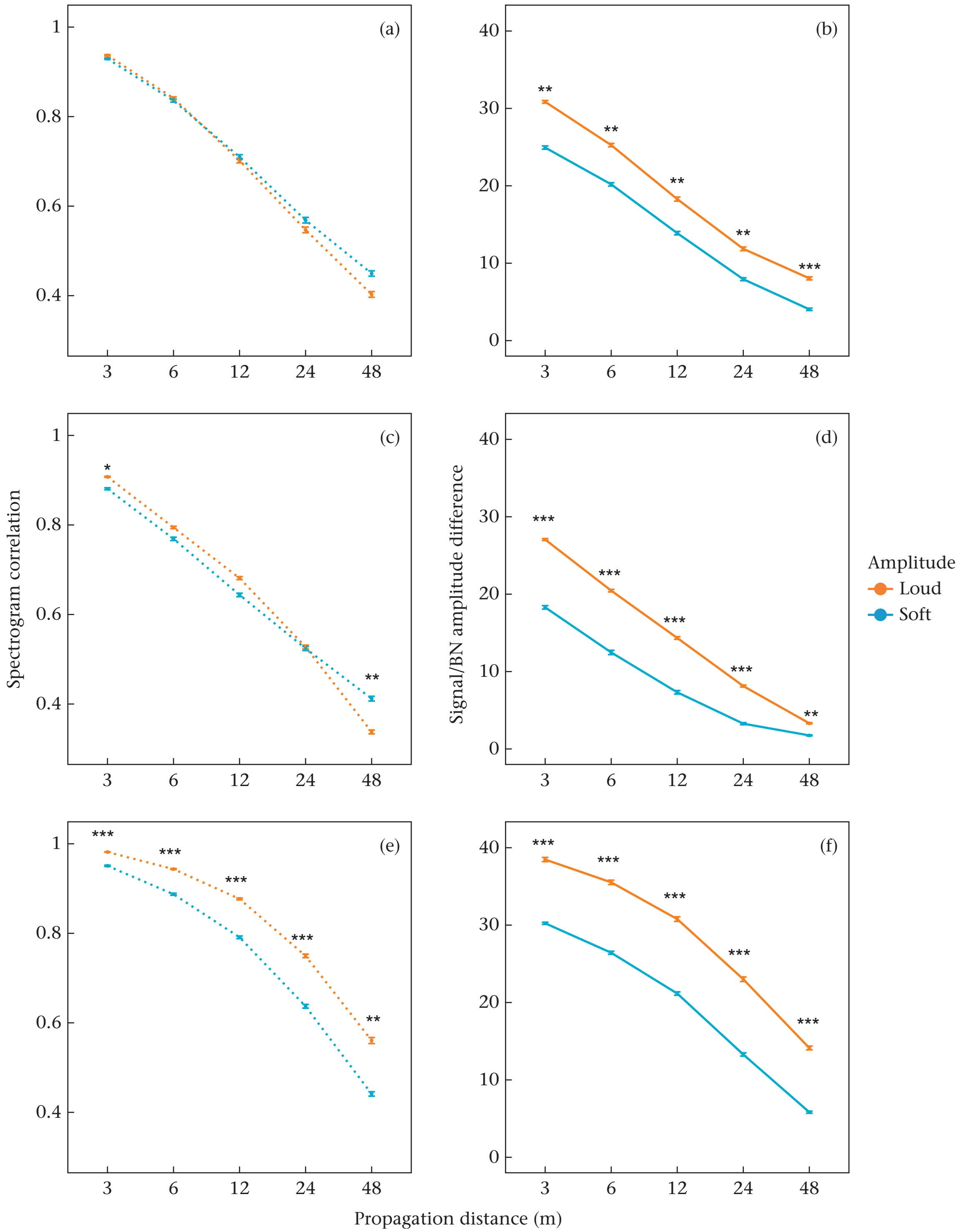

Figure 8. For each species in their native habitat [(a, b) banded mongooses in Mweya; (c, d) dwarf mongooses in Sorabi; (e, f) meerkats in Kalahari], (a, c, e) spectrogram correlation (mean ± SE) and (b, d, f) amplitude difference values (mean ± SE) of their vocalizations categorized as either ‘loud’ or ‘soft’. Spectrogram correlation and amplitude difference values are based on propagations carried out with ‘natural’ amplitude conditions to evaluate the effect of amplitude shifts on sound degradation and attenuation. BN: background noise. All *P* values were adjusted with Bonferroni corrections. **P* < 0.05; ***P* < 0.01; ****P* < 0.001.

transmission-friendly condition. Further investigation of this unexpected result brought evidence that the same effect was observed for the transmission of banded and dwarf mongoose vocalizations in the Kalahari. In addition, meerkat vocalizations propagated similarly in Mweya and Sorabi to those of banded and dwarf mongooses. This rules out an effect inherent to meerkat vocalizations, and instead identifies the origin of this phenomenon as the Kalahari habitat. The most likely explanation for this comes from the fact that, in the Kalahari, the ‘open’ condition involved a relatively soft, sandy ground structure (as opposed to a much harder, compact ground in Mweya and Sorabi; Cant, 2000; Manser et al., 2014; Scholes et al., 2002). Attenuation of specific frequencies

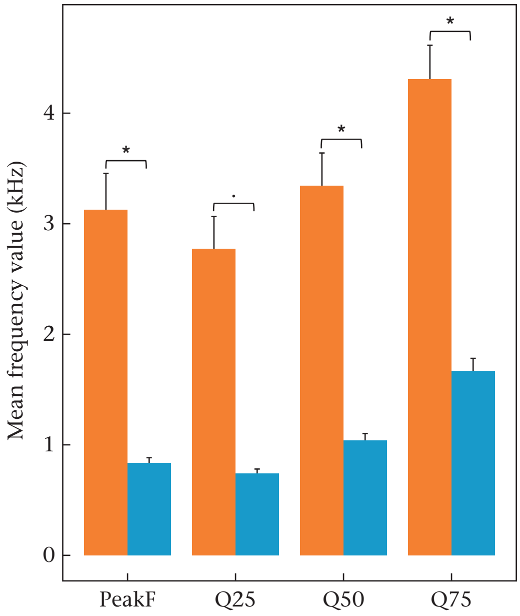

Figure 9. Mean + SE of the peak frequency (PeakF) and the 25th (Q25), 50th (Q50) and 75th (Q75) percentile frequencies of loud and soft calls (pooled from all vocalizations from the three species considered in this study). $^{*}P < 0.05$, $^{\bullet}P = 0.052$.

has been shown to vary depending on the soil porosity, and ground attenuation in the Kalahari could thus be more important in the more porous soil typical of our 'open' vegetation cover condition (Aylor, 1972; Oelze, Darmody, & O'Brien, 2001).

Contrary to the open condition of the Kalahari discussed above, vegetation cover is most prominent in Mweya, as well as to a lesser extent in Sorabi. Foliage, branches and trunks can reflect, absorb and block sound waves, in particular leading to interference for higher frequencies (Aylor, 1972; Wiley & Richards, 1978). This could explain why dwarf mongoose vocalizations, which have the highest frequency values (Fig. 4), are the most degraded among the study species (Fig. 3). Note that other potential parameters could affect sound transmission, which we could not document in this study. In particular, investigating the effect of humidity could prove relevant, given that a decrease in relative humidity can lead to an increase in atmospheric absorption, and therefore an increase in attenuation for high-frequency sounds (e.g. Delany, 1977; Ingård, 1953). Future studies of the AAH may therefore find it worthwhile to integrate examination of the effect of seasonal changes in humidity conditions and differing levels of background noise on signal transmission.

