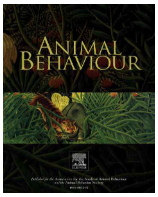
Animal Behaviour 230 (2025) 123373

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Alerting components in animal vocalization

Vlad Demartsev [a], [b], [*], Yair Geva [c], Pablo Alba-González [c], Lee Koren [d], Amiyaal Ilany [c], [e], Eli Geffen [c]

[a] Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany
[b] Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Konstanz, Germany
[c] School of Zoology, Tel Aviv University, Tel Aviv, Israel
[d] The Mina and Everard Goodman Faculty of Life Sciences, Bar-Ilan University, Ramat-Gan, Israel
[e] The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, Israel

ARTICLE INFO

Article history:
Received 7 February 2025
Initial acceptance 18 March 2025
Final acceptance 29 July 2025
Available online 30 October 2025
MS. number: 25-00096

Keywords:
animal communication
attention
bioacoustics
framework
saliency
signalling efficiency

Effective communication relies on signals that are detectable and informative, yet the structural acoustic properties supporting these qualities are not always the same. Alerting components (introductory elements that capture the receiver's attention) can enhance signalling efficiency. While such elements are likely to be common in both human and animal communication, standardized evaluation criteria for alerting components are lacking. We propose a framework to identify and evaluate acoustic alerting components based on three criteria. (1) Signal properties: structural features enhancing signal propagation and effective range. (2) Signaller perspective: flexible use by signallers based on receiver attention. (3) Receiver perspective: increased likelihood and speed of responses to the signal. We applied this framework to test whether ‘wail’ elements in rock hyrax, *Procavia capensis*, songs serve as alerting components. Our findings indicate that wails exhibit several features consistent with an alerting function: they degrade minimally over medium communicative ranges, frequently occur at the beginning of songs and appear less often at the end. Playback experiments showed a higher probability of conspecific responses to songs with intact wails than to songs with reduced wails. Our framework offers a tool to study alerting components across species, revealing strategies for effective communication in complex environments. Understanding the mechanisms underlying the usage and effectiveness of alerting components can provide insights into how animals capture and evaluate attention and the cognitive processes supporting these capabilities.

Acoustic signals evolve to balance environmental transmission and receiver perception, but these goals often conflict. The acoustic adaptation hypothesis (Morton, 1975) suggests that signals are shaped to be robust to environmental degradation at the relevant communication range. Additionally, the signal perception and processing hypothesis (Endler, 1993) suggests that signals are shaped to reliably evoke behavioural responses by transducing into neural outputs. However, with some evolutionary forces acting in opposition (Freitas et al., 2025), signal structures optimized for propagation may not evoke strong behavioural responses, and vice versa (Guilford & Dawkins, 1993). As a result, we often find signals with suboptimal acoustic structures for propagation in native habitats, highlighting trade-offs in signal design. For example, the long-distance calls of the common marmoset, *Callithrix jacchus*, do not appear to be specifically adapted for transmission in its native habitat (Morrill et al., 2013). Similarly, banded mongoose, *Mungos mungo*, calls appear to be transmitted better in a non-native rather than in their native habitat (Garcia Arasco et al., 2022). The sensory drive hypothesis attempts to unify the two main selection pressures on signal design and predicts the coevolution of signals, sensory mechanisms and microhabitat choice (Cummings & Endler, 2018).

Alerting components, which are introductory call elements that capture attention, can bridge some of the constraints by recruiting the receiver's ‘attentional energy’ and priming them for complex messages (Bermeitinger & Frings, 2015; Richards, 1981). Auditory attention enhances receivers' responsiveness in the frequency range of the signal by modifying the neuronal receptive fields in the auditory cortex (Fritz et al., 2007). This allows better isolation of the stimuli from background noise and better resolution of its acoustic dimensions compared to the case in a preattentive state (Fritz et al.,

---

[*] Corresponding author.
E-mail address: demartsev@gmail.com (V. Demartsev).

https://doi.org/10.1016/j.anbehav.2025.123373

2007; Kayser et al., 2005). When the ‘message’ components of the signal are costly and elaborate (Nelson et al., 2016), effectively capturing receiver attention and increasing the likelihood of response helps to balance the cost—benefit ratio of the signalling event. This mechanism is widely used in human speech (e.g. starting an utterance with ‘look’, ‘listen’ or ‘excuse me’; Aijmer, 2018), serving to signal an intention to communicate (Scott-Phillips, 2015) and to monitor the engagement of communication partners (Senju & Hasegawa, 2005). Besides humans (Tomasello, 2016), alerting components have been found in signals of multiple animal species, including among birds (Brenowitz, 1982), anurans (Gerhardt, 1976) and other mammals (Mitchell et al., 2006).

To fulfil the function of increasing the detectability of signals (Wiley, 2006), alerting components are expected to be conspicuous (Ord & Stamps, 2008) and robust to spatial degradation and environmental interference (Morton, 1975). However, the specific signal characteristics supporting these qualities often vary, influenced by the acoustic characteristics of the environment, species-specific communication distance and ecological constraints (e.g. detectability by predators). Possible examples of alerting components, observed in the roars of red deer, *Cervus elaphus* (Reby & Charlton, 2012), and in the barks of dingoes, *Canis familiaris dingo* (Déaux et al., 2016), include perceptually harsh sounds that contain nonlinear phenomena (NLP; Massenet et al., 2025). Sounds containing NLP often evoke strong behavioural responses (Massenet et al., 2025; Townsend & Manser, 2011). The artificial addition of an NLP component (white noise) to alarm calls of yellow-bellied marmots, *Marmota flaviventris*, disrupted their foraging behaviour, possibly due to increased attention and vigilance (Blumstein & Recapet, 2009). However, calls containing NLP are often broadband and exhibit uneven attenuation, with higher frequencies attenuating more rapidly than lower frequencies. This differential energy loss can lead to a change in the perceived characteristics of the signal and, in some cases, affect its recognition by the receivers.

Other possible examples of alerting components include tonal sounds, wherein most of the energy is concentrated within a narrow and low-frequency range, which are less susceptible to differential degradation (Richards, 1981). In multiple bird species, narrow frequency, tonal and widely spaced introductory notes are followed by rapid trills and frequency sweeps. The structure of the trills degrades due to reverberation, but the introductory tonal signals could be favoured to reduce degradation and masking by environmental noise (Dubois & Martens, 1984). In fact, signal organization of tonal and unmodulated introductory elements followed by syntactically and acoustically complex structures has been described in calls of multiple taxa. In sooty mangabey, *Cercocebus torquatus atys*, territorial whoop-gobble calls start with simple, low-pitched notes and continue with a complex series of mixed-type syllables (Range & Fischer, 2004). In white-crowned sparrows, *Zonotrichia leucophrys*, songs begin with a simple, possibly alerting, whistle followed by complex trill and buzz-type elements (Nelson et al., 2016). Similarly, the songs of male Javan silvery gibbons, *Hylobates moloch*, begin with a series of relatively tonal notes (with low-frequency modulation) and gradually transition to more complex trills and modulated song syllables (Geissmann et al., 2005). With the differences in the vocal anatomy in the various taxa (Fitch & Suthers, 2016), it is unlikely that these similarities in signal structure would be driven by specific physiological/anatomical constraints on vocal production. This could, however, indicate convergence towards a signal structure that overcomes constraints of environmental degradation (Richards, 1981) and alerts the receivers towards the messaging components of a signal.

No standardized criteria exist to evaluate alerting components, despite their prevalence in natural communication (Grafe & Wanger, 2007; Mitchell et al., 2006; Nelson, 2017). There are several nonmutually exclusive criteria that can indicate such a function; for example, spatial propagation, robustness to masking noise and evocative acoustic features. Furthermore, recent evidence shows that animals are capable of flexible and intentional use of signals to draw the receivers' attention (Salmi et al., 2022). A focused investigation of alerting signal phenomena could reveal to what extent they are used in conjunction with the evaluation and awareness of the receivers' attention. Considering the lack of established benchmarks and testing procedures for the evaluation of alerting functionality, we propose a framework to identify acoustic alerting components based on three criteria. Acoustic alerting components should (1) have structural features enhancing spatial propagation and effective range (signal properties), (2) be used flexibly by signallers based on environmental interference and receiver attention (signaller perspective) and (3) increase the likelihood and speed of receivers’ responses to the signal (receiver perspective). In Table 1, we outline these three main criteria with six predictions (P) and test procedures for evaluating the alerting function.

Here, we use our proposed framework (Table 1) to evaluate the introductory elements of rock hyrax, *Procavia capensis*, songs as alerting components. Rock hyraxes, social mammals with a well-described vocal repertoire (Demartsev, Gordon, et al., 2019;

Table 1
Criteria for testing the alerting function of an acoustic signal

Criterion	Prediction	Property description	Test procedures
Signal properties	P1 spatial degradation	Alerting components will demonstrate enhanced spatial propagation properties: low decay over transmission distances (Nelson et al., 2016; Richards, 1981) within the typical communication ranges of the species	Sound propagation trials for quantifying the distance-dependent acoustic degradation of the signal (Araya-Salas et al., 2025)
	P2 robustness to interference	Alerting components will be resistant to masking by environmental noise through high amplitude, frequency range and duration (Ord & Stamps, 2008; Wiley, 2006) and generally will accumulate more saliency within the auditory scene (Kayser et al., 2005)	Analysis of auditory masking under varying levels of environmental noise. Identification of features that are salient and robust to natural interference (Brumm & Slabbekoorn, 2005)
Signaller perspective	P3 adjustment for attention	Receiver reactions, indicating signal detection, will lead to the omission of the alerting component from subsequent signalling (Botting & Bastian, 2019; Hostetter et al., 2007)	Testing for the occurrence of alerting component as a function of the audience's behavioural responses (Hostetter et al., 2001) and under varying levels of environmental noise (Peters et al., 2007)
	P4 adjustment for interference	Under masking conditions, alerting components will be included and persist in the signalling event (Peters et al., 2007)	
Receiver perspective	P5 response probability	Under similar environmental conditions, receivers will be more likely to respond to a signal with an alerting component than without it (Wiley, 2006, 2013)	Playback trials, testing the receiver response (vocal, vigilance, general orienting behaviours), probability and latency to stimuli primed by alerting components of varying intensity and salience (Blumstein & Recapet, 2009).
	P6 response latency	Signals preceded by an alerting component will be detected and responded to faster in comparison to signals with message components only (Richards, 1981)	

Fourie, 1977), are a suitable model for testing technical and biological criteria of alerting signals. Male hyraxes produce long and syntactically complex vocal displays termed ‘songs’ (Koren & Geffen, 2008, 2011). While the energetic cost of singing appears low (Ilany et al., 2013), hyrax males adjust their singing effort when they have an alert audience. More specifically, events that induce heightened alertness and orienting behaviour in conspecifics (alarm/distress calls, predator presence, physical fights) also trigger male singing. These ‘event-induced’ songs tend to be longer and more complex in comparison to ‘spontaneous’ singing (Demartsev et al., 2014; Ilany et al., 2011). Previously, we suggested that singing might be associated with increased costs of exposure to predators or competitors (Ilany et al., 2011). So, increased signalling effort when the audience is already attentive could be a means of balancing the costs and benefits of singing (Demartsev et al., 2014). The progression of the songs (from the beginning to the end) resembles musical structures designed to maximize attention and lead the audience towards a climactic ending of the performance (Demartsev et al., 2017). Overall, the singing displays of hyrax males appear to recruit and maintain audience attention on both behavioural and structural levels. However, it is not clear if it includes designated alerting elements as yet another solution for maximizing the probability of reaching potential receivers.

