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Original Article

Harsh vocal elements affect counter-singing dynamics in male rock hyrax

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Morton's motivation-structural (MS) rules suggest that the acoustic structure of a signal can reflect the caller's motivation and internal state. In many species, low-frequency and noisy (harsh) sounds have been found to comply with MS rules, accompanying agonistic interactions and functioning as a badge of aggression and dominance. Male rock hyraxes (*Procavia capensis*) often produce long and complex advertisement calls (songs) both "spontaneously" and in counter-singing sessions with other males. Hyrax songs include a "snort" vocal element, which is a harsh sound produced only by mature, dominant males. We predicted that the number of snort elements in the song would affect the dynamics of male hyrax counter-singing. We performed 3 series of playback experiments of natural and artificially manipulated songs on a wild hyrax population. We found that the probability of initiating counter-singing by nearby males increased together with the number of snorts in the stimulus song. Furthermore, the receivers replied to the synthetic "snort-only" vocal sequences at an equal rate as to their origin song as long as the snort elements maintained their original position within the signal. Our findings suggest that the snort component is one of the main information transfer channels in male hyrax singing and can elicit conspecific singing even when isolated from other vocal elements. In addition, the position of snort elements (their temporal pattern and rhythm) bears a possible significance in keeping the overall signal meaningful. Finally, our findings support previous claims that harsh sounds constitute one of the key components in vocal communication.

Key words: **harsh sounds, motivation-structural rules, multichannel signal, vocal communication.**

INTRODUCTION

According to Morton's motivation-structural (MS) rules, there is a relationship between the acoustic structure of sounds and the motivation underlying their use. Sounds produced in aggressive circumstances are often wide bandwidth (i.e., harsh) and low frequency, whereas sounds produced in appeasing contexts are high frequency and tonal (Morton 1977; August and Anderson 1987; Briefer 2012). MS rules are related to the idea that animals seek to project a larger body size during agonistic interactions and smaller size during friendly interactions (Taylor and Reby 2010). Such vocal projection of body size could evolve into a reliable signal in social communication. Although MS rules are not universally valid and there are species that present exceptions [e.g., pigtail macaques, *Macaca nemestrina* (Gouzoules and Gouzoules 1989) and yellow-bellied marmots, *Marmota flaviventris* (Blumstein and Recapet 2009)], many avian and mammalian species exhibit vocalization patterns that are in line with the MS hypothesis (August and Anderson 1987). Baboons (*Papio cynocephalus ursinus*) offer a good example as their loud barks vary acoustically according to context. Tonal calls are given when an individual is at risk of becoming separated from the group, while harsh calls are given when a predator has been seen (Seyfarth and Cheney 2003).

Harsh sounds contain acoustic nonlinearities such as frequency jumps and deterministic chaos (Slaughter et al. 2013). Harsh vocalizations also have more salient formants (Charlton et al. 2014) that may be favored for aggressive signaling, possibly because they have been found to provide a good estimate of body size and fighting ability (Vannoni and McElligott 2008). Moreover, in both humans and other animals, sounds associated with high arousal tend to be harsher (Briefer 2012). The noisy acoustical structure of harsh sounds is evocative (Townsend and Manser 2011); it can enhance receiver responsiveness (Blumstein and Recapet 2009) and help prevent receiver desensitization (Ramachandran 1996). For example, meerkats (*Suricata suricatta)* responded more strongly to harsh alarm calls compared to tonal ones (Townsend and Manser 2011). However, an opposite behavior has been reported in red deer sexual display, in which harsh roars received less response than less harsh, "common" roars (Garcia et al. 2014).

The rock hyrax (*Procavia capensis*) is a social mammal that uses acoustic communication as its main channel of informational transfer (Fourie 1977). Hyrax males often engage in singing sessions to advertise their quality (Demartsev et al. 2014) and about 25% of all songs are male–male counter-singing events (Ilany