Despite the significant differences in sound transmission due to vegetation cover, habitat itself does not seem to determine fully the transmission variation between the three species vocalizations. For instance, meerkats and banded mongooses show a similar degradation pattern of their vocalizations overall (Fig. 3), but they dwell in habitats that differ in terms of acoustic degradation (Fig. 5). To date, a large number of studies performed on mammals do not necessarily support the AAH (Daniel & Blumstein, 1998; Ey & Fischer, 2009; Holzmann & Areta, 2020; Peters & Peters, 2010). Our results showing only partial support (at least when focusing on each species separately) in the Herpestidae family indicate that habitat is indeed not the only selective force shaping vocal repertoires. This is particularly true for the banded mongoose population used in this study, which showed no support at all for the AAH. Factors other than the environment might play a role in the evolution of species-specific vocalizations. For example, laryngeal and vocal tract anatomy are known to impose significant constraints on sound production (Taylor & Reby, 2010) and are often directly related to body size (Briefer & McElligott, 2011; Garcia, Herbst, Bowling, Dunn, & Fitch, 2017; Reby & McComb, 2003). Looking at our study species (whose body sizes range from 400 g in dwarf mongooses to 600–900 g in meerkats and to 1.5 kg in banded mongooses; Manser et al., 2014), future studies investigating the underpinnings of vocal repertoire evolution should account for such morphometric aspects. Note that our results (Fig. 4), showing overall higher-frequency vocalizations in dwarf mongooses (the smallest species), but lower-frequency vocalizations in meerkats (and not in banded mongooses, the largest species), emphasize the need for follow-up research on acoustic allometry in this family. Similarly, quantifying overall animal vocal activity at the three field sites may prove valuable to assess the degree to which interspecific acoustic competition can influence effective sound transmission due to increased background noise. The case of banded mongooses is of particular interest here since this is where our data show no support for the AAH and at the same time where heterospecific (in particular bird) vocal activity was estimated as the loudest and most ubiquitous (M. Garcia, personal observation).

As both degradation and attenuation can affect the acoustic structure of vocalizations, they can impair the effective decoding of biological information encoded within them. At the same time, these phenomena can themselves provide functionally valuable information to the receiver, for example about the distance and/or direction of the vocalizing animal (the so-called 'ranging hypothesis'; Morton, 1982; Naguib & Wiley, 2001). Further research involving in-depth analysis of transmission of specific acoustic features is currently underway to evaluate (1) which of these features carry different information types (e.g. individual identity, arousal level) and (2) how information content is actively used to coordinate group dynamics within species. In particular, determining the active acoustic space of species-specific call types (see e.g. in koalas, *Phascolarctos cinereus*; Charlton, Reby, Ellis, Brumm, & Fitch, 2012) will improve our understanding of the behavioural context in which these vocalizations are uttered and used for group cohesion in mongooses. This could, for instance, provide insights into differences in foraging strategies between banded mongooses (with group spread averaging 23 m when foraging or lying down; Meniri, n.d.) dwarf mongooses (where nearest neighbours are usually found within 2.5 m; Kern & Radford, 2021) and meerkats (where nearest neighbours are usually found within 5 m and group spread during foraging is about 14 m; Doolan & Macdonald, 1996; Gall & Manser, 2017). Similarly, mongoose vocalizations could be structured to transmit over biologically relevant distances that reflect typical group-specific spatial distributions across various contexts (Fotheringham, Martin, & Ratcliffe, 1997; Tubaro & Segura, 1994). Finally, we point out that it is possible that only some acoustic features are adjusted to the environment, while other features might depend more on other factors (such as phylogeny, call context, caller arousal or short-term variation in social surrounding or ambient noise level; Forstmeier, Burger, Temnow, & Derégnaucourt, 2009; Luther & Gentry, 2013; Morton, 1977). Future work, in particular investigating mongooses' perceptual abilities and vocal anatomy, should help better understand the selective pressures shaping vocal diversity in the Herpestidae family.

Degradation and Species-specific Behavioural Adjustments

Classifying call types into two categories based on their natural sound production amplitude, namely loud and soft vocalizations, we found that, when standardizing amplitude for all call types, soft vocalizations transmitted with less degradation than loud vocalizations (although only for large distances in meerkats). As this approach allowed us to control for natural amplitude variation

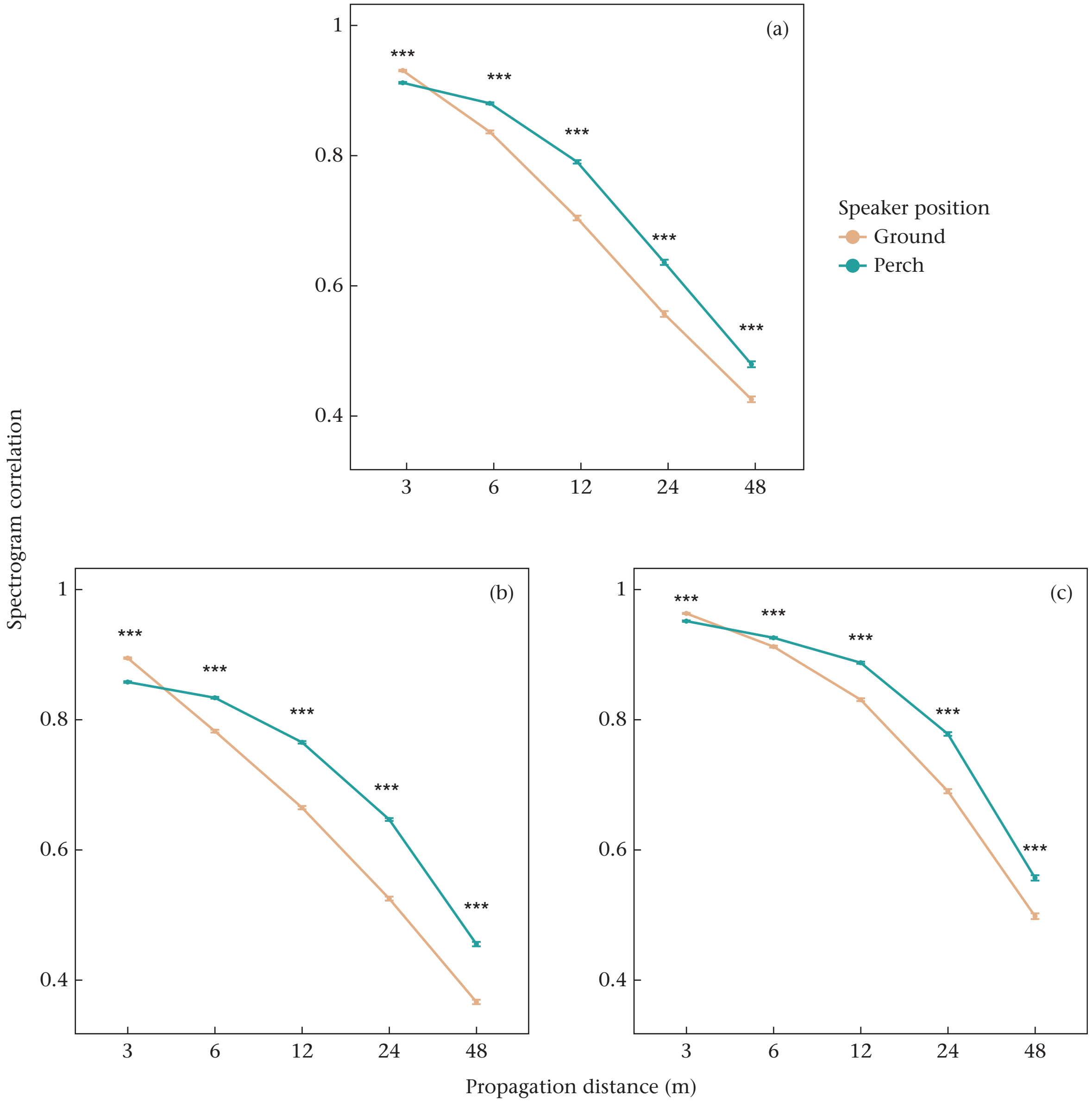

Figure 10. For each species in their native habitat [(a) banded mongooses in Mweya; (b) dwarf mongooses in Sorabi; (c) meerkats in Kalahari], spectrogram correlation values (mean ± SE) obtained with vocalizations propagated with their 'natural' amplitude and the speaker placed either on the ground or on a perch. All *P* values were adjusted with Bonferroni corrections. $***P < 0.001$.