Hyrax songs consist of three distinct vocal elements (Fig. 1, Audio S1 in the Supplementary Material), which are repeated and combined into multielement sequences (bouts). Consecutive bouts are typically delimited by a silence of more than 1 s, and a song can thus contain hundreds of vocal elements, split into dozens of bouts (Kershenbaum, 2014; Kershenbaum et al., 2012). Wails are usually the opening elements of the bouts and songs (Koren & Geffen, 2008) with an average duration of 0.6 s and up to 1.3 s (Koren & Geffen, 2011). Chucks are short (average 0.1 s) elements that are serially repeated throughout the bouts (average 12.8 elements per bout, range 0–51). Snorts are the rarest element, mostly produced by older adult males, and appear in the second half of the song. While chucks and snorts were previously shown to reflect individual singer traits such as weight, age and dominance (Koren & Geffen, 2008, 2011; Weissman et al., 2020), wails have not been linked to a trait or function. The relatively long duration of wails (Fig. 1) may make them more salient to the audience, as the auditory threshold (sound pressure level required for detection) is lower for longer sounds (Heil, 2014). Previous reports have shown that some animals increase the duration of the alerting component under noisy conditions, possibly to improve detectability (Peters et al., 2007). Furthermore, the tonal and unmodulated wail segments could be more robust to degradation related to distance and reverberation. Together with the observation of wails being produced mainly in the opening parts of the song, we hypothesized that they could function as alerting components, produced before the information-bearing chucks and snorts.

To test the alerting functionality of rock hyraxes' wails, we performed a multilevel analysis of: (1) sound propagation experiments, measuring spatial degradation (P1) and robustness to interference (P2) of the three song elements; (2) the appearance of wails in the different stages of naturally produced songs; (3) the signallers' adjustment for attention (P3) examining if the rate at which wails are excluded from song bouts is conditioned on receiving conspecific responses; (4) the receiver response probability (P5) and response latency (P6) to natural and manipulated songs with reduced or disrupted wails. Testing for signaller adjustment for interference (P4, Table 1) was not possible, as environmental noise levels and acoustic interference measurements were not included in the long-term field protocols. By testing 5 out of 6 predictions described by our framework (Table 1), we are able to determine to what extent wails can fulfil the alerting component functionality.

METHODS

Study System

We collected the data at the Ein Gedi Natural Reserve, Israel (31°28′N, 35°24′E) between 2000 and 2015, following previously established protocols (Demartsev et al., 2014; Ilany et al., 2011). We trapped rock hyraxes using live box traps (Tomahawk Live Trap, https://livetrap.com) placed in shaded locations and baited with cabbage and kohlrabi. We set the traps at dawn, inspected them after 3–4 h and locked them open until the next trapping session. We anaesthetized the trapped animals by intramuscular injection of ketamine hydrochloride (10 mg/kg). We individually marked each hyrax with a subcutaneous transponder (Datamars Inc., https://datamars.com) and either an ear tag (pups and juveniles, ca. 0.25 g per tag) or a lightweight numbered collar (adult individuals, ca. 5 g). Over the 16-year study period, we anaesthetized and

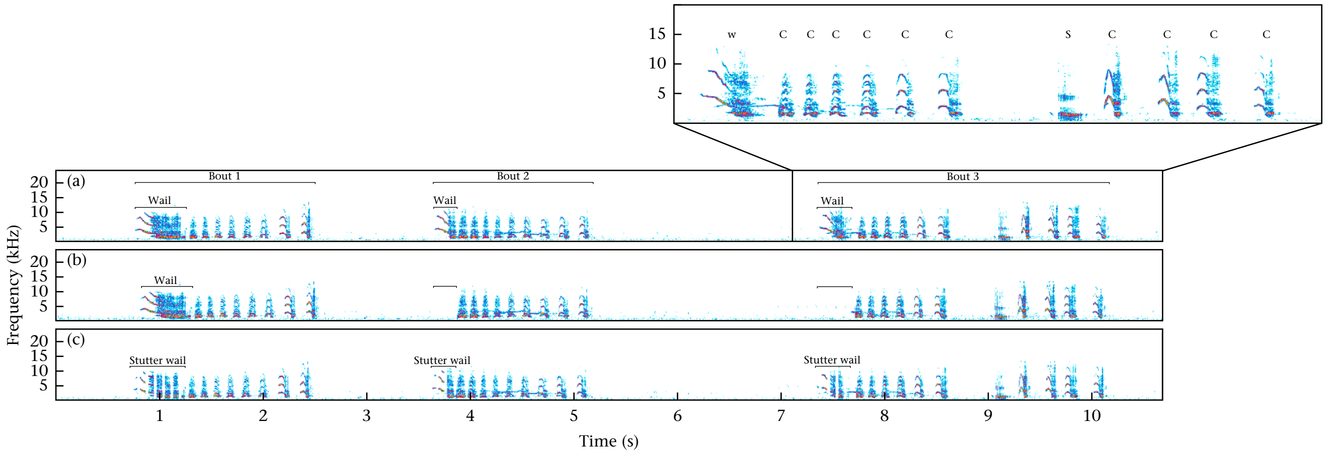


Figure 1. Sample spectrogram showing three consecutive bouts of an average male hyrax song and the track structure used in the playback trials. (a) Control (natural wails): natural, unaltered songs. The insert shows a detailed structure of Bout 3, demonstrating the common order of elements within (W = wail, C = chuck and S = snort). (b) Treatment 1 (reduced wails): songs in which we randomly replaced 70% of all wail elements with background noise sections of the same length. Songs had the same number and order of bouts as the originals. (c) Treatment 2 (stutter wails): songs in which we segmented the wail elements into 5–6 equally spaced parts by inserting a short section of background noise.

marked a total of 378 individual animals, with a mean (± SD) yearly capture rate of 63.4 ± 20.4 individuals. Unless required by the protocols of specific projects, we released the recaptured individuals without anaesthesia and subsequent treatment. In years where hyraxes were captured for marking only, the rates (± SD) of recaptured individuals undergoing anaesthesia and further procedures were only 3.2% ± 2.9. In years when we undertook biologger deployment and retrieval (Bordes et al., 2022) or collected metabolic rate measurements (Ilany et al., 2013), the rates (± SD) of further intervention on recaptured individuals were 60.0% ± 10.4.

Behavioural Observations and Vocalization Recordings

The annual field seasons lasted from April to August and we observed hyraxes daily, during their morning activity periods, using 10 × 42 Monarch binoculars and a Fieldscope ED82 telescope with up to ×75 zoom magnification (both Nikon, https://imaging.nikon.com). For each observed animal, we documented its ID (based on collars and/or ear tags), location and behaviour (e.g. moving, eating, lying, vocalizing). In the case of vocalizations, we noted all types of calls (e.g. song, alarm trill). We recorded male songs, used for structural analyses and as templates for playback experiments, from a distance of 10–50 m, using a Sennheiser ME67 shotgun microphone (frequency response 50–20 000 Hz ± 2.5 dB), powered by a Sennheiser K6 module, covered with a Sennheiser MZW70-1 blimp windscreen and hand-held using an MZS20–1 shock mount with a pistol grip (Sennheiser Electronic, Germany, https://www.sennheiser.com). We recorded the audio in mono either using a Marantz PMD-222 cassette recorder (Marantz, Japan, https://www.marantz.com) and later digitized it, or using a Tascam HD-P2 digital audio recorder (TASCAM Corporation, CA, U.S.A., https://tascam.com), with a sampling frequency of 48 kHz and a sampling width of 24 bits (Ilany et al., 2011).

Sound Propagation Trials (Signal Properties, P1 and P2)

We expected wails in hyrax song to have better spatial propagation properties and to be more robust to environmental interference (noise masking or scattering by wind) than chuck and snort elements. To test that we performed sound propagation trials from 28–30 July 2023, between 1800 hours and 2000 hours (UTC + 3). We performed the trials at two locations (31°27′46.0″N, 35°23′20.0″E and 31°27′18.7″N, 35°23′00.6″E), both in a typical rock hyrax habitat in our study area. We selected the locations to allow for at least 100 m of flat terrain, unobstructed by dense vegetation and far from sources of anthropogenic noise. We selected three natural hyrax songs, which we had previously recorded at the field site, with minimal noise interference and only one vocalizing male. Each of the selected songs included all three elements with the following mean element frequency (± SD) per song: wail, 34.7 ± 11.5; chuck, 198.9 ± 61.2; snort, 5.3 ± 7.6. To minimize the low-frequency noise, we applied a high-pass filter of 200 Hz to each track and shortened the silent sections (between the hyrax calls) to standardize the duration of the tracks to 110–130 s. We then normalized the amplitude of the calls in the tracks to 75% of the dynamic range. We used Avisoft-SASLab Pro 5.3.2 (Avisoft Bioacoustics, Germany, https://avisoft.com) for all audio editing and cleaning steps.