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et al. 2011). In other species, such duel-type contests were found to facilitate comparison of male performance or intended to jam the signal of the competitor (Vehrencamp et al. 2007). Hyrax songs were shown to transmit multiple messages as different song parameters correlated with different performer traits (Koren and Geffen 2009). In addition, hyrax songs were suggested to constitute a multichannel signal in which same (redundant) and different information is encoded in parallel pathways (Bro-Jørgensen 2010; Koren and Geffen 2011). Hyrax songs are composed of 3 repetitive elements—wails, chucks, and snorts (Koren and Geffen 2009). Wail and chuck are high-frequency, tonal sounds, whereas snort is low frequency and noisy (Supplementary Figures S2 and S3) (Koren and Geffen 2009) and thus, according to MS rules, can be associated with aggression and dominance. Snorts often develop last during the ontogenesis of song maturation (Koren and Geffen 2009) and are the least frequent element in male hyrax singing (Demartsev et al. 2014), suggesting that their production may be physically or acoustically constrained (Koren and Geffen 2009). Like other loud and broadband sounds, snorts may be used to emphasize formant frequencies. In the rock hyrax, formants were found to be tightly linked to androgen levels and social status (Koren and Geffen 2009), traits that are associated with agonistic interactions between males. The link between formant frequencies and social rank (i.e., fighting ability) suggests that formants, and consequently snorts, broadcast information regarding the physical and motivational state of the caller to any receiver.

Our ability to individually identify participants in vocal interaction and their clear response (reply or no reply) makes our study system suitable for the assessment of whether cues of social rank or motivation are encoded in the harsh elements of a vocal signal. In addition, our system allows us to examine how social and/or motivational cues are perceived by receivers and affect their behavior.

In this work, we conducted playback experiments using natural and manipulated hyrax songs in order to assess the effect of snorts on the reply rate of conspecific males. As snort elements might indicate aggression, we predicted that the number of these elements in a male song would affect the motivation of male receivers to reply. More specifically, as we suspect counter-singing to be a type of contest, we predicted that high-ranking and resident males would reply more frequently to a hostile, snort-rich signal than to snort-poor songs. Low-ranking males were predicted to reply mostly to subtle, snort-poor songs and to remain silent during potentially aggressive, snort-rich signals. In line with our first prediction, we also predicted that the omission of snort elements from a song would reduce the perceived level of signal aggression, allowing more males to respond.

MATERIALS AND METHODS

Ethical statement

This study was conducted under a permit from the Israeli Nature and Parks Authority, which is the government agency responsible for supervising all wildlife research in Israel, for trapping, sampling, and handling hyraxes in the wild. The annual permit numbers are 2011/38061, 2012/38400, 2013/38803, 2014/40185, and 2015/40768. Throughout the entire course of our 16-year field study, no long-term stress or interference effects were detected in the individual animals or in the population. Both the general population numbers and the integrity of the specific social groups in the research area remained stable.

Field protocol

The study was conducted at the Ein Gedi Nature Reserve in Israel (31°28′N, 35°24′E) as part of a long-term project running since 1999. The data for the current study were collected between 2011 and 2015. During each field season (April–August), hyraxes were observed for 4–5 days per week. Field procedures followed previously published protocols (Koren et al. 2008; Koren and Geffen 2009; Barocas et al. 2011; Ilany et al. 2013). Briefly, rock hyraxes were trapped using live box traps (Tomahawk Live Trap Co, Tomahawk, WI) baited with cabbage and kohlrabi. The traps were set at dawn, inspected after 3–4 h and locked open until the next trapping session. Trapped animals were anesthetized by intramuscular injection of ketamine hydrochloride (0.1 ml/kg). Each hyrax was individually marked with a subcutaneous transponder (DataMars SA) and either an ear tag (~0.25 g per tag) or a light numbered collar (~5 g). Over the course of the study (1999–2015), about 400 hyraxes were individually marked and no adverse effects from the transponders or the collars were observed. Captured hyraxes were weighed and measured. Following anesthesia recovery (at least 120 min), the animals were released back at their capture sites and resumed full normal activity. All treatments were performed in the shade to avoid overheating.

Behavioral observations, social rank, and residency status

Hyraxes were observed during morning activity hours, about 4 h each day, using 10 × 42 binoculars (Monarch, Nikon) and a telescope with up to ×75 zoom magnification (Fieldscope ED82, Nikon).

Each year (2011–2015), male hyraxes' residency status (i.e., bachelor or resident) was determined according to the social network algorithms described in Barocas et al. (2011). Briefly, resident males were observed in a stable association with a group of females, sharing sleeping dens and feeding sites as well as tolerated in the vicinity of the pups. Bachelor males showed no stable association with other individuals and were observed only in brief positive interactions with females during the mating season. All observed agonistic interactions were recorded following our previously published protocol (Koren et al. 2008). A matrix of annual encounters was prepared for each research site for all pairwise agonistic interactions when a clear act of aggression by 1 individual resulted in evasive action being taken by a second individual. On average, 18 (±2.4) agonistic interactions were recorded per season, and involved 11.3 (±3.2) participant males. Annual social rank was calculated for each individual using the David's score (DS) procedure (Gammell et al. 2003; Barocas et al. 2011). Social rank scores were normally distributed.