across different call types, and given the potential stronger degradation of higher frequencies (Wiley & Richards, 1978), we interpreted these degradation patterns as attributable to the acoustic structure of these vocalizations. Supporting this interpretation, looking at acoustic energy distributions, soft vocalizations were characterized by lower frequencies than loud vocalizations (Fig. 9). This raised the question of whether, by varying their vocal behaviour (i.e. by a differential amplitude adjustment), mongooses could benefit from enhanced propagation of their vocalizations, thereby achieving greater transmission over larger distances. Indeed, when looking at the propagation of these two categories produced at their natural amplitudes, we found that for banded and dwarf mongooses both loud and soft vocalizations transmitted equally well in their native habitat, thus cancelling the difference seen when using standardized amplitudes. Even more striking is the case of meerkats where loud vocalizations were better transmitted than soft vocalizations, reversing the results obtained with standardized amplitudes (Figs, 7 and 8). These observations are reminiscent of the Lombard effect (Brumm & Slabbekoorn, 2005), which describes how an increase in signal amplitude can usually increase the signal-to-noise ratio of a given vocalization and counteract the constraints imposed by the background noise. In line with this effect, we saw that the natural amplitude values were consistently higher for loud vocalizations than for soft vocalizations (Fig. 8). Our transmission results thus highlight a trade-off between acoustic structure and loudness, indicating that mongooses could compensate for the less efficient structure of loud vocalizations by producing them at high amplitudes to optimize their transmission though species-specific habitats.

Finally, another strategy by which signallers could improve signal transmission and potentially increase detection by conspecifics living in the same environment is by changing their spatial position. Studies have found that by switching the height of the perch, some species of birds and primates can improve the effective transmission of their song, especially in forested habitats (Mathevon, Aubin, & Dabelsteen, 1996; Nemeth, Dabelsteen, Pedersen, & Winkler, 2006). Our analysis showed that vocalizations produced from a perch were systematically transmitted with less degradation than those produced from the ground for distances greater than 3 m (Fig. 10). Although sentinel behaviour is thought to have evolved as a means of better detecting predators and increasing vigilance efficiency (Bednekoff, 1997), our results indicate that the elevated position of sentinels also leads to improved signal transmission (Fig. A2), highlighting a hitherto unrecognized adaptive benefit to this behaviour. The improvement in sound transmission resultant from an elevated loudspeaker position was also found for banded mongoose vocalizations; yet this species does not display sentinel behaviour. This may be explained by the fact that banded mongooses dwell in densely vegetated habitats with multiple predators (e.g. lions, hyaenas, birds of prey), where reduced visibility combined with the time spent leaving an elevated position could lead to a higher predation risk (in comparison with being close to shelter if remaining on the ground). With regard to their survival, the costs associated with displaying sentinel behaviour may thus outweigh the benefits, even if the latter include more efficient transmission of vocalizations.

Conclusion

The study of vocal signal structure and usage in relation to the environment is key to understanding animal communication systems. Using a comparative approach, for the first time involving multiple call types per species, we investigated the transmission patterns of meerkat, banded mongoose and dwarf mongoose vocalizations both in their native and in non-native habitats. We did not find clear support for the AAH across the Herpestidae family (although results were consistent with the AAH for meerkats and partially for dwarf mongooses), indicating that not all vocalizations are systematically adapted to optimal transmission in their own habitat. However, a finer examination of vegetation cover revealed that this feature could play an important role in mongoose communication, with sound degradation increasing with vegetation density across habitats. Furthermore, we showed that vocal usage and behavioural modifications in these species can help them overcome some of the constraints imposed by their environment. Specifically, signal transmission can be improved by means of amplitude adjustment, especially for those call types that are more affected by degradation. Moreover, by calling from a perch rather than ground level, mongooses find an advantage in that their vocalizations will be transmitted with less degradation in their environment. In short, our results reveal a complex interplay of species repertoire, habitat, vegetation cover and caller behaviour on the transmission of vocal signals, thereby demonstrating the need to take a holistic, multidimensional approach to examining the AAH and the evolution of vocal behaviour.

Author Contributions

M.G. and M.M. designed the study; A.N.R. and M.A.C. helped implement the experimental design; M.G. performed propagation experiments and collected the data (with the help of S.K. in Mweya); A.G.A. and M.G. analysed the data; A.G.A., S.K.W. and M.G. performed the statistical analyses; A.G.A. and M.G. drafted the manuscript; all authors contributed to revising the manuscript.

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Supplementary material

Supplementary material associated with this article can be found, in the online version at https://doi.org/10.1016/j.anbehav.2022.02.016.

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Appendix

Table A1
Summary output of the analyses testing for Temperature and Wind differences between AM, NOON and PM conditions

	AM/NOON	AM/PM	NOON/PM
Temperature	27.02 ± 0.26/33.95 ± 0.22 ***	27.02 ± 0.26/30.42 ± 0.34 ***	33.95 ± 0.22/30.42 ± 0.34 ***
Wind	1.33 ± 0.03/1.27 ± 0.05 NS	1.33 ± 0.03 /1.06 ± 0.05 ***	1.27 ± 0.05/1.06 ± 0.05 *

Temperature and wind differences between conditions were tested using Kruskal–Wallis tests followed by pairwise Wilcoxon rank sum comparisons with Bonferroni corrections for multiple testing. Mean ± SE are indicated for each condition and all *P* values were adjusted with Bonferroni corrections. Temperatures are expressed in degrees Celsius and wind speed in m/s.
*$P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table A2
Summary output of the GLMM testing for the effect of species identity (and its interaction with recording distance) on spectrogram correlations in the Kalahari

		Estimate	SE	*t*	*P*
General	BD–DW	0.53	0.12	4.27	0.0001
	BD–MK	−0.18	0.13	−1.4	0.482
	DW–MK	−0.72	0.12	−5.75	<0.0001
3 m	BD–DW	0.4	0.13	3.17	0.005
	BD–MK	−0.11	0.13	−0.82	1
	DW–MK	−0.51	0.13	−4.03	0.0002
6 m	BD–DW	0.55	0.13	4.4	<0.0001
	BD–MK	−0.24	0.13	−1.78	0.226
	DW–MK	−0.79	0.13	−6.28	<0.0001
12 m	BD–DW	0.51	0.13	4.4	0.0001
	BD–MK	−0.26	0.13	−2	0.136
	DW–MK	−0.78	0.13	−6.51	<0.0001
24 m	BD–DW	0.55	0.13	4.4	<0.0001
	BD–MK	−0.26	0.13	−2	0.135
	DW–MK	−0.81	0.13	−6.51	<0.0001
48 m	BD–DW	0.65	0.13	5.18	<0.0001
	BD–MK	−0.05	0.13	−0.36	1
	DW–MK	−0.7	0.13	−5.56	<0.0001

This summary table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing). BD: banded mongooses; DW: dwarf mongooses; MK: meerkats.