We broadcasted the tracks from a FoxPro Scorpion X1B speaker with a TX200 wireless remote controller (FOXPRO Inc., PA, U.S.A., https://www.gofoxpro.com). To compare the spatial propagation of the three song elements we recorded the broadcasted tracks at four distances (10, 25, 50 and 100 m) using a Tascam HD-P2 audio recorder and a tripod-mounted Sennheiser ME67 microphone with an MZW70-1 blimp windscreen, angled directly at the speaker. In each location, we broadcasted each of the three tracks twice, resulting in 12 samples per recording distance. To account for the effects of sound distortion due to wind speed and direction, as well as the potential for masking due to wind noise, we recorded wind speed throughout the trials using a Benetech Windmeter GM816 (http://www.benetechco.net). We calculated the median wind speed for each recording and considered it as a proxy for environmental noise levels during the playback. We received wind direction data from the Israeli Meteorological Service ground weather station located at 31°25′12.0″N, 35°23′13.6″E, approximately 4 km from the experimental sites. We calculated the angular differences between the wind direction and the axis of sound transmission (wind bearing), with 0° indicating full alignment between the wind direction and the sound transmission axis and 180° indicating that the wind direction is directly opposite to the sound transmission axis.

Postprocessing and sound decay analysis

We visually and auditorily inspected the audio files in Raven Pro 1.6.5 (K. Lisa Yang Center for Conservation Bioacoustics, NY, U.S.A., https://www.ravensoundsoftware.com), applied a high-pass filter of 200 Hz to minimize low-frequency noise and manually annotated each vocal element. We assigned a common identifier to the same vocal element exemplars recorded at different distances. We then performed a spectrogram correlation analysis using the spcc function from the R package baRulho (Araya-Salas et al. , 2025), which estimates the similarity of two sound waves using time–frequency cross-correlation (Araya-Salas & Smith-Vidaurre, 2017). Within each transmission ‘transect’, we defined a call recorded at 10 m as a reference level and compared it to the same sound recorded at 25, 50 and 100 m.

We used a mixed model to test for the effect of the vocal element (i.e. wail, chuck or snort), distance from the speaker, median wind speed and wind bearing relative to the speaker on spectrogram cross-correlation. As the difference between the vocal elements was the prime interest of the study, we included two-way interaction terms between the vocal element and all the recording distance and wind-related variables. We set the trial's unique identifier as a random effect and estimated the effect size by the total effect (Saltelli, 2002). To estimate the collinearity of predictors, we used the variance inflation factor (VIF), with a cutoff value of VIF < 10, and calculated *P* values using randomizations.

Song Structure Analysis (Signaller Perspective, P3)

As potential alerting components, wails were expected to consistently appear at the beginning of the song and to be omitted or reduced when an audience is likely to be alert. To establish that, we used our hyrax song library, recorded between 2000 and 2015 (Demartsev et al., 2014; Demartsev, Kershenbaum, et al., 2019). We used songs with documented singer ID and behavioural/environmental contexts of the singing event as logged by human observers. In this work, we refined the classification of the singing context described in Demartsev et al. (2014) and divided singing events into spontaneous (songs initiated without any observable external trigger), countersinging (songs initiated as a response to singing by other males or in parallel to songs of other males) and event-induced (songs initiated as a response to a stressful event, e.g. presence of a predator, alarm calling). We defined the singing context at the bout level rather than at the song level. In a spontaneous singing event, we defined all bouts as spontaneous. In a counter-singing event, we noted the time when the conspecific singing response was detected, marked the preceding bouts as spontaneous and the following bouts as counter-singing. In cases when the focal individual started singing in response to a conspecific song, we defined all bouts as countersinging. In event-induced events, we defined all bouts as event-induced.

Overall, we analysed 210 natural songs by 18 males. These included 2065 spontaneous bouts (from complete songs that were performed without observable triggers or parts of songs performed before conspecific response), 1378 countersinging bouts (from complete songs that were performed as a response to conspecific singing or parts of songs performed after the conspecific response was heard) and 574 event-induced bouts (from complete songs initiated after or during a song inducing event). For each song, we extracted the number of song bouts, the sequence of elements in each bout and the duration of each vocal element. To test whether the wails are associated with the beginning of singing bouts, we calculated the frequency per bout of all possible dyadic combinations that contain the wail element: chuck–wail, snort–wail, wail–chuck, wail–snort, wail–wail, bout start–wail (i.e. wail as the first call of the bout) and wail-bout end (i.e. wail as the last call of the bout). We used a logistic mixed model to test whether the frequency of the wail vocal combinations differs between bouts and between song types (spontaneous, countersinging and event-induced). We set male identity * proportion of song duration as a random slope and evaluated the effect size by the total effect (Saltelli, 2002).

To test whether the occurrence and duration of wails decrease in the terminal bouts of a song and whether the rate of wail exclusion is affected by conspecific singing, we used a nominal logistic mixed model for the wail occurrence per singing bout (binary) data and a normal mixed model for the wail duration per bout. As the predictors in these models, we used the relative position of the bout in the song (i.e. the proportion of song duration) and song type (spontaneous, countersinging and event-induced). We set the singers identity as a random effect in both models, calculated the effect size by the total effect (Saltelli, 2002) and calculated *P* values using randomizations.

Field Playback Trials (Receiver Perspective, P5 and P6)

We expected that the omission of wails from the song would impair its detectability by the recipients and subsequently increase response latency and reduce overall responsiveness. To test this, we conducted a series of field playback trials in April–August 2020 and 2021 (during peak male hyrax singing activity). We conducted 118 playback trials at five locations with a mean of 23.6 trials per location (range 13–33), in the Ein Gedi Natural Reserve (Table A1). The targeted receivers were not part of the marked hyrax population but from groups that were opportunistically observed. We followed a previously established playback protocol (Demartsev, Ilany, et al., 2016). Briefly, to maintain playback rates similar to those of natural hyrax singing events observed at the field site and to minimize habituation, we restricted the number of trials to two per day per site, with a minimum interval of 30 min. To eliminate the potential effects of acquaintance between the senders and receivers (Goll et al., 2017), we only used songs that were recorded at least 3 km from the playback sites and at least 7 years before the date of the experiment, thus mimicking a song of an unfamiliar individual. We transmitted the tracks using a FoxPro Scorpion X1B speaker placed in a concealed spot within a 20–30 m radius of an identified male hyrax or a group of at least four adult individuals. We calibrated the amplitude of playback tracks to match the natural level of hyrax singing (ca. 80 dB; Ilany et al., 2011). Once no natural hyrax vocalizations or environmental disturbances were observed for at least 5 min, we activated the playback.

Playback trials consisted of three different treatments. (1) Control (natural wails, 40 trials): natural, unaltered songs (Fig. 1a, Audio S1). (2) Treatment 1 (reduced wails, 39 trials). To test whether the abundance of wails affects the frequency and the latency of singing responses, we randomly replaced ca. 70% of the wails with background noise sections of the same length. Songs had the same number and order of bouts and nonwail elements as the original donor tracks (Fig. 1b, Audio S2). (3) Treatment 2 (stutter wails, 39 trials). To test whether wails' continuous and nonmodulated structure facilitates saliency and contributes to the frequency and latency of singing responses, we segmented all wails into 5–6 equally spaced parts. We inserted short sections (ca. 0.04 s) of background noise, equally spaced along the element, and kept approximately 65% of its duration (Fig. 1c, Audio S3).

As control tracks and templates for Treatment 1 and 2 manipulations, we selected eight songs produced by different males with an average ± SD song duration of 2.4 ± 0.9 min, net vocal duration of 26.7 s and syntactic complexity of 0.42 ± 0.05 (Demartsev, Kershenbaum, et al., 2019). The manipulation of Treatment 1 tracks resulted in songs with a mean of 33.3% (range 30.8–36.4%) of the original wail duration, which translated into a 28.5% reduction of the songs' net vocal duration. We decided to reduce the number of wail elements and not omit them completely to limit the reduction in the net duration of the signal and to maintain an overall resemblance to the songs' natural syntactic structure. The manipulation of Treatment 2 tracks resulted in songs with a mean of 64.3% (range 58.5–64.4%) of the original wail duration, which translated into a 15.2% reduction in the songs' net vocal duration. To prevent artefacts from the sound editing process, we applied a DC offset filter and normalized the amplitude of the calls in the manipulated tracks to 75% of the dynamic range.

We played a selected natural playback track and its alterations (i.e. Treatments 1 and 2) to each of the targeted social groups while randomizing the order of control and treatment track playbacks. For each trial, we noted the receivers' responses as either 'singing' or 'not singing' as a binary variable and recorded the playback track and any hyrax vocalization emitted during the trial using the same equipment used for our routine collection of hyrax vocalization. We considered a 'singing' response as singing by at least one male initiated within 2.5 min from the end of playback. The 2.5 min threshold was based on the observed response time to natural male hyrax singing events.

From the audio recordings of 'singing' responses, we extracted the latency between the beginning of the playback trial and the onset of the reply. In cases when more than one male responded, we only analysed the first response. We used a generalized estimating equation (GEE) logistic mixed model for the binary reply data and a normal mixed model for the latency to reply data to compare the experimental treatments. We set the playback site and song ID as random effects in both models and calculated *P* values using randomizations whenever the *F* test was used. All statistical models in this study were calculated using JMP, version 18 (SAS Institute, Inc., U.S.A., https://www.sas.com) and SPSS, version 29 (IBM Corp., U.S.A., https://www.ibm.com).

Ethical Note

All field procedures for this study were conducted in accordance with the Israeli Nature and Parks Authority guidelines and regulations under the following annual permit numbers: 2000/8871, 2001/8871, 2002/14674, 2003/14674, 2004/17687, 2005/17687, 2007/27210, 2008/31138, 2009/32871, 2010/37520, 2011/38061, 2012/38400, 2013/38803, 2014/40185, 2015/40768, 2016/41174, 2017/41507, 2018/41880, 2019/42182, 2020/42434, 2021/42663, 2022/42985, 2023/43316. As our research was carried out exclusively in the field and involved only free-ranging animals, a separate approval of the Tel Aviv University Institutional Animal Care and Use Committee was not required. All data collection and experimental procedures followed previously established protocols and were performed by trained personnel. Over the course of this long-term study, no detrimental effects have been observed on the individual animals, social groups or population levels.