Vocalization recording and playback experiments

The long-range vocalizations used for our playback experiments were recorded from a distance of 10–50 m with a Sennheiser ME 67 shotgun microphone (frequency response 50–20 000 Hz ± 2.5 dB) powered by a Sennheiser K6 module, and covered with a Sennheiser MZW70-1 blimp windscreen (Sennheiser Electronic GmbH & Co. K. G., Wedemark, Germany). The microphone was handheld using an MZS20-1 shock-mount with a pistol grip. Vocalizations were recorded in mono (Tascam HD-P2 digital audio recorder; TASCAM Corporation, Montebello, CA), with a sampling frequency of 48 kHz and a sampling width of 24 bits (Ilany et al. 2011).

Playback experiments were performed using a remote-activated FoxPro Scorpion X1B speaker with a TX200 wireless remote controller (FOXPRO Inc., Lewistown, PA), following our previously published protocols (Ilany et al. 2011; Demartsev et al. 2014). The speaker was placed before dawn in 1 of 33 concealed spots in an area frequently visited by focal hyraxes. The speaker was activated once we had observed and identified at least 1 stationary male hyrax within a 20–30 m radius, and only if no natural hyrax vocalization had been heard at least 5 min prior to playback initiation. Each of the songs used for playback experiments was 1.5–2 min in length, which is the common range of duration for hyrax singing (Demartsev et al. 2014). The songs were played according to their original duration, with no repetition/looping in any single playback trial. The volume of playbacks was calibrated by preliminary trials to match the normal level of hyrax singing (about 80 dB) (Ilany et al. 2013). We restricted the number of playbacks to 2 per day in order to minimize disturbance to hyrax daily routine and natural vocal interactions, as well as to prevent the hyraxes in the area from becoming accustomed to the speaker location and to avoid desensitization to the playback experiments. All behavioral responses of the individuals located within the 30 m radius of the speaker during playbacks were noted. We considered a singing response as any reply by at least one of the present males within 2.5 min from the end of playback. The 2.5 min threshold was set according to our previously published protocols (Demartsev et al. 2014) and based on the frequency of male hyrax singing (Ilany et al. 2013). In cases of several males responding, only the first reply was considered for the playback analysis.

We conducted three sets of playback experiments (Figure 1, Appendix 1).

Set A (differential snort content)

In this set, we aimed to evaluate the effect of snort content of natural, unmodified songs, on the probability of reply. We selected songs from our previously recorded natural song library based on sound quality and the number of snort elements. Songs were randomly selected throughout the playback sessions (the number of repetitions for each song is indicated in Appendix 1). In order to eliminate receiver familiarity with the singer, we used songs recorded several years previously and distant from the experiment site (at least 3 km). The list of songs used for playbacks included 14 natural songs, each performed by a different adult male, containing 0–78 snort elements (Appendix 1). This set of songs is an objective representation of the snort number range observed in male hyrax songs (n = 274 naturally recorded songs) (Demartsev et al. 2014). The songs in Set A were played during the 2011–2015 seasons, from 11 locations, to 53 different male hyraxes, mean of 2.6 ± 2.3 playbacks per individual. We grouped the songs selected for playbacks into 3 song types: N_{NONE}—songs with zero snorts/song, a clearly distinct category that comprises almost 50% of all male songs in our research area; N_{POOR}—songs with fewer than 10 snorts/song, a category containing a below average number of snorts (mean snorts/song = 9) and composed of the majority (~70%) of songs containing snorts; and N_{RICH}—songs with more than 11 snorts/song, a category containing an above average number of snorts and composed of ~30% of all songs containing snorts (Figure 1, Supplementary Figure S1).