Table A3
Summary output of the GLMM testing for the effect of species identity (and its interaction with recording distance) on spectrogram correlations in Mweya

		Estimate	SE	*t*	*P*
General	BD–DW	0.45	0.1	4.59	<0.0001
	BD–MK	−0.12	0.1	−1.21	0.675
	DW–MK	−0.57	0.1	−5.87	<0.0001
3 m	BD–DW	0.32	0.1	3.19	0.004
	BD–MK	−0.13	0.1	−1.23	0.660
	DW–MK	−0.44	0.1	−4.48	<0.0001
6 m	BD–DW	0.37	0.1	3.79	0.0005
	BD–MK	−0.2	0.1	−1.95	0.153
	DW–MK	−0.58	0.1	−5.84	<0.0001
12 m	BD–DW	0.46	0.1	4.63	<0.0001
	BD–MK	−0.22	0.1	−2.09	0.110
	DW–MK	−0.67	0.1	6.83	<0.0001
24 m	BD–DW	0.53	0.1	5.36	<0.0001
	BD–MK	−0.09	0.1	−0.87	1
	DW–MK	−0.62	0.1	−6.28	<0.0001
48 m	BD–DW	0.56	0.1	5.69	<0.0001
	BD–MK	0.02	0.1	0.17	1
	DW–MK	−0.54	0.1	−5.51	<0.0001

This summary table includes estimates, SE, *t* ratios and significance value from pairwise comparison (adjusted with Bonferroni correction due to multiple testing). BD: banded mongooses; DW: dwarf mongooses; MK: meerkats.

Table A4
Summary output of the GLMM testing for the effect of species identity (and its interaction with recording distance) on spectrogram correlations in Sorabi

		Estimate	SE	*t*	*P*
General	BD–DW	0.36	0.1	3.63	0.0009
	BD–MK	−0.11	0.1	−1.04	0.892
	DW–MK	−0.46	0.1	−4.73	<0.0001
3 m	BD–DW	0.33	0.1	3.31	0.003
	BD–MK	−0.13	0.1	−1.28	0.606
	DW–MK	−0.46	0.1	−4.65	<0.0001
6 m	BD–DW	0.35	0.1	3.56	0.001
	BD–MK	−0.2	0.1	−1.94	0.155
	DW–MK	−0.56	0.1	−5.61	<0.0001
12 m	BD–DW	0.27	0.1	2.71	0.02
	BD–MK	−0.17	0.1	−1.67	0.287
	DW–MK	−0.44	0.1	−4.47	<0.0001
24 m	BD–DW	0.35	0.1	3.54	0.001
	BD–MK	−0.08	0.1	−0.77	1
	DW–MK	−0.43	0.1	−4.35	<0.0001
48 m	BD–DW	0.48	0.1	4.83	<0.0001
	BD–MK	0.05	0.1	0.51	1
	DW–MK	−0.42	0.1	−4.29	0.0001

This summary table includes estimates, SE, *t* ratios and significance value from pairwise comparison (adjusted with Bonferroni correction due to multiple testing). BD: banded mongooses; DW: dwarf mongooses; MK: meerkats.

Table A5
Acoustic features discriminating between calls of meerkats, banded mongooses and dwarf mongooses

	BD		DW		MK		LMM		
	Mean	SE	Mean	SE	Mean	SE	Estimates		*P*
Peak frequency	0.94	0.1	4.04	0.39	0.74	0.04	BD–MK	−0.76	0.242
							BD–DW	−3.41	<0.0001
							MK–DW	2.64	<0.0001
Q25	0.92	0.1	3.5	0.35	0.66	0.04	BD–MK	−0.56	0.406
							BD–DW	−3.1	<0.0001
							MK–DW	2.54	<0.0001
Q50	1.58	0.14	3.931	0.38	0.92	0.05	BD–MK	−0.18	0.921
							BD–DW	−2.66	<0.0001
							MK–DW	2.49	<0.0001
Q75	2.78	0.22	4.63	0.4	1.48	0.08	BD–MK	0.88	0.201
							BD–DW	−1.39	0.021
							MK–DW	2.27	<0.0001

This summary table includes mean, SE and results from LMMs (testing for differences in acoustic features between species). Significance values were adjusted with Bonferroni correction due to multiple testing. BD: banded mongooses; DW: dwarf mongooses; MK: meerkats. Mean and SE for Peak frequency, Q25, Q50 and Q75 are expressed in kHz.

Table A6
Summary output of the GLMM testing for the effect of habitat (and its interaction with recording distance) on spectrogram correlations for meerkats

		Estimate	SE	*t*	*P*
General	Kalahari–Mweya	0.19	0.01	22.91	<0.0001
	Kalahari–Sorabi	0.21	0.01	25.19	<0.0001
	Mweya–Sorabi	0.02	0.01	2.03	0.128
3 m	Kalahari–Mweya	0.24	0.02	8.79	<0.0001
	Kalahari–Sorabi	0.25	0.02	11.81	<0.0001
	Mweya–Sorabi	0.01	0.02	2.93	0.010
6 m	Kalahari–Mweya	0.24	0.02	11.73	<0.0001
	Kalahari–Sorabi	0.25	0.02	12.57	<0.0001
	Mweya–Sorabi	0.01	0.02	0.74	1
12 m	Kalahari–Mweya	0.27	0.02	14.87	<0.0001
	Kalahari–Sorabi	0.34	0.02	19.1	<0.0001
	Mweya–Sorabi	0.07	0.02	4.09	0.0001
24 m	Kalahari–Mweya	0.03	0.02	13.67	<0.0001
	Kalahari–Sorabi	0.15	0.02	9.64	<0.0001
	Mweya–Sorabi	−0.07	0.02	−4.11	0.0001
48 m	Kalahari–Mweya	0.03	0.01	2.26	0.071
	Kalahari–Sorabi	0.03	0.01	2.18	0.088
	Mweya–Sorabi	−0.01	0.01	−0.11	1

This summary table includes estimates, SE, *t* ratios and significance value from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A7
Summary output of the GLMM testing for the effect of habitat (and its interaction with recording distance) on spectrogram correlations for dwarf mongooses

		Estimate	SE	*t*	*P*
General	Kalahari–Mweya	0.09	0.01	11.67	<0.0001
	Kalahari–Sorabi	−0.03	0.01	−3.97	0.0002
	Mweya–Sorabi	−0.12	0.01	−15.73	<0.0001
3 m	Kalahari–Mweya	0.19	0.02	9.61	<0.0001
	Kalahari–Sorabi	0.22	0.02	11.37	<0.0001
	Mweya–Sorabi	0.03	0.02	1.66	0.292
6 m	Kalahari–Mweya	0.09	0.02	5.12	<0.0001
	Kalahari–Sorabi	0.04	0.02	2.52	0.035
	Mweya–Sorabi	−0.04	0.02	−2.62	0.027
12 m	Kalahari–Mweya	0.21	0.01	13.14	<0.0001
	Kalahari–Sorabi	0.02	0.01	1.35	0.529
	Mweya–Sorabi	−0.19	0.01	−11.76	<0.0001
24 m	Kalahari–Mweya	0.05	0.01	3.4	0.002
	Kalahari–Sorabi	−0.21	0.01	−14.06	<0.0001
	Mweya–Sorabi	−0.27	0.01	−17.26	<0.0001
48 m	Kalahari–Mweya	−0.09	0.02	−5.76	<0.0001
	Kalahari–Sorabi	−0.22	0.01	−13.67	<0.0001
	Mweya–Sorabi	−0.12	0.02	−7.66	<0.0001

This summary table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A8
Summary output of the GLMM testing for the effect of habitat (and its interaction with recording distance) on spectrogram correlations for banded mongooses