RESULTS

Sound Propagation Trials (Signal Properties, P1 and P2)

When comparing the distance-dependent degradation of the wail to the two other song elements, we found that at median distances, wails showed high acoustic stability. When recorded 25 m from the sound source, wails exhibited relatively high spectral cross-correlation values (overall mean ± SE: 0.77 ± 0.01), indicating low signal degradation, and were statistically comparable to snorts (overall mean ± SE: 0.79 ± 0.03; Tukey post hoc test: $t_{266} = 0.7$, $P = 0.74$). Both wails and snorts demonstrated significantly higher cross-correlation values than chucks (overall mean ± SE: 0.72 ± 0.01; wails: $t_{308} = 2.6$, $P = 0.026$; snorts: $t_{230} = 3.9$, $P < 0.001$), which were the most degraded. At longer distances, while snorts remained the most reliably transmitted element, showing the highest spectral cross-correlation at 50 and 100 m distances (overall mean ± SE: 0.75 ± 0.02), both wails and chucks rapidly degraded (overall mean ± SE: wails 0.61 ± 0.01, chucks 0.60 ± 0.01; Fig. 2a, Table 2).

Regarding the influence of wind conditions, the transmission quality of snorts appeared relatively unaffected by wind direction and speed. For both chucks and wails, spectral cross-correlation

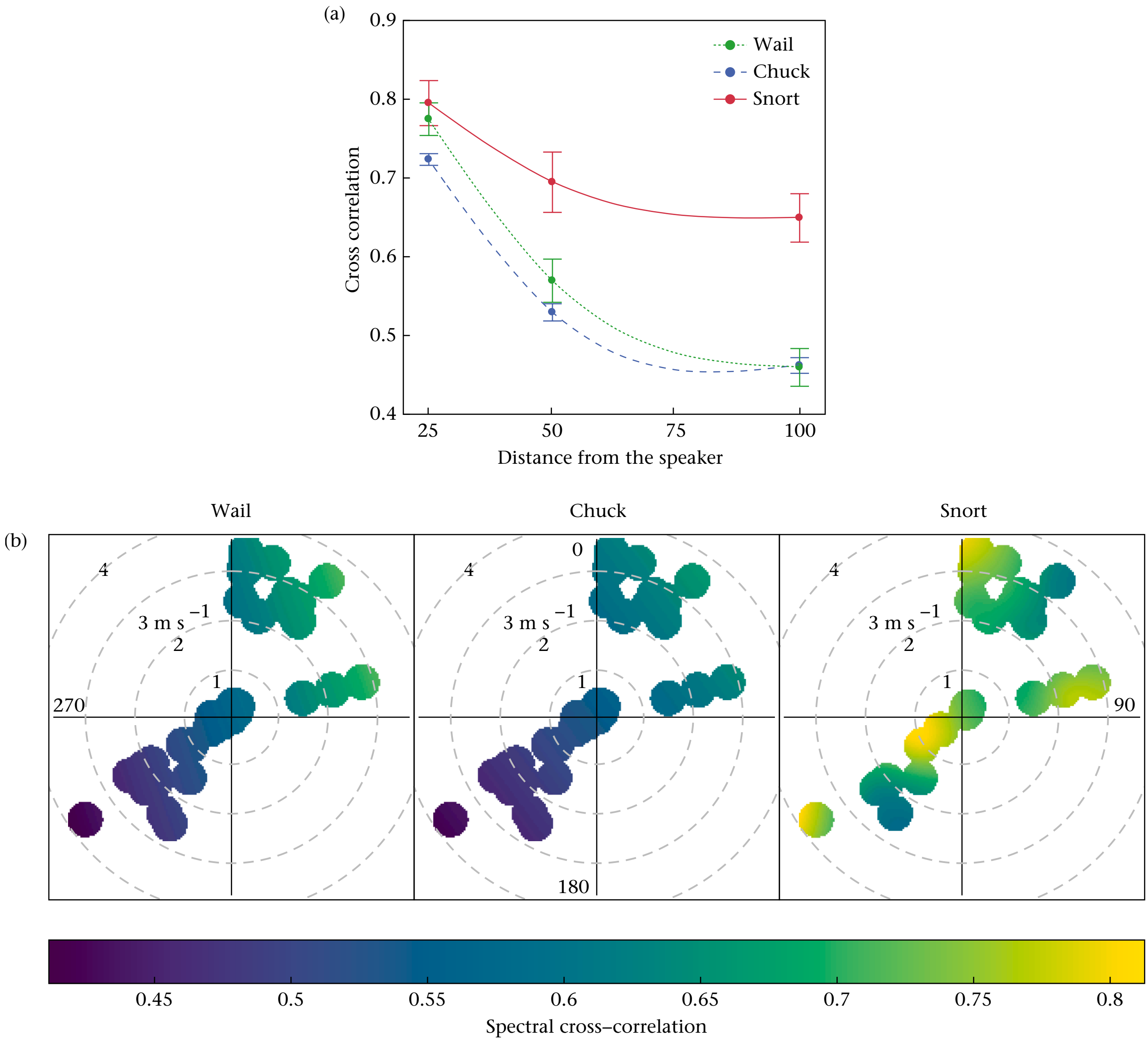


Figure 2. Distance and wind-dependent decay of the song elements. (a) The Y axis represents the spectral cross-correlation of the song elements recorded at 25, 50 and 100 m distance from the sound source (X axis) compared to the reference recording made at 10 m. Dot and whisker markers are the mean (± 95% confidence interval, CI) of the measured spectral correlation values. The connecting curves illustrate the continuous relationship between distance and spectral decay. (b) Spectral cross-correlation of the song elements as a function of wind speed (m/s), denoted by the dashed rings, and wind direction displayed as a relative bearing, with 0° indicating wind direction that aligns with the direction of the sound transmission transect. The positions of the dots represent the median wind speed values (m/s) and median relative wind direction, measured during the sound propagation trials. The colours of the dots represent the spectral cross-correlation values of each song element, per respective environmental conditions, compared to the reference recording made at 10 m.

Table 2
Effect of recording distance and wind speed on the spectral cross-correlation of hyrax song elements

Model term	*df*	*F*	*P*	Total effect	VIF
Song vocal element	2, 216	17.8	**<0.001**	0.486	3.1
Distance from the speaker	1, 3962	290.3	**<0.001**	0.366	7.1
Wind speed median	1, 4163	21.2	**<0.001**	0.063	7.3
Wind bearing difference	1, 4156	63.2	**<0.001**	0.174	7.9
SVE * Distance from the speaker	2, 3956	7.0	**0.001**		7.4
SVE * Wind speed median	2, 4160	6.2	**0.002**		7.6
SVE * Wind bearing difference	2, 4158	8.6	**<0.001**		8.2

The effect of song vocal element (SVE), distance from the speaker, median wind speed, wind bearing relative to the speaker and two-way interactions on spectral cross-correlation. Sound ID was set as a random effect. The effect size was estimated by the total effect. Collinearity of predictors was estimated by the variance inflation factor (VIF). *P* values were calculated using randomisations. Significant terms are denoted in bold.

values decreased (indicating higher degradation) when the wind bearing was opposite to the sound transmission axis and increased (lower degradation) when it was aligned (Fig. 2b–Table 2). While visual inspection of the results (Fig. 2b) suggested that under strong winds, wails might have higher cross-correlation values (lower degradation) than chucks when the sound axis aligns with the wind direction, all three-way and four-way interaction terms (including element type * distance * wind effects) were not statistically significant ($P \geq 0.166$ in all cases).

Overall, the model results showed that the type of vocal element and the distance from the speaker were the most influential predictors (i.e. had the highest effect size) on the spectral cross-correlation. In contrast, wind speed and bearing showed relatively minor influence on element degradation (Table 2).

Song Structure Analysis (Signaller Perspective, P3)

As alerting components are more likely to have a functional benefit at the start of the signal, we tested whether the wails have a typical location within a singing bout and whether this location is affected by the singing context (song and bout type). Wails appeared at the beginning (start-wail) of nearly every bout in the songs (mean ± SD = 0.87 ± 0.12; Fig. 3), regardless of the bout being spontaneous, countersinging or event-induced. Generally, we found a significant difference between the proportions of the seven element combinations that contained wails (likelihood ratio $\chi^2_6 = 71.4$, $P < 0.0001$, total effect = 0.94), but no differences between bout types ($\chi^2_2 = 0.7$, $P = 0.696$, total effect < 0.01) or between males ($\chi^2_{17} = 3.7$, $P = 0.999$, total effect = 0.05). We also did not detect significant interaction between singer identity and element combinations ($\chi^2_{102} = 12.7$, $P = 0.999$).

To determine whether wails tend to be emitted at certain phases of the hyrax song, we looked at the probability of wail occurrence and duration as a function of song progression. We found that overall, both the probability of wail occurrence and their duration significantly decreased towards the end of the song (Fig. 4b–d; Table 3). When considering the singing context, we found a significant interaction between bout type and position of the bout in the song in both the probability of wail occurrence ($P < 0.001$; Fig. 4b–Table 3) and wail duration ($P < 0.01$; Fig. 4d–Table 3). In event-induced bouts, the probability of wail occurrence as the songs progressed decreased at a higher rate than in both spontaneous and countersinging bouts (Fig. 4c). However, the difference in slopes was significant only in event-induced and spontaneous bouts comparison (Tukey test, odds ratio = 2.5, $P = 0.003$). Similarly, wail duration decreased with song progression, with a significant difference in slopes between event-induced and spontaneous bouts (Tukey test, $P = 0.03$). Wail duration decreased at a lower rate in spontaneous bouts relative to event-induced bouts; however, the overall effect size (i.e. total effect) of bout type in the model was small (total effect = 0.03; Table 3). We found a similar, albeit nonsignificant, trend between event-induced and countersinging bouts ($P = 0.06$).