Set B (element omission)

In this set of experiments, we evaluated the effect of signal reduction due to omission of vocal elements on the probability of reply. Three natural "snort-rich" tracks, which contained 78, 72, and 62 snort elements (Tracks 3, 12, and 13, Appendix 1; Figure 1, Supplementary Figure S2a and Supplementary Audio S4), were used as the control and a template for element omission manipulation. The control templates were digitally manipulated using Avisoft SAS LabPro software version 5.2.07 (Avisoft Bioacoustics, Berlin, Germany). Two synthetic versions of each original recording were created:

S_{NONE}. To determine whether removal of the snort elements would decrease receivers' reply rate in comparison to the natural, snort-rich recording, all snort elements were omitted from the N_{RICH} tracks and replaced by background noise (Tracks 3_N, 12_N, and 13_N,

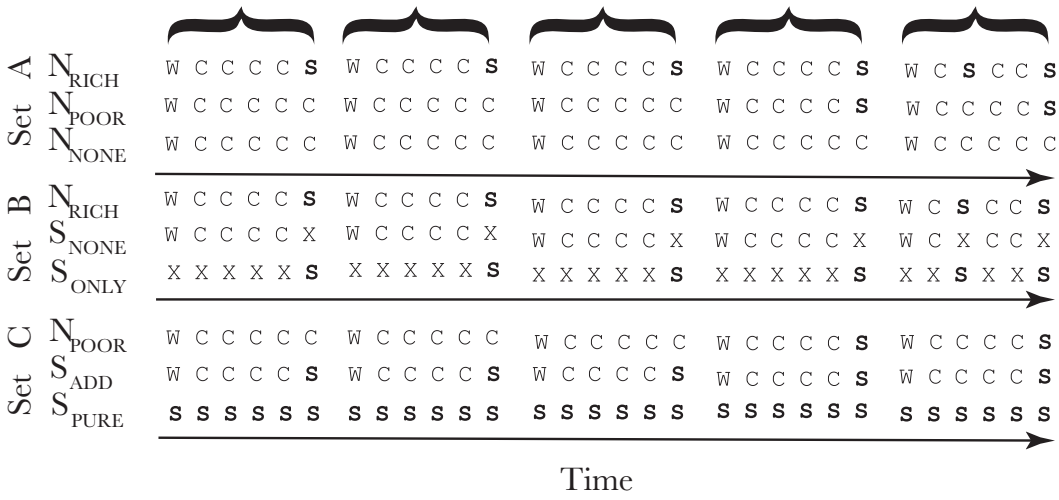

Figure 1

A diagram representing the structure of male hyrax songs used as treatments in our playback experiments. Each line shows a fragment of a different song treatment as a series of the different vocal elements (i.e., W—Wail, C—Chuck, and S—Snort). Element deletion and replacement with background noise is denoted by X. Brackets show the boundaries of a single singing bout. Each group of treatments was assigned a specific experimental set: Set A—natural songs with differential number of snort vocal elements, Set B—artificial element omission, and Set C—artificial snort addition.

Appendix 1; Supplementary Figure S2b and Supplementary Audio S5). The resulting songs had the same bout structure and duration as the N_{RICH} tracks but lacked the snort elements.

S_{ONLY}. To determine to what extent snort sequence, isolated from the original syntactical content, is sufficient in stimulating a singing reply from receivers, all wail and chuck elements from the N_{RICH} tracks were replaced by background noise (Tracks 3_O, 12_O, and 13_O, Appendix 1; Supplementary Figure S2c and Supplementary Audio S6). This resulted in "snort-only" songs containing only snort elements but maintaining the overall duration and general bout structure of the natural songs.

The results received from S_{ONLY} and S_{NONE} playbacks were pooled and analyzed together with the data received from the corresponding N_{RICH} tracks 3, 12, and 13 in Set A. Overall, songs assigned to Set B were played between 2013 and 2015 seasons, from 9 locations, to 33 different male hyraxes, mean of 3.2 ± 2.9 playbacks per individual.

Set C (snort addition)

In this set of experiments, we examined the effect of artificial addition of snort elements (i.e., elevation of the snort signal) on the probability of reply. Three natural "snort-poor" recordings containing 2–3 snort elements (Track 7, 14, and 4, Appendix 1; Figure 1, Supplementary Figure S3a and Supplementary Audio S7) were used as a control and templates for the manipulation. Two artificial versions of each original recording were created:

S_{ADD}. To determine whether the artificial addition of snort elements would increase receivers' reply rate in comparison to the natural snort-poor recording, we added 11, 21, and 17 snort elements to the N_{POOR} tracks (Tracks 7_A, 14_A, and 4_A, Appendix 1; Supplementary Figure S3b and Supplementary Audio S8). The added snort elements originated from the corresponding natural template and were integrated at the end of each singing pulse (i.e., bout), following a typical 0.05 sec interelement silence interval. The artificial snort elements replaced the last element in the bout in order to maintain the song's overall element number. Since snorts often appear as the final element in a given bout, and we added snorts in proportion to the number of bouts in the template song, such artificial addition of snorts did not seem to produce an abnormal signal or disrupt the general bout structure and rhythm of the natural song.