		Estimate	SE	*t*	*P*
General	Kalahari–Mweya	0.13	0.01	16.96	<0.0001
	Kalahari–Sorabi	0.13	0.01	16.57	<0.0001
	Mweya–Sorabi	−0.01	0.01	−0.6	1
3 m	Kalahari–Mweya	0.21	0.02	9.6	<0.0001
	Kalahari–Sorabi	0.28	0.02	13.12	<0.0001
	Mweya–Sorabi	0.07	0.02	3.49	0.002
6 m	Kalahari–Mweya	0.21	0.02	11.25	<0.0001
	Kalahari–Sorabi	0.22	0.02	11.87	<0.0001
	Mweya–Sorabi	0.01	0.02	0.52	1
12 m	Kalahari–Mweya	0.23	0.01	13.97	<0.0001
	Kalahari–Sorabi	0.25	0.01	15.23	<0.0001
	Mweya–Sorabi	0.02	0.01	1.13	0.778
24 m	Kalahari–Mweya	0.05	0.01	3.2	0.004
	Kalahari–Sorabi	−0.03	0.01	−2.25	0.073
	Mweya–Sorabi	−0.08	0.01	−5.38	<0.0001
48 m	Kalahari–Mweya	0.03	0.01	−1.95	0.154
	Kalahari–Sorabi	−0.07	0.01	−4.74	<0.0001
	Mweya–Sorabi	−0.04	0.01	−2.71	0.020

This summary table includes estimates, SE, t ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A9
Summary output of the GLMM testing for the effect of vegetation cover (and its interaction with recording distance) on spectrogram correlations for meerkats in the Kalahari

		Estimate	SE	*t*	*P*
General	Dense–Intermediate	−0.1	0.01	−8.17	<0.0001
	Dense–Open	−0.06	0.01	−4.59	<0.0001
	Intermediate–Open	0.04	0.01	3.11	0.006
3 m	Dense–Intermediate	0.08	0.03	2.35	0.057
	Dense–Open	−0.02	0.04	−0.52	1
	Intermediate–Open	−0.1	0.04	−2.67	0.023
6 m	Dense–Intermediate	−0.05	0.03	1.51	0.395
	Dense–Open	−0.01	0.03	−0.1	1
	Intermediate–Open	−0.05	0.03	−1.48	0.412
12 m	Dense–Intermediate	−0.13	0.03	−4.77	<0.0001
	Dense–Open	−0.07	0.03	−2.59	0.029
	Intermediate–Open	0.05	0.03	1.82	0.205
24 m	Dense–Intermediate	−0.26	0.02	−11.33	<0.0001
	Dense–Open	−0.1	0.02	−4.18	0.0001
	Intermediate–Open	0.16	0.02	6.34	<0.0001
48 m	Dense–Intermediate	−0.27	0.02	−12.54	<0.0001
	Dense–Open	−0.11	0.02	−4.88	<0.0001
	Intermediate–Open	0.16	0.02	6.83	<0.0001

This summary table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A10
Summary output of the GLMM testing for the effect of vegetation cover (and its interaction with recording distance) on spectrogram correlations for banded mongooses in Mweya

		Estimate	SE	*t*	*P*
General	Dense–Intermediate	−0.29	0.01	−21.91	<0.0001
	Dense–Open	−0.57	0.01	−40.8	<0.0001
	Intermediate–Open	−0.27	0.01	−19.66	<0.0001
3 m	Dense–Intermediate	−0.32	0.03	−8.88	<0.0001
	Dense–Open	−0.49	0.04	−13.27	<0.0001
	Intermediate–Open	−0.17	0.04	−4.56	<0.0001
6 m	Dense–Intermediate	−0.31	0.03	−10.33	<0.0001
	Dense–Open	−0.65	0.03	−20.41	<0.0001
	Intermediate–Open	−0.34	0.03	−10.48	<0.0001
12 m	Dense–Intermediate	−0.4	0.03	−14.7	<0.0001
	Dense–Open	−0.73	0.03	−26	<0.0001
	Intermediate–Open	−0.34	0.03	−11.8	<0.0001
24 m	Dense–Intermediate	−0.41	0.03	−15.76	<0.0001
	Dense–Open	−0.64	0.03	−24.21	<0.0001
	Intermediate–Open	−0.23	0.03	−8.71	<0.0001
48 m	Dense–Intermediate	−0.04	0.03	−1.41	0.478
	Dense–Open	−0.33	0.03	−12.58	<0.0001
	Intermediate–Open	−0.29	0.02	−11.27	<0.0001

This summary table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A11
Summary output of the GLMM testing for the effect of vegetation cover (and its interaction with recording distance) on spectrogram correlations for dwarf mongooses in Sorabi

		Estimate	SE	*t*	*P*
General	Dense–Intermediate	−0.28	0.01	−22.93	<0.0001
	Dense–Open	−0.48	0.01	−39.93	<0.0001
	Intermediate–Open	−0.21	0.01	−16.45	<0.0001
3 m	Dense–Intermediate	−0.32	0.03	−10.63	<0.0001
	Dense–Open	−0.43	0.03	−14.1	<0.0001
	Intermediate–Open	−0.1	0.03	−3.23	0.004
6 m	Dense–Intermediate	−0.49	0.03	−18.64	<0.0001
	Dense–Open	−0.7	0.03	−26.33	<0.0001
	Intermediate–Open	−0.21	0.03	−7.27	<0.0001
12 m	Dense–Intermediate	−0.36	0.02	−14.46	<0.0001
	Dense–Open	−0.55	0.02	−22.48	<0.0001
	Intermediate–Open	−0.19	0.02	−7.61	<0.0001
24 m	Dense–Intermediate	−0.06	0.02	−2.74	0.018
	Dense–Open	−0.29	0.02	−12.28	<0.0001
	Intermediate–Open	−0.22	0.02	−9.23	<0.0001
48 m	Dense–Intermediate	−0.15	0.02	−6.09	<0.0001
	Dense–Open	−0.45	0.02	−18.58	<0.0001
	Intermediate–Open	−0.3	0.02	−12.13	<0.0001

This summary table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A12
Summary output of the GLMM testing for the effect of vegetation cover (and its interaction with recording distance) on spectrogram correlations for meerkats in Mweya

		Estimate	SE	*t*	*P*
General	Dense–Intermediate	−0.2	0.01	−13.13	<0.0001
	Dense–Open	−0.57	0.02	−35.35	<0.0001
	Intermediate–Open	−0.37	0.01	−22.9	<0.0001
3 m	Dense–Intermediate	−0.26	0.04	−6.47	<0.0001
	Dense–Open	−0.33	0.04	−8.03	<0.0001
	Intermediate–Open	−0.07	0.04	−1.65	0.297
6 m	Dense–Intermediate	−0.24	0.03	−6.8	<0.0001
	Dense–Open	−0.54	0.04	−14.45	<0.0001
	Intermediate–Open	−0.29	0.04	−7.88	<0.0001
12 m	Dense–Intermediate	−0.3	0.03	−9.52	<0.0001
	Dense–Open	−0.77	0.03	−22.83	<0.0001
	Intermediate–Open	−0.47	0.03	−13.78	<0.0001
24 m	Dense–Intermediate	−0.3	0.03	−9.94	<0.0001
	Dense–Open	−0.78	0.03	−24.91	<0.0001
	Intermediate–Open	−0.48	0.03	−15.54	<0.0001
48 m	Dense–Intermediate	0.08	0.03	2.74	0.019
	Dense–Open	−0.43	0.03	−14.11	<0.0001
	Intermediate–Open	−0.51	0.03	−17.12	<0.0001

This summary table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A13
Summary output of the GLMM testing for the effect of vegetation cover (and its interaction with recording distance) on spectrogram correlations for meerkats in Sorabi