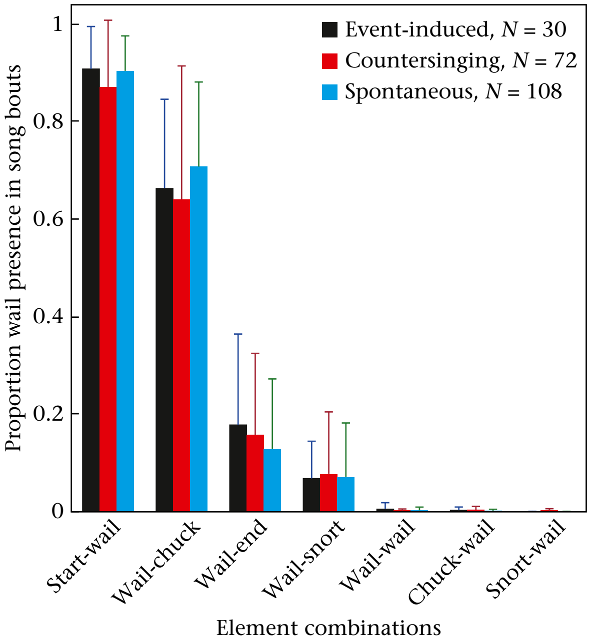


Figure 3. Mean (± SD) of the frequency of the wail vocal combinations per bout in the three song types (spontaneous, countersinging and event-induced). Wails appear most frequently as the first call of a singing bout and are predominantly followed by chucks.

Field Playback Trials (Receiver Perspective, P5 and P6)

The reply rate to natural wail controls was significantly higher than to manipulated songs (mixed model Tukey test, $\chi^2 = 6.8$, $P = 0.033$; Fig. 5a and b). The reply rate for both reduced wails songs ($P = 0.028$) and stutter wails songs ($P = 0.063$) was lower than for natural songs (Fig. 5b). Furthermore, we found a significant difference in the reply latency between the treatments (mixed model, $F_{2,37} = 4.1$, $P = 0.049$ by randomizations). The reply latency to the stutter wails treatments was significantly longer than to the natural wail songs (Tukey test, $P = 0.032$ by randomizations; Fig. 5c). No difference in reply latency was detected between natural wail and reduced wail songs (Tukey test, $P = 0.548$ by randomizations) or between reduced wail and stutter wail songs (Tukey test, $P = 0.124$ by randomizations).

DISCUSSION

In this study, we introduced and applied a framework to structurally and functionally evaluate whether or not an acoustic signal serves as an alerting component. In applying this framework to rock hyrax songs, we tested five of our framework's six total prediction criteria (P1–6). Rock hyrax wails degrade minimally over medium communicative ranges (P1) but do not show significant resistance to wind interference (P2). Wails frequently occur at the beginning of songs and are relatively quickly omitted from event-induced songs (P3). Conspecifics are more likely to respond to songs with intact wails than to songs with reduced wails (P5), but the response latency is not consistently affected (P6). Taken

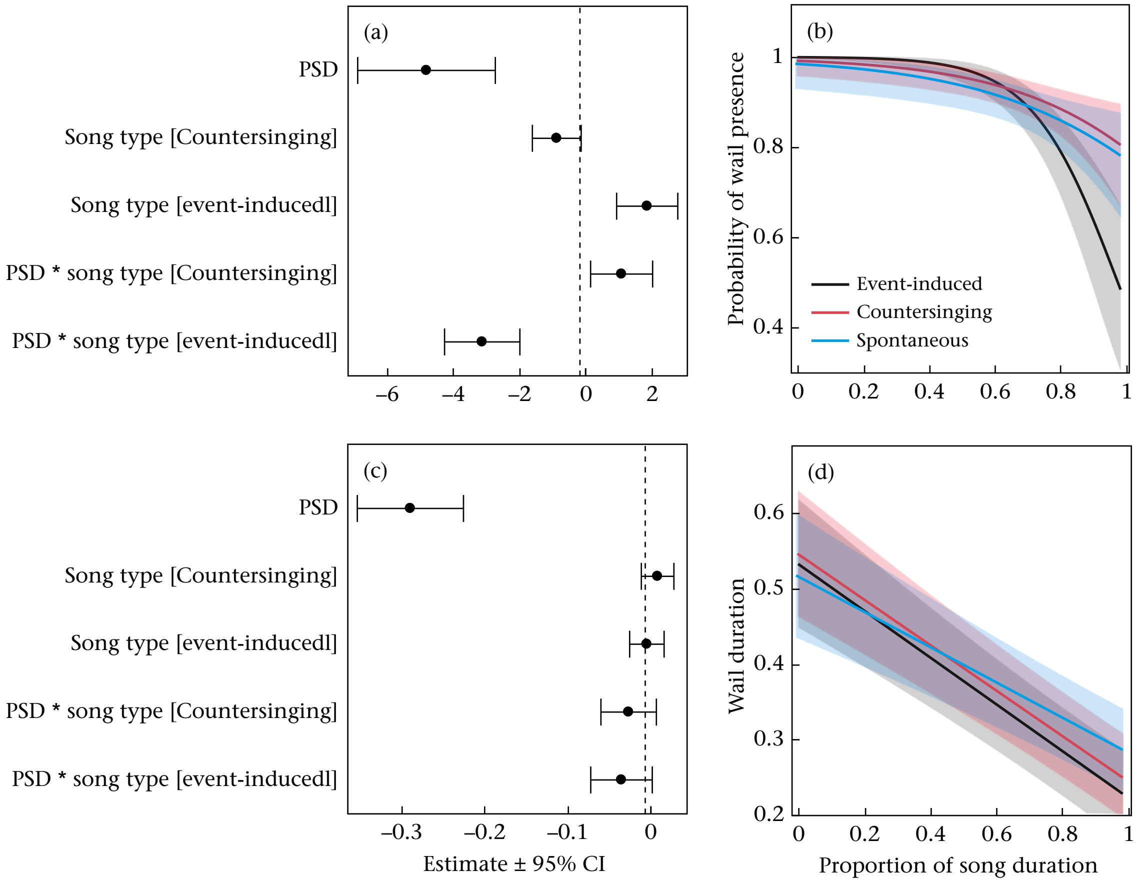


Figure 4. The omission of wails as a function of song progression. (a) The model estimates ± 95% confidence intervals, CI (whiskers), of the proportion of song duration (PSD), song type and their interaction, for wail presence. (b) The predicted probability of wail presence as a function of PSD. Shaded areas represent the 95% CI on the model estimates. (c) The model estimates (± 95% CI, whiskers) of the PSD, song type and their interaction, for wail duration. (d) The predicted probability of wail duration as a function of PSD. Shaded areas represent the 95% CI on the model estimates.

Table 3
The occurrence and the duration of wail elements as a function of the phase and type of hyrax song

Model term	*df*	*F*	*P*	Total effect
Wail presence				
Proportion of song duration	1, 16	38.9	**<0.001**	0.99
Song type	1, 4211	13.0	**<0.001**	0.22
Proportion of song duration * song type	1, 4211	15.7	**<0.001**	
Wail duration				
Proportion of song duration	1, 13	91.2	**<0.001**	0.97
Song type	2, 3628	2.8	0.051	0.03
Proportion of song duration * song type	2, 3429	6.8	**0.010**	

The effect of the relative position of a bout in the song (proportion of song duration), song type (spontaneous, countersinging and event-induced) and their interaction on wail presence (nominal logistic model) and wail duration (normal distribution model). The effect size was evaluated by the total effect. Male identity * Proportion of song duration was set as a random slope. *P* values were calculated using randomizations. Significant terms are denoted in bold.

together, we found that the wail elements fully meet three of the criteria, and partially meet a fourth, providing mixed support for our hypothesis on their alerting function.

Our findings in hyrax songs highlight that evidence for an alerting function can be mixed, and not all evaluation criteria need to be met. Factors like habitat structure, communication distances and social organization inevitably affect the specific mechanism through which alerting elements achieve their functionality. Therefore, comparing different sounds within a species' acoustic repertoire using this framework can reveal their relative alerting potential, even if no single sound type perfectly fits all criteria. Furthermore, while alerting components often have enhanced spatial propagation properties and are more robust to interference and noise masking than the messaging components, this may not always be necessary. The alerting function could also be achieved through species-specific introductory elements, potentially simple, repeated sounds that extend signal duration or establish a predictable rhythm, increasing contrast against background noise (Wiley, 2006).

The ultimate benchmark of the signals' alerting significance is the receiver's responses to them. Our framework integrates the physical propagation properties with signaller- and receiver-related signalling dynamics, offering a comprehensive evaluation procedure for the alerting functionality. While our experiments focused on the duration and structure of wails, this approach is readily adaptable for testing the importance of other features. Depending on the perception and communicative environment of the study species, frequency composition, bandwidth, amplitude modulation, rate or rhythmicity could each be systematically altered. Beyond reducing features, artificially enhancing specific acoustic or structural parameters could further strengthen the argument for their inherent alerting properties. Combined reduction and enhancement experiments can help reveal perceptual thresholds for alerting features and distinguish between inherent and learned responses. Evaluating the flexible usage of alerting components by the signaller, based on the

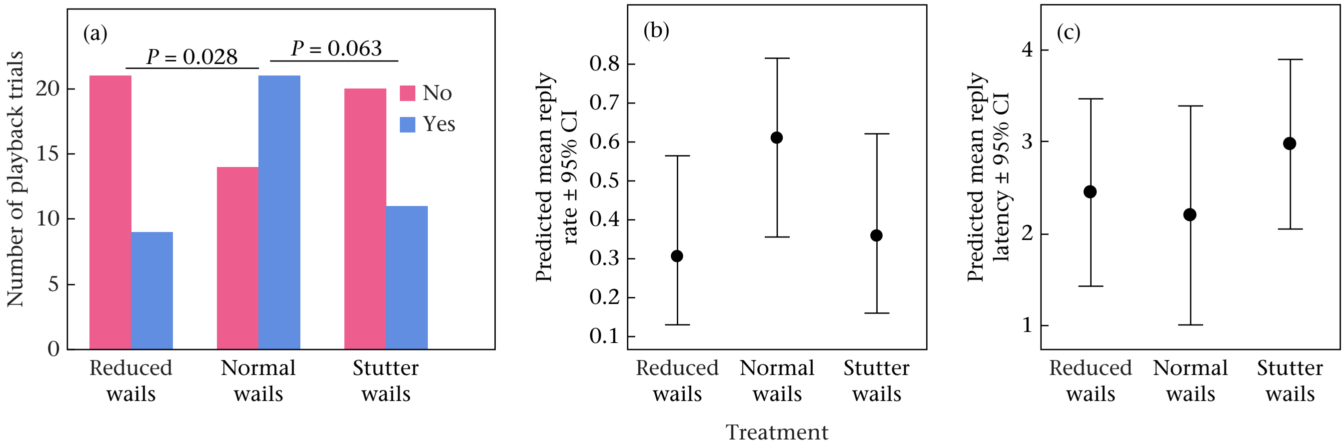


Figure 5. Playback trial outcomes. (a) The number of playback trials that received and did not receive) a conspecific singing reply by experimental conditions. (b) Model estimates ± 95% CI (whiskers) of predicted reply probabilities by experimental condition. (c) Model estimates ± 95% CI of predicted reply latency by experimental condition.

receiver's responses, can demonstrate to what extent animals perceive audience attention. Overall, the modularity of this framework enables its application across diverse species and signalling systems.

Signal Properties (P1 and P2)

We hypothesized that the duration and composite structure (containing both harmonic and NLP segments) of wails would make them more salient and robust to environmental interference compared to the shorter chucks or, relatively rare, harsh snorts. Hyrax songs and singing bouts typically begin with an introductory wail followed by a rapid series of chucks. Our analysis showed that wails were indeed more acoustically stable than chucks at a 25 m range, although this advantage diminished at 50 m and 100 m. These results could be analogous to the observations in other species, such as the introductory whistles in white-crowned sparrow, *Z. leucophrys*, songs, which degrade less with distance than subsequent complex phrases (Nelson et al., 2016). Similarly, coyote, *Canis latrans*, howls were relatively stable compared to harsh bark vocalizations (Mitchell et al., 2006). Wind direction and speed affected wails and chucks similarly. Higher spectral cross-correlation values were measured for calls recorded during stronger winds that were aligned with the axis of sound transmission. This indicates lower signal degradation, probably attributable to increased effective sound wave velocity and reduced scattering as the sound propagated downwind (Cheinet et al., 2018). The moderate wind speeds (up to 4 m/s) measured during our sound propagation trials, combined with the use of a wind-protected microphone, may not have been sufficient to fully test the resilience of signals to noise masking. Systematic tests under varied levels of natural or simulated noise interference, combined with direct measurements of background noise, would provide a clearer and more robust test of signals' resilience to masking.

The most stably transmitted elements in hyrax songs across all distances and wind conditions were the snorts, probably due to their low-frequency composition. Snorts contain NLP (Weissman et al., 2019) and are known to be evocative on their own, inducing conspecific responses even when other song elements are missing (Demartsev, Ilany, et al., 2016). NLP-containing elements have been shown to be evocative in red deer, *C. elaphus* (Reby & Charlton, 2012), dingo, *C. f. dingo* (Déaux et al., 2016) and yellow-bellied marmots, *M. flaviventris* (Blumstein & Recapet, 2009). However, snorts typically appear later in hyrax songs, are absent in young males' songs and are relatively rare overall (Koren & Geffen, 2008). The potential costs of their production (Weissman et al., 2019) and dense informational content (Demartsev, Ilany, et al., 2016) make snorts less likely to have a primary alerting function. Wails, being consistently present at the start of songs across all males and showing reliable transmission at short-to-medium ranges, appear to have higher alerting value.

Signaller Perspective (P3 and P4)

Wails appear at the opening of songs but become less common and often completely omitted as the songs progress. Such a pattern aligns with the expectation that alerting components precede message-bearing components, to enhance initial detection (Rowe, 1999). Alerting components can be dropped, with the signalling effort shifting toward the message components. This transition can be a part of a stereotypical signal structure or driven by the perception of the receivers' attention. In hyrax songs, in the latter half of the song, the syntactic complexity increases (Demartsev et al., 2017), information-rich snorts (Weissman et al., 2019) appear and wails are often shortened or omitted. This can be analogous to the introductory notes in male red junglefowl, *Gallus gallus*, alarm events. These notes trigger orienting responses towards the caller and are omitted from subsequent alarm calls (Evans & Bayly, 2003). Similarly, in spotted hyenas, *Crocuta crocuta*, long-distance whoop bouts often start with preliminary whoops, which have a simpler structure and could act as a warm-up or alerting signal before the message-bearing part (Lehmann et al., 2022).

While it is expected that alerting components will be omitted as the signaller perceives the receiver as attentive (Ben Mocha & Burkart, 2021), studies assessing dynamic attention awareness in animals often report mixed results (Botting & Bastian, 2019). Our current findings in this respect are also inconclusive. We previously hypothesized that countersinging (responding to another song) and event-induced (triggered by external events, such as alarms) songs both imply perceived audience attention (Demartsev et al., 2014). However, we found that while the wail omission was significantly faster in event-induced bouts, there was no difference between countersinging and spontaneous bouts. Event-induced songs follow salient events known to capture the attention of nearby individuals (Demartsev et al., 2014). So, faster omission of wails supports the hypothesis that perceived receiver attention facilitates a quicker transition from alerting to messaging components. A possible explanation for the difference in the rates of wail omission between countersinging and event-induced bouts could be the timing of attention capture and perception. Event-induced songs begin after an external event has probably already focused the audience's (Demartsev et al., 2014) and signaller's attention. This alignment of the trigger with the start of the song can influence the entire structural progression of the vocalization from its onset, leading to a faster omission of wails. On the other hand, countersinging often arises during an ongoing vocalization, meaning the initial singer might not immediately detect and process the response. This delay could slow the adjustment in the singing behaviour (wail omission) and obscure the influence of audience attention on song characteristics.

Alternatively, the higher arousal associated with predator-related or agonistic events, which trigger event-induced songs, could drive the rapid omission rates of wails. The requirement of motor preparation for producing complex movement (Rajan & Doupe, 2013) and the 'warming up' hypothesis predict improvement of a motor task with recent practice (Schraft et al., 2017). Wails are the first to appear in the ontogeny of hyrax songs (V. Demartsev, A. Ilany, L. Koren, E.Geffen, personal observations) and thus may be the easiest elements to produce. Initiating a song with a wail sequence may provide the necessary neural priming and/or motor warm-up for the complex, terminal bouts of the song. Higher levels of arousal are known to accelerate vocal performance (e.g increased call rate in marmoset monkeys, *Callithrix jacchus*; Borjon et al., 2016) and could speed up the song progression and wail omission.

While we could not test signallers' adjustment to interference (P4), our general prediction is that, under noisy conditions, wails would be sustained for a larger proportion of the song and/or that the duration of individual wail elements would increase. Such adjustments could enhance the signal's contrast and salience, similar to the case in Australian lizards, *Amphibolurus muricatus*, which increase the duration of alerting tail flicks in response to motion noise (Peters, 2008; Peters et al., 2007). Other potential solutions to mitigate the effect of noise include increasing amplitude and frequency shift to escape masking (Brumm et al., 2004; Hage et al., 2013). Showing the selective application of these adjustments to specific signal components would provide strong evidence for their designated alerting functionality. This specificity could minimize the potential costs associated with increased amplitude or duration of the whole signal.

Receiver Perspective (P5 and P6)

Our playback experiments showed that receivers were less likely to respond vocally to reduced wail or stutter wail playback tracks. This supports our prediction that wails might increase the detectability of songs. The reply latency was affected by the manipulation of wails in the stutter wail treatment, but the effect was relatively small. The composite structure of wails (stable harmonic segment followed by an NLP-containing pulse; Demartsev, Gordon, et al., 2019) might enhance their salience and localizability, contributing to the observed difference in reply rates. However, the relatively small effect on reply latency might be due to the nature of hyrax song evaluation. As songs are relatively long (mean = 2.0 min, maximum = 8.1 min), alerting components are expected to be most beneficial at the beginning of the signal. However, the receiver's decision to respond depends on the receiver's social status (Demartsev, Ilany, et al., 2016) and the song's features (Demartsev, Bar Ziv, et al., 2016). Thus, signal evaluation probably relies on the gradual accumulation of information over time (Goll et al., 2017). So, the time required for this evaluation might overshadow initial detection speed differences facilitated by alerting components.

An alternative interpretation of the reduced response rates to manipulated tracks is that the modifications altered the signal's informational content or perceived integrity, rather than just its detectability. Removing wails might have changed the songs in a way that discouraged replies, similar to how removing snorts previously reduced responses (Demartsev, Bar Ziv, et al., 2016). Removing wails also reduced the net vocal duration of the signal and could have affected the response probability. However, we have previously shown that the syntactic structure of hyrax songs is a stronger driver of response probability than the general sound density (Demartsev, Bar Ziv, et al., 2016) and this is likely to be the case in this study. It's also possible that the manipulated tracks were perceived as novel or ambiguous, leading receivers to hesitate or require a longer processing time.

Conclusion

In summary, our findings underscore the complex interplay between signal structure, signaller behaviour and receiver perception in shaping the alerting function of acoustic signals. While wails in rock hyrax songs could serve as an alerting component, the full extent to which they facilitate communication efficiency requires further investigation. Future studies, aiming for a deeper understanding of how alerting components are used in animal signals, could focus on their causal effects on signalling success; for instance, by conducting controlled playback experiments to measure receiver vigilance responses, changes in activity, or specific vocal replies across varied social and environmental conditions. Another vital research avenue involves examining the evolutionary trade-offs associated with producing highly detectable signals. This includes addressing the potential energetic costs of increased amplitude or duration, or enhanced conspicuousness to unintended receivers, such as predators or competitors.

Author Contributions

Vlad Demartsev: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Yair Geva:** Investigation, Data curation. **Pablo Alba González:** Writing – review & editing, Investigation. **Lee Koren:** Writing – review & editing, Project administration, Methodology, Investigation, Conceptualization. **Amiyaal Ilany:** Writing – review & editing, Methodology, Funding acquisition, Investigation, Conceptualization. **Eli Geffen:** Writing – review & editing, Visualization, Supervision, Resources, Project administration, Funding acquisition, Formal analysis, Conceptualization.

Data Availability

All data and relevant scripts used for analysis and for generating the figures are available at Mendeley https://doi.org/10.17632/ks7r8y6y2d.1. See Demartsev et al. (2025).

Declaration of Interest

The authors have no conflicts of interest to declare.