		Estimate	SE	*t*	*P*
General	Dense–Intermediate	−0.34	0.01	−27.73	<0.0001
	Dense–Open	−0.74	0.01	−58.1	<0.0001
	Intermediate–Open	−0.39	0.01	−29.64	<0.0001
3 m	Dense–Intermediate	−0.38	0.03	−11.25	<0.0001
	Dense–Open	−0.56	0.03	−16.39	<0.0001
	Intermediate–Open	−0.18	0.04	−4.86	<0.0001
6 m	Dense–Intermediate	−0.47	0.03	−16.73	<0.0001
	Dense–Open	−0.92	0.03	−31.02	<0.0001
	Intermediate–Open	−0.45	0.03	−14.03	<0.0001
12 m	Dense–Intermediate	−0.48	0.02	−19.55	<0.0001
	Dense–Open	−0.94	0.02	−37.08	<0.0001
	Intermediate–Open	−0.47	0.03	−17.33	<0.0001
24 m	Dense–Intermediate	−0.18	0.02	−7.93	<0.0001
	Dense–Open	−0.63	0.02	−27.36	<0.0001
	Intermediate–Open	−0.45	0.02	−19.04	<0.0001
48 m	Dense–Intermediate	−0.21	0.02	−9.37	<0.0001
	Dense–Open	−0.62	0.02	−28.34	<0.0001
	Intermediate–Open	−0.41	0.02	−18.38	<0.0001

This summary table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A14
Summary output of the GLMM testing for the effect of vegetation cover (and its interaction with recording distance) on spectrogram correlations for banded mongooses in the Kalahari

		Estimate	SE	*t*	*P*
General	Dense–Intermediate	−0.08	0.01	−6.32	<0.0001
	Dense–Open	−0.05	0.01	−3.46	0.002
	Intermediate–Open	0.03	0.01	2.49	0.038
3 m	Dense–Intermediate	0.15	0.03	4.2	0.0001
	Dense–Open	−0.01	0.04	−0.29	1
	Intermediate–Open	−0.16	0.04	−4.14	0.0001
6 m	Dense–Intermediate	0.18	0.03	6.27	<0.0001
	Dense–Open	−0.01	0.03	−0.2	1
	Intermediate–Open	−0.19	0.03	−5.96	<0.0001
12 m	Dense–Intermediate	−0.11	0.02	−4.51	<0.0001
	Dense–Open	−0.08	0.03	−2.94	0.010
	Intermediate–Open	0.03	0.03	1.24	0.641
24 m	Dense–Intermediate	−0.32	0.02	−13.65	<0.0001
	Dense–Open	−0.07	0.02	−3	0.008
	Intermediate–Open	0.24	0.02	9.77	<0.0001
48 m	Dense–Intermediate	−0.3	0.02	−13.09	<0.0001
	Dense–Open	−0.06	0.02	−2.51	0.036
	Intermediate–Open	0.24	0.02	9.73	<0.0001

This summary table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A15
Summary output of the GLMM testing for the effect of vegetation cover (and its interaction with recording distance) on spectrogram correlations for dwarf mongooses in the Kalahari

		Estimate	SE	*t*	*P*
General	Dense–Intermediate	−0.1	0.01	−7.91	<0.0001
	Dense–Open	−0.02	0.01	−1.46	0.430
	Intermediate–Open	0.08	0.01	6.02	<0.0001
3 m	Dense–Intermediate	0.12	0.03	3.88	0.0003
	Dense–Open	−0.02	0.03	−0.71	1
	Intermediate–Open	−0.15	0.03	−4.27	0.0001
6 m	Dense–Intermediate	0.24	0.03	8.77	<0.0001
	Dense–Open	−0.02	0.03	−0.81	1
	Intermediate–Open	−0.26	0.03	−8.88	<0.0001
12 m	Dense–Intermediate	−0.08	0.02	−3.16	0.005
	Dense–Open	−0.02	0.03	−0.84	1
	Intermediate–Open	0.06	0.03	2.1	0.108
24 m	Dense–Intermediate	−0.41	0.02	−16.67	<0.0001
	Dense–Open	0.01	0.03	0.6	1
	Intermediate–Open	0.43	0.03	16.23	<0.0001
48 m	Dense–Intermediate	−0.37	0.03	−13.95	<0.0001
	Dense–Open	−0.04	0.03	−1.45	0.444
	Intermediate–Open	0.32	0.03	11.72	<0.0001

This summary table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A16
Summary output of the GLMM testing for the effect of calling loudness (and its interaction with recording distance) on spectrogram correlations for meerkats in the Kalahari

		Estimate	SE	*t*	*P*
General	Loud–Soft	−0.15	0.16	−0.91	0.362
3 m	Loud–Soft	−0.1	0.16	0.61	0.544
6 m	Loud–Soft	−0.01	0.16	−0.06	0.950
12 m	Loud–Soft	−0.13	0.16	−0.82	0.410
24 m	Loud–Soft	−0.3	0.16	−1.86	0.063
48 m	Loud–Soft	−0.39	0.16	−2.4	0.016

This summary table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A17
Summary output of the GLMM testing for the effect of calling loudness (and its interaction with recording distance) on spectrogram correlations for banded mongooses in Mweya

		Estimate	SE	*t*	*P*
General	Loud–Soft	−0.46	0.15	−3.05	0.002
3 m	Loud–Soft	−0.24	0.15	−1.55	0.122
6 m	Loud–Soft	−0.4	0.15	−2.65	0.008
12 m	Loud–Soft	−0.52	0.15	−3.42	0.0006
24 m	Loud–Soft	−0.55	0.15	−3.68	0.0002
48 m	Loud–Soft	−0.57	0.15	−3.79	0.0002

This summary table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A18
Summary output of the GLMM testing for the effect of calling loudness (and its interaction with recording distance) on spectrogram correlations for dwarf mongooses in Sorabi

		Estimate	SE	*t*	*P*
General	Loud–Soft	−0.75	0.06	−11.59	<0.0001
3 m	Loud–Soft	−0.65	0.07	−9.36	<0.0001
6 m	Loud–Soft	−0.81	0.07	−11.88	<0.0001
12 m	Loud–Soft	−0.7	0.07	−10.38	<0.0001
24 m	Loud–Soft	−0.77	0.07	−11.5	<0.0001
48 m	Loud–Soft	−0.82	0.07	−12.15	<0.0001

This summary table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A19
Summary output of the GLMM testing for the effect of calling loudness (and its interaction with recording distance) on spectrogram correlations for meerkats in the Kalahari

		Estimate	SE	*t*	*P*
General	Loud–Soft	0.6	0.13	4.63	<0.0001
3 m	Loud–Soft	0.72	0.13	5.36	<0.0001
6 m	Loud–Soft	0.6	0.13	5.04	<0.0001
12 m	Loud–Soft	0.61	0.13	4.65	<0.0001
24 m	Loud–Soft	0.53	0.13	4.09	<0.0001
48 m	Loud–Soft	0.47	0.13	3.66	0.0003

The analysis for this summary table is based on vocalizations played back at their ‘natural’ amplitude. The table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A20
Summary output of the GLMM testing for the effect of calling loudness (and its interaction with recording distance) on spectrogram correlations for banded mongooses in Mweya

		Estimate	SE	*t*	*P*
General	Loud–Soft	−0.04	0.13	−0.34	0.730
3 m	Loud–Soft	0.11	0.13	0.83	0.407
6 m	Loud–Soft	0.04	0.13	0.31	0.755
12 m	Loud–Soft	−0.04	0.13	−0.31	0.758
24 m	Loud–Soft	−0.08	0.13	−0.66	0.511
48 m	Loud–Soft	−0.25	0.13	−1.9	0.057

The analysis for this summary table is based on vocalizations played back at their ‘natural’ amplitude. The table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A21
Summary output of the GLMM testing for the effect of calling loudness (and its interaction with recording distance) on spectrogram correlations for dwarf mongooses in Sorabi