Acknowledgments

We acknowledge the essential logistical support and hospitality provided by the staff of the Ein Gedi Nature Reserve and the Ein Gedi Field School. We extend our sincere thanks to the Nature and Parks Authority for their permission to conduct this research and for their logistical support. We are grateful for the invaluable contributions of our former students, field assistants and guests at the field site. We appreciate A. Ashbury's constructive suggestions, which significantly improved the structure and clarity of this paper. Finally, we thank all members of the CoCoMo group for their valuable feedback on the early drafts and conceptualization of this paper. The long-term hyrax study was supported by grants from the Israel Science Foundation (577/99, 488/05, 461/09, 550/14, 767/16, 244/19, 245/19, 422/22, 539/24) and the U.S.-Israel Binational Science Foundation (2015088, 2019156). Parts of this work were carried out while V.D. was an Alexander von Humboldt-Stiftung postdoctoral fellow and also funded by the German Research Foundation (DFG) under Germany's Excellence Strategy (EXC 2117 –422037984).

Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123373.

References

Aijmer, K. (2018). Positioning of self in interaction: Adolescents' use of attention-getters. In K. Beeching, C. Ghezzi, & P. Molinelli (Eds.), *Positioning the self and others* (pp. 177–195). John Benjamins Publishing Company.

Araya-Salas, M., Grabarczyk, E. E., Quiroz-Oliva, M., García-Rodríguez, A., & Rico-Guevara, A. (2025). Quantifying degradation in animal acoustic signals with the R package baRulho. *Methods in Ecology and Evolution, 16*(3), 456–467. https://doi.org/10.1111/2041-210x.14481

Araya-Salas, M., & Smith-Vidaurre, G. (2017). warbleR: An R package to streamline analysis of animal acoustic signals. *Methods in Ecology and Evolution, 8*(2), 184–191. https://doi.org/10.1111/2041-210X.12624

Ben Mocha, Y., & Burkart, J. M. (2021). Intentional communication: Solving methodological issues to assigning first-order intentional signalling. *Biological Reviews, 96*(3), 903–921. https://doi.org/10.1111/brv.12685

Bermeitinger, C., & Frings, C. (2015). Rhythm and attention: Does the beat position of a visual or auditory regular pulse modulate T2 detection in the attentional blink? *Frontiers in Psychology, 6*, 1847. https://doi.org/10.3389/fpsyg.2015.01847

Blumstein, D. T., & Recapet, C. (2009). The sound of arousal: The addition of novel non-linearities increases responsiveness in marmot alarm calls. *Ethology, 115* (11), 1074–1081. https://doi.org/10.1111/j.1439-0310.2009.01691.x

Bordes, C. N. M., Beukeboom, R., Goll, Y., Koren, L., & Ilany, A. (2022). High-resolution tracking of hyrax social interactions highlights nighttime drivers of animal sociality. *Communications Biology, 5*(1), 1378. https://doi.org/10.1038/s42003-022-04317-5

Borjon, J. I., Takahashi, D. Y., Cervantes, D. C., & Ghazanfar, A. A. (2016). Arousal dynamics drive vocal production in marmoset monkeys. *Journal of Neurophysiology, 116*(2), 753–764. https://doi.org/10.1152/jn.00136.2016

Botting, J., & Bastian, M. (2019). Examining the use of auditory signals as 'attention-getters' in zoo-housed gorillas (*Gorilla gorilla gorilla*) and orangutans (*Pongo pygmaeus* and hybrid). *International Journal of Primatology, 40*(4), 573–586. https://doi.org/10.1007/s10764-019-00100-2

Brenowitz, E. A. (1982). Long-range communication of species identity by song in the red-winged blackbird. *Behavioral Ecology and Sociobiology, 10*(1), 29–38. https://doi.org/10.1007/BF00296393

Brumm, H., & Slabbekoorn, H. (2005). Acoustic communication in noise. In P. J. B. Slater, C. T. Snowdon, T. J. Roper, H. J. Brockmann, & M. Naguib (Eds.), *Advances in the Study of Behavior* (Vol. 35, pp. 151–209). Academic Press.

Brumm, H., Voss, K., Köllmer, I., & Todt, D. (2004). Acoustic communication in noise: Regulation of call characteristics in a New World monkey. *Journal of Experimental Biology, 207*(3), 443–448. https://doi.org/10.1242/jeb.00768

Cheinet, S., Cosnefroy, M., Königstein, F., Rickert, W., Christoph, M., Collier, S. L., Dagallier, A., Ehrhardt, L., Ostashev, V. E., Stefanovic, A., Wessling, T., & Wilson, D. K. (2018). An experimental study of the atmospheric-driven variability of impulse sounds. *Journal of the Acoustocal Society of America, 144*(2), 822. https://doi.org/10.1121/1.5047750

Cummings, M. E., & Endler, J. A. (2018). 25 years of sensory drive: The evidence and its watery bias. *Current Zoology, 64*(4), 471–484. https://doi.org/10.1093/cz/zoy043

Déaux, E. C., Allen, A. P., Clarke, J. A., & Charrier, I. (2016). Concatenation of 'alert' and 'identity' segments in dingoes' alarm calls. *Scientific Reports, 6*(1), Article 30556. https://doi.org/10.1038/srep30556

Demartsev, V., Bar Ziv, E., Shani, U., Goll, Y., Koren, L., & Geffen, E. (2016). Harsh vocal elements affect counter-singing dynamics in male rock hyrax. *Behavioral Ecology, 27*(5), 1397–1404. https://doi.org/10.1093/beheco/arw063

Demartsev, V., Geva, Y., Gonzalez, P. A., Koren, L., Ilany, A., & Geffen, E. (2025). *Alerting components in animal vocalization*. https://doi.org/10.17632/ks7r8y6y2d.1 [Data File].

Demartsev, V., Gordon, N., Barocas, A., Bar Ziv, E., Ilany, T., Goll, Y., Ilany, A., & Geffen, E. (2019). The 'Law of Brevity' in animal communication: Sex-specific signaling optimization is determined by call amplitude rather than duration. *Evolution Letters, 3*(6), 623–634. https://doi.org/10.1002/evl3.147

Demartsev, V., Ilany, A., Barocas, A., Bar Ziv, E., Schnitzer, I., Koren, L., & Geffen, E. (2016). A mixed strategy of counter-singing behavior in male rock hyrax vocal competitions. *Behavioral Ecology and Sociobiology, 70*(12), 2185–2193. https://doi.org/10.1007/s00265-016-2222-z

Demartsev, V., Ilany, A., Kershenbaum, A., Geva, Y., Margalit, O., Schnitzer, I., Barocas, A., Bar-Ziv, E., Koren, L., & Geffen, E. (2017). The progression pattern of male hyrax songs and the role of climactic ending. *Scientific Reports, 7*(1), 2794. https://doi.org/10.1038/s41598-017-03035-x

Demartsev, V., Kershenbaum, A., Ilany, A., Barocas, A., Bar Ziv, E., Koren, L., & Geffen, E. (2014). Male hyraxes increase song complexity and duration in the presence of alert individuals. *Behavioral Ecology, 25*(6), 1451–1458. https://doi.org/10.1093/beheco/aru155

Demartsev, V., Kershenbaum, A., Ilany, A., Barocas, A., Weissman, Y., Koren, L., & Geffen, E. (2019). Lifetime changes in vocal syntactic complexity of rock hyrax males are determined by social class. *Animal Behaviour, 153*, 151–158. https://doi.org/10.1016/j.anbehav.2019.05.011

Dubois, A., & Martens, J. (1984). A case of possible vocal convergence between frogs and a bird in Himalayan torrents. *Journal für Ornithologie, 125*(4), 455–463. https://doi.org/10.1007/BF01640137

Endler, J. A. (1993). Some general comments on the evolution and design of animal communication systems. *Philosophical Transactions of the Royal Society B: Biological Sciences, 340*(1292), 215–225. https://doi.org/10.1098/rstb.1993.0060

Evans, C., & Bayly, K. (2003). Dynamic changes in alarm call structure: A strategy for reducing conspicuousness to avian predators? *Behaviour, 140*(3), 353–369. https://doi.org/10.1163/156853903321826675

Fitch, W. T., & Suthers, R. A. (2016). Vertebrate vocal production: An introductory overview. In R. A. Suthers, W. T. Fitch, R. R. Fay, & A. N. Popper (Eds.), *Vertebrate sound production and acoustic communication* (Vol. 53, pp. 1–18). Springer. https://doi.org/10.1007/978-3-319-27721-9_1.

Fourie, P. B. (1977). Acoustic communication in the rock hyrax (*Procavia capensis*). *Zeitschrift für Tierpsychologie, 44*(2), 194–219.

Freitas, B., D'Amelio, P. B., Mila, B., Thebaud, C., & Janicke, T. (2025). Meta-analysis of the acoustic adaptation hypothesis reveals no support for the effect of vegetation structure on acoustic signalling across terrestrial vertebrates. *Biological Reviews, 100*(2), 815–833. https://doi.org/10.1111/brv.13163

Fritz, J. B., Elhilali, M., David, S. V., & Shamma, S. A. (2007). Auditory attention — Focusing the searchlight on sound. *Current Opinion in Neurobiology, 17*(4), 437–455. https://doi.org/10.1016/j.conb.2007.07.011

Garcia Arasco, A., Manser, M., Watson, S. K., Kyabulima, S., Radford, A. N., Cant, M. A., & Garcia, M. (2022). Testing the acoustic adaptation hypothesis with vocalizations from three mongoose species. *Animal Behaviour, 187*, 71–95. https://doi.org/10.1016/j.anbehav.2022.02.016

Geissmann, T., Bohlen-Eyring, S., & Heuck, A. (2005). The male song of the Javan silvery gibbon (*Hylobates moloch*). *Contributions to Zoology, 74*(1–2), 1–25. https://doi.org/10.1163/18759866-0740102001

Gerhardt, H. (1976). Significance of two frequency bands in long distance vocal communication in the green treefrog. *Nature, 261*(5562), 692–694.