		Estimate	SE	*t*	*P*
General	Loud–Soft	0.04	0.09	0.47	0.638
3 m	Loud–Soft	0.21	0.09	2.28	0.022
6 m	Loud–Soft	0.13	0.09	1.43	0.154
12 m	Loud–Soft	0.16	0.09	1.81	0.070
24 m	Loud–Soft	0.02	0.09	0.28	0.777
48 m	Loud–Soft	−0.32	0.09	−3.56	0.0004

The analysis for this summary table is based on vocalizations played back at their ‘natural’ amplitude. The table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A22
Summary output of the GLMM testing for the effect of calling loudness (and its interaction with recording distance) on amplitude difference values (between vocalization peak amplitude and background noise amplitude) for meerkats in the Kalahari

		Estimate	SE	*z*	*P*
General	Loud–Soft	−0.0349	0.0052	−6.685	<0.0001
3 m	Loud–Soft	−0.0213	0.0053	−4.028	0.0001
6 m	Loud–Soft	−0.0262	0.0053	−4.956	<0.0001
12 m	Loud–Soft	−0.0324	0.0053	−6.106	<0.0001
24 m	Loud–Soft	−0.0429	0.0053	−8.08	<0.0001
48 m	Loud–Soft	−0.0515	0.0053	−9.675	<0.0001

The analysis for this summary table is based on vocalizations played back at their ‘natural’ amplitude. The table includes estimates, SE, *z* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A23
Summary output of the GLMM testing for the effect of calling loudness (and its interaction with recording distance) on amplitude difference values (between vocalization peak amplitude and background noise amplitude) for banded mongooses in Mweya

		Estimate	SE	*z*	*P*
General	Loud–Soft	−0.0227	0.0066	−3.446	0.0006
3 m	Loud–Soft	−0.0191	0.0067	−2.867	0.004
6 m	Loud–Soft	−0.0191	0.0067	−2.861	0.004
12 m	Loud–Soft	−0.0206	0.0067	−3.083	0.002
24 m	Loud–Soft	−0.0242	0.0067	−3.61	0.0003
48 m	Loud–Soft	−0.0306	0.0067	−4.572	<0.0001

The analysis for this summary table is based on vocalizations played back at their ‘natural’ amplitude. The table includes estimates, SE, *z* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A24

Summary output of the GLMM testing for the effect of calling loudness (and its interaction with recording distance) on amplitude difference values (between vocalization peak amplitude and background noise amplitude) for dwarf mongooses in Sorabi

		Estimate	SE	*z*	*P*
General	Loud–Soft	−0.0341	0.0039	−8.717	<0.0001
3 m	Loud–Soft	−0.0337	0.004	−8.366	<0.0001
6 m	Loud–Soft	−0.0404	0.004	−9.999	<0.0001
12 m	Loud–Soft	−0.044	0.0041	−10.843	<0.0001
24 m	Loud–Soft	−0.038	0.0041	−9.327	<0.0001
48 m	Loud–Soft	−0.0146	0.0041	−3.574	0.0004

The analysis for this summary table is based on vocalizations played back at their ‘natural’ amplitude. The table includes estimates, SE, *z* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing).

Table A25

Acoustic features discriminating between loud and soft calls

	Soft calls		Loud calls		LMM	
	Mean	SE	Mean	SE	Estimates	*P*
Peak frequency	0.84	0.05	3.13	0.33	−2.05	0.041
Q25	0.74	0.04	2.77	0.29	−1.84	0.052
Q50	1.04	0.06	3.34	0.3	−2.12	0.034
Q75	1.67	0.11	4.31	0.3	−2.48	0.023

This summary table includes mean, SE and results from LMMs (testing for differences in acoustic features between loud and soft vocalizations). Significance values were adjusted with Bonferroni correction due to multiple testing. Mean and SE for peak frequency, Q25, Q50 and Q75 are expressed in kHz.

Table A26

Summary output of the GLMM testing for the effect of loudspeaker position (and its interaction with recording distance) on spectrogram correlations for meerkats in the Kalahari

		Estimate	SE	*t*	*P*
General	Ground–Perch	−0.21	0.01	−24.75	<0.0001
3 m	Ground–Perch	0.24	0.02	9.33	<0.0001
6 m	Ground–Perch	−0.14	0.02	−6.64	<0.0001
12 m	Ground–Perch	−0.45	0.02	−24.64	<0.0001
24 m	Ground–Perch	−0.47	0.01	−31.07	<0.0001
48 m	Ground–Perch	−0.25	0.01	−18.77	<0.0001

This summary table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing). Ground: vocalizations played at their natural amplitude with the loudspeaker placed on the ground. Perch: vocalizations played at their natural amplitude with the loudspeaker placed on a perch.

Table A27

Summary output of the GLMM testing for the effect of the loudspeaker position (and its interaction with recording distance) on spectrogram correlations for banded mongooses in Mweya

		Estimate	SE	*t*	*P*
General	Ground–Perch	−0.21	0.01	−22.59	<0.0001
3 m	Ground–Perch	−0.23	0.03	8.83	<0.0001
6 m	Ground–Perch	−0.29	0.02	−12.86	<0.0001
12 m	Ground–Perch	−0.43	0.02	−22.37	<0.0001
24 m	Ground–Perch	−0.34	0.02	−19.28	<0.0001
48 m	Ground–Perch	−0.23	0.02	−12.99	<0.0001

This summary table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing). Ground: vocalizations played at their natural amplitude with the loudspeaker placed on the ground. Perch: vocalizations played at their natural amplitude with the loudspeaker placed on a perch.

Table A28

Summary output of the GLMM testing for the effect of the loudspeaker position (and its interaction with recording distance) on spectrogram correlations for dwarf mongooses in Sorabi

		Estimate	SE	*t*	*P*
General	Ground–Perch	−0.28	0.01	−40.8	<0.0001
3 m	Ground–Perch	0.32	0.02	17.24	<0.0001
6 m	Ground–Perch	−0.29	0.02	−18.1	<0.0001
12 m	Ground–Perch	−0.49	0.01	−33.78	<0.0001
24 m	Ground–Perch	−0.51	0.01	−38.32	<0.0001
48 m	Ground–Perch	−0.42	0.01	−31.53	<0.0001

This summary table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing). Ground: vocalizations played at their natural amplitude with the loudspeaker placed on the ground. Perch: vocalizations played at their natural amplitude with the loudspeaker placed on a perch.

Table A29

Summary output of the GLMM testing for the effect of the loudspeaker position (and its interaction with recording distance) on spectrogram correlations for meerkat sentinel calls in the Kalahari

		Estimate	SE	*t*	*P*
General	Ground–Perch	−0.15	0.01	−14.7	<0.0001
3 m	Ground–Perch	0.7	0.03	24.31	<0.0001
6 m	Ground–Perch	−0.07	0.02	−3.06	0.002
12 m	Ground–Perch	−0.51	0.02	−22.93	<0.0001
24 m	Ground–Perch	−0.58	0.02	−30.92	<0.0001
48 m	Ground–Perch	−0.3	0.02	−16.43	<0.0001

This summary table includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing). Ground: sentinel calls played at their natural amplitude with the loudspeaker placed on the ground. Perch: sentinel calls played at their natural amplitude with the loudspeaker placed on a perch.

Table A30

Summary output of the GLMM testing for the effect of the loudspeaker position (and its interaction with recording distance) on spectrogram correlations for dwarf mongoose sentinel calls in Sorabi

		Estimate	SE	*t*	*P*
General	Ground–Perch	−0.33	0.01	−29.1	<0.0001
3 m	Ground–Perch	0.38	0.03	12.15	<0.0001
6 m	Ground–Perch	−0.24	0.03	−9.02	<0.0001
12 m	Ground–Perch	−0.56	0.02	−23.4	<0.0001
24 m	Ground–Perch	−0.61	0.02	−28.29	<0.0001
48 m	Ground–Perch	−0.61	0.02	−29.26	<0.0001

This summary includes estimates, SE, *t* ratios and significance values from pairwise comparison (adjusted with Bonferroni correction due to multiple testing). Ground: sentinel calls played at their natural amplitude with the loudspeaker placed on the ground. Perch: sentinel calls played at their natural amplitude with the loudspeaker placed on a perch.