Goll, Y., Demartsev, V., Koren, L., & Geffen, E. (2017). Male hyraxes increase countersinging as strangers become 'nasty neighbours'. *Animal Behaviour, 134*, 9–14. https://doi.org/10.1016/j.anbehav.2017.10.002

Grafe, T. U., & Wanger, T. C. (2007). Multimodal signaling in male and female foot-flagging frogs *Staurois guttatus* (Ranidae): An alerting function of calling. *Ethology, 113*(8), 772–781. https://doi.org/10.1111/j.1439-0310.2007.01378.x

Guilford, T., & Dawkins, M. S. (1993). Receiver psychology and the design of animal signals. *Trends in Neurosciences, 16*(11), 430–436. https://doi.org/10.1016/0166-2236(93)90068-W

Hage, S. R., Jiang, T., Berquist, S. W., Feng, J., & Metzner, W. (2013). Ambient noise induces independent shifts in call frequency and amplitude within the Lombard effect in echolocating bats. *Proceedings of the National Academy of Sciences, 110*(10), 4063–4068. https://doi.org/10.1073/pnas.1211533110

Heil, P. (2014). Towards a unifying basis of auditory thresholds: Binaural summation. *Journal of the Association for Research in Otolaryngology, 15*(2), 219–234. https://doi.org/10.1007/s10162-013-0432-x

Hostetter, A. B., Cantero, M., & Hopkins, W. D. (2001). Differential use of vocal and gestural communication by chimpanzees (*Pan troglodytes*) in response to the attentional status of a human (*Homo sapiens*). *Journal of Comparative Psychology, 115*(4), 337. https://doi.org/10.1037/0735-7036.115.4.337

Hostetter, A. B., Russell, J. L., Freeman, H., & Hopkins, W. D. (2007). Now you see me, now you don't: Evidence that chimpanzees understand the role of the eyes in attention. *Animal Cognition, 10*, 55–62. https://doi.org/10.1007/s10071-006-0031-x

Ilany, A., Barocas, A., Kam, M., Ilany, T., & Geffen, E. (2013). The energy cost of singing in wild rock hyrax males: Evidence for an index signal. *Animal Behaviour, 85*(5), 995–1001. https://doi.org/10.1016/j.anbehav.2013.02.023

Ilany, A., Barocas, A., Koren, L., Kam, M., & Geffen, E. (2011). Do singing rock hyraxes exploit conspecific calls to gain attention? *PLoS One, 6*(12), Article e28612. https://doi.org/10.1371/journal.pone.0028612

Kayser, C., Petkov, C. I., Lippert, M., & Logothetis, N. K. (2005). Mechanisms for allocating auditory attention: An auditory saliency map. *Current Biology, 15*(21), 1943–1947. https://doi.org/10.1016/j.cub.2005.09.040

Kershenbaum, A. (2014). Entropy rate as a measure of animal vocal complexity. *Bioacoustics – The International Journal of Animal Sound and Its Recording, 23*(3), 195–208. https://doi.org/10.1080/09524622.2013.850040

Kershenbaum, A., Ilany, A., Blaustein, L., & Geffen, E. (2012). Syntactic structure and geographical dialects in the songs of male rock hyraxes. *Proceedings of the Royal Society B: Biological Sciences, 279*(1740), 2974–2981. https://doi.org/10.1098/rspb.2012.0322

Koren, L., & Geffen, E. (2008). Complex call in male rock hyrax (*Procavia capensis*): A multi-information distributing channel. *Behavioral Ecology and Sociobiology, 63*(4), 581–590. https://doi.org/10.1007/s00265-008-0693-2

Koren, L., & Geffen, E. (2011). Individual identity is communicated through multiple pathways in male rock hyrax (*Procavia capensis*) songs. *Behavioral Ecology and Sociobiology, 65*(4), 675–684. https://doi.org/10.1007/s00265-010-1069-y

Lehmann, K. D. S., Jensen, F. H., Gersick, A. S., Strandburg-Peshkin, A., & Holekamp, K. E. (2022). Long-distance vocalizations of spotted hyenas contain individual, but not group, signatures. *Proceedings of the Royal Society B: Biological Sciences, 289*(1979), Article 20220548. https://doi.org/10.1098/rspb.2022.0548

Massenet, M., Mathevon, N., Anikin, A., Briefer, E. F., Fitch, W. T., & Reby, D. (2025). Nonlinear phenomena in vertebrate vocalizations: Mechanisms and communicative functions. *Philosophical Transactions of the Royal Society B: Biological Sciences, 380*(1923), Article 20240002. https://doi.org/10.1098/rstb.2024.0002

Mitchell, B. R., Makagon, M. M., Jaeger, M. M., & Barrett, R. H. (2006). Information content of coyote barks and howls. *Bioacoustics, 15*(3), 289–314. https://doi.org/10.1080/09524622.2006.9753555

Morrill, R. J., Thomas, A. W., Schiel, N., Souto, A., & Miller, C. T. (2013). The effect of habitat acoustics on common marmoset vocal signal transmission. *American Journal of Primatology, 75*(9), 904–916. https://doi.org/10.1002/ajp.22152

Morton, E. S. (1975). Ecological sources of selection on avian sounds. *American Naturalist, 109*(965), 17–34. https://doi.org/10.1086/282971

Nelson, D. A. (2017). Geographical variation in song phrases differs with their function in white-crowned sparrow song. *Animal Behaviour, 124*, 263–271. https://doi.org/10.1016/j.anbehav.2016.05.016

Nelson, D. A., Szeyller, E., & Poesel, A. (2016). Alerting and message components of white-crowned sparrow song differ in structure and environmental transmission. *Behaviour, 153*(3), 263–285. https://doi.org/10.1163/1568539X-00003341

Ord, T. J., & Stamps, J. A. (2008). Alert signals enhance animal communication in 'noisy' environments. *Proceedings of the National Academy of Sciences of the United States of America, 105*(48), 18830–18835. https://doi.org/10.1073/pnas.0807657105

Peters, R. A. (2008). Environmental motion delays the detection of movement-based signals. *Biology Letters, 4*(1), 2–5. https://doi.org/10.1098/rsbl.2007.0422

Peters, R. A., Hemmi, J. M., & Zeil, J. (2007). Signaling against the wind: Modifying motion-signal structure in response to increased noise. *Current Biology, 17*(14), 1231–1234. https://doi.org/10.1016/j.cub.2007.06.035

Rajan, R., & Doupe, A. J. (2013). Behavioral and neural signatures of readiness to initiate a learned motor sequence. *Current Biology, 23*(1), 87–93. https://doi.org/10.1016/j.cub.2012.11.040

Range, F., & Fischer, J. (2004). Vocal repertoire of sooty mangabeys (*Cercocebus torquatus atys*) in the Taï National Park. *Ethology, 110*(4), 301–321. https://doi.org/10.1111/j.1439-0310.2004.00973.x

Reby, D., & Charlton, B. D. (2012). Attention grabbing in red deer sexual calls. *Animal Cognition, 15*(2), 265–270. https://doi.org/10.1007/s10071-011-0451-0

Richards, D. G. (1981). Alerting and message components in songs of rufous-sided towhees. *Behaviour, 76*(3–4), 223–249. https://doi.org/10.1163/156853981x00095

Rowe, C. (1999). Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour, 58*(5), 921–931. https://doi.org/10.1006/anbe.1999.1242

Salmi, R., Szczupider, M., & Carrigan, J. (2022). A novel attention-getting vocalization in zoo-housed western gorillas. *PLoS One, 17*(8), Article e0271871. https://doi.org/10.1371/journal.pone.0271871

Saltelli, A. (2002). Sensitivity analysis for importance assessment. *Risk Analysis, 22*(3), 579–590. https://doi.org/10.1111/0272-4332.00040

Schraft, H. A., Medina, O. J., McClure, J., Pereira, D. A., & Logue, D. M. (2017). Within-day improvement in a behavioural display: Wild birds 'warm up'. *Animal Behaviour, 124*, 167–174. https://doi.org/10.1016/j.anbehav.2016.12.026

Scott-Phillips, T. C. (2015). Meaning in animal and human communication. *Animal Cognition, 18*(3), 801–805. https://doi.org/10.1007/s10071-015-0845-5

Senju, A., & Hasegawa, T. (2005). Direct gaze captures visuospatial attention. *Visual Cognition, 12*(1), 127–144. https://doi.org/10.1080/13506280444000157

Tomasello, M. (2016). Chapter 7 – What did we learn from the ape language studies? In B. Hare, & S. Yamamoto (Eds.), *Bonobos: Unique in mind, brain, and behavior* (pp. 95–104). https://doi.org/10.1093/oso/9780198728511.003.0007

Townsend, S. W., & Manser, M. B. (2011). The function of nonlinear phenomena in meerkat alarm calls. *Biology Letters, 7*(1), 47–49. https://doi.org/10.1098/rsbl.2010.0537

Weissman, Y. A., Demartsev, V., Ilany, A., Barocas, A., Bar-Ziv, E., Koren, L., & Geffen, E. (2020). A crescendo in the inner structure of snorts: A reflection of increasing arousal in rock hyrax songs? *Animal Behaviour, 166*, 163–170. https://doi.org/10.1016/j.anbehav.2020.06.010

Weissman, Y. A., Demartsev, V., Ilany, A., Barocas, A., Bar-Ziv, E., Shnitzer, I., Geffen, E., & Koren, L. (2019). Acoustic stability in hyrax snorts: Vocal tightrope-walkers or wrathful verbal assailants? *Behavioral Ecology, 30*(1), 223–230. https://doi.org/10.1093/beheco/ary141

Wiley, R. H. (2006). Signal detection and animal communication. In H. J. Brockmann, P. J. B. Slater, C. T. Snowdon, T. J. Roper, M. Naguib, & K. E. Wynne-Edwards (Eds.), *Advances in the study of behavior* (Vol. 36, pp. 217–247). Academic Press.

Wiley, R. H. (2013). Signal detection, noise, and the evolution of communication. In H. Brumm (Ed.), *Animal communication and noise* (pp. 7–30). Springer. https://doi.org/10.1007/978-3-642-41494-7_2.

Appendix

Table A1
Count of playbacks at each location by experimental treatment

Location	Treatment type	*N*
David	30% wails	3
	Normal wails	7
	Stutter wails	3
School	30% wails	4
	Normal wails	4
	Stutter wails	6
Shed	30% wails	9
	Normal wails	9
	Stutter wails	13
Terrace	30% wails	8
	Normal wails	11
	Stutter wails	8
Waterfall	30% wails	15
	Normal wails	9
	Stutter wails	9