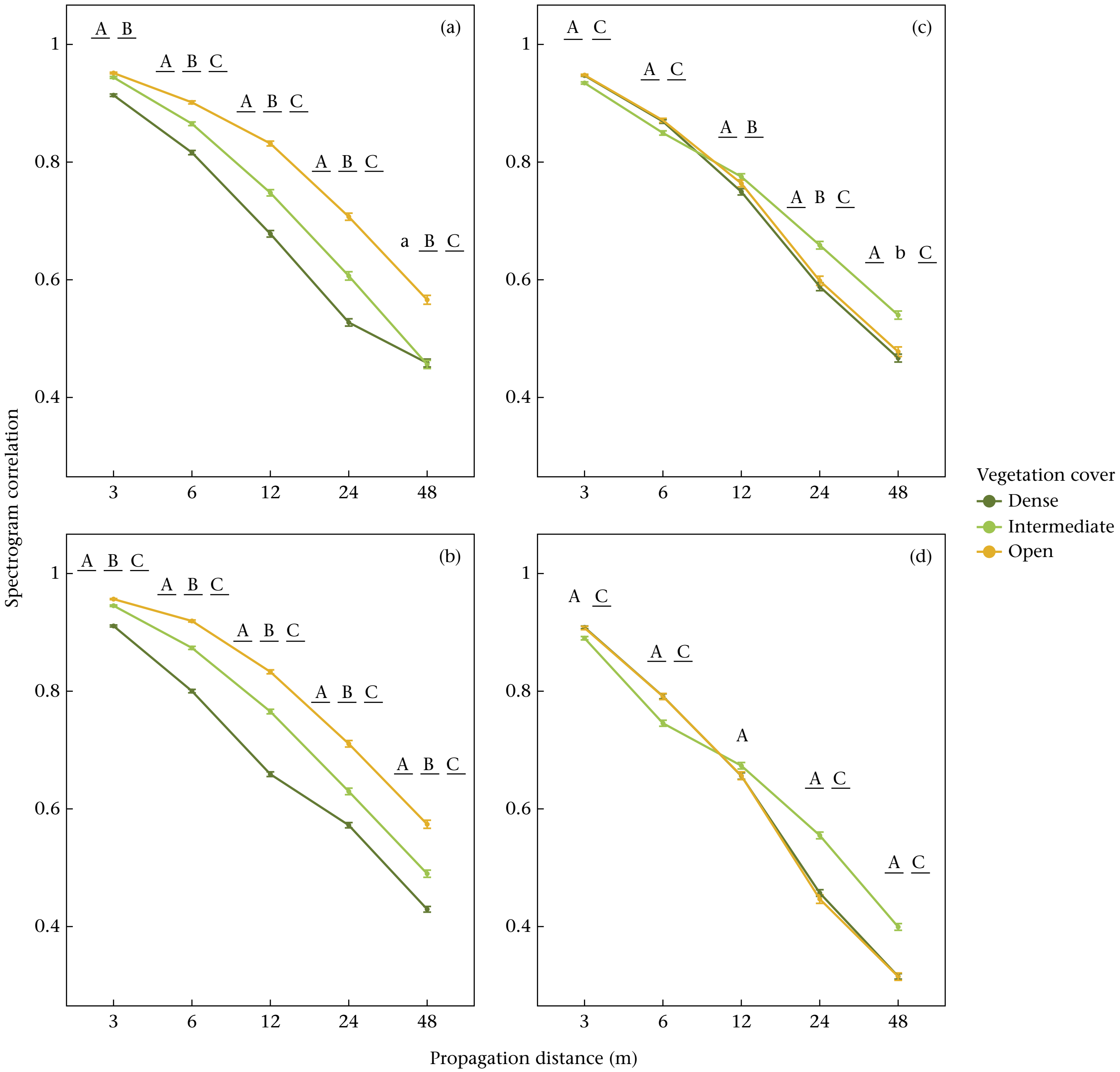

Figure A1. For meerkats in (a) Mweya and (b) Sorabi and for (c) banded and (d) dwarf mongooses in the Kalahari, spectrogram correlation values (mean ± SE) of their vocalizations in open, intermediate and dense landscapes. All P values were adjusted with Bonferroni corrections. Tests and significance levels are indicated as follows: ‘A’ significant difference between ‘dense’ and ‘intermediate’; ‘B’ significant difference between ‘dense’ and ‘open’; ‘C’ significant difference between ‘intermediate’ and ‘open’; lowercase letters indicate $P < 0.05$; uppercase letters not underscored indicate $P < 0.01$; uppercase and underscored letters indicate $P < 0.001$.

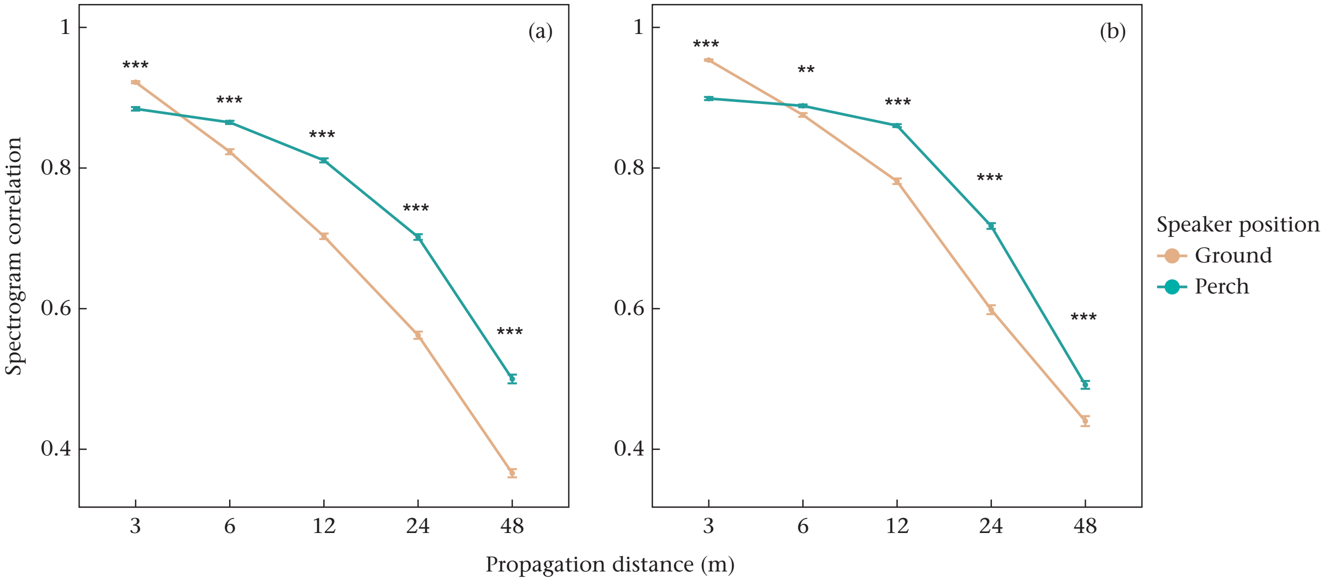

Figure A2. For meerkats and dwarf mongooses in their native habitat [(a) dwarf mongooses in Sorabi; (b) meerkats in Kalahari], spectrogram correlation values (mean ± SE) obtained with sentinel calls propagated with their 'natural' amplitude and the speaker placed either on the ground or on a perch. All *P* values were adjusted with Bonferroni corrections. $^{**}P < 0.01$; $^{***}P < 0.001$.