S_{PURE}. To determine whether a snort-only sequence could be recognized as a conspecific signal by the receiver hyrax males and would generate a singing reply, we replaced all vocal elements from the natural N_{POOR} recording with snorts (Tracks 7_P, 14_P, and 4_P, Appendix 1; Supplementary Figure S3c and Supplementary Audio S9). Since snort elements are typically longer than chucks, they could not be inserted in the exact locations of the original wail or chuck elements. However, we controlled for natural intervals between elements in an attempt to maintain the existing sound/silence interval in the song. This resulted in a snort-only sequence maintaining nearly the same duration, rhythm, and bout structure of the original song. The results obtained from S_{ADD} and S_{PURE} playbacks were pooled and analyzed together with the data received from the corresponding N_{POOR} tracks 7, 14, and 4 in Set A. Overall, songs assigned to Set C were played between 2013 and 2015 seasons, from 13 locations, to 33 different male hyraxes, mean of 2.9 ± 3.6 playbacks per individual.

Statistical analysis

We selected to examine 5 relevant independent variables as effects on the probability of reply in our experiments: playback type, which featured the treatment levels in each of the experiments (Appendix 1); residency status (resident or bachelor) of the receiver/responder; body weight of the receiver/responder; social rank (David's score) of the receiver/responder; and song duration, which was relevant only in set A (Appendix 1).

To examine for song and individual effects on the probability of reply (binary dependent response), we used a logistic regression under the framework of the generalized estimating equations (GEE). GEE is an extension of generalized linear models (GLM) for correlated data (i.e., mixed model), and specifically designed for repeated measures within the same subjects (Overall and Tonidandel 2004). We set individual/group and playback identities as random effects in all GEE analyses. The Wald χ^2 was used for testing the significance of each effect. Multiple comparisons were conducted using the sequential Bonferroni correction. GEE model fitting was done in SPSS (version 22, SPSS Inc.).

Fisher exact test was used for contingency analysis of reply rates to natural and manipulated playback tracks. Spearman correlation was performed to test the effect of number of track repetitions on reply rate.

RESULTS

During the 2011–2015 field seasons, we performed 273 playback experiments to determine the effect of the snort element composition in hyrax songs on male conspecifics' reply rate. The playbacks were assigned to 3 experimental sets, comprising 138, 105, and 96 playbacks, respectively (Table 1, Figure 2). Overall, hyraxes replied similarly to the manipulated song playbacks (42% reply rate, $n = 135$) as to the natural song playbacks (36% reply rate, $n = 138$; Fisher exact test, $P = 0.324$), suggesting that song manipulation per se had no effect on the perception of the signal by the receivers.

Table 1

The effect of playback type, song duration, male residence status (resident or bachelor), male body weight, and male social rank on the probability of reply

Term	Wald χ^2	df (n)	P
Set A (differential snort content)			
Natural song playbacks (53 males)			
Number of snorts/song	4.45	1 (138)	**0.035**
Playback type (N_{RICH}, N_{POOR}, N_{NONE})	5.45	2 (138)	0.065
Song duration	0.40	1 (138)	0.525
Residence status	0.16	1 (72)	0.693
Body weight	0.45	1 (72)	0.501
Social rank	0.03	1 (72)	0.864
Playback type * Song duration	6.25	2 (138)	**0.044**
Residence status * Playback type	2.42	2 (72)	0.298
Residence status * Body weight	0.00	1 (72)	0.947
Residence status * Social rank	0.72	1 (72)	0.395
Set B (snort omission)			
Synthetic song playbacks (33 males)			
Playback type (N_{RICH}, S_{NONE}, S_{ONLY})	5.54	2 (105)	0.063
Set C (snort addition)			
Synthetic song playbacks (33 males)			
Playback type (N_{POOR}, S_{PURE}, S_{ADD})	12.40	2 (96)	**0.002**

Number of experiments is in brackets. Significance relationship P values are marked in bold. Legends for the abbreviation of playback types are outlined in Appendix 1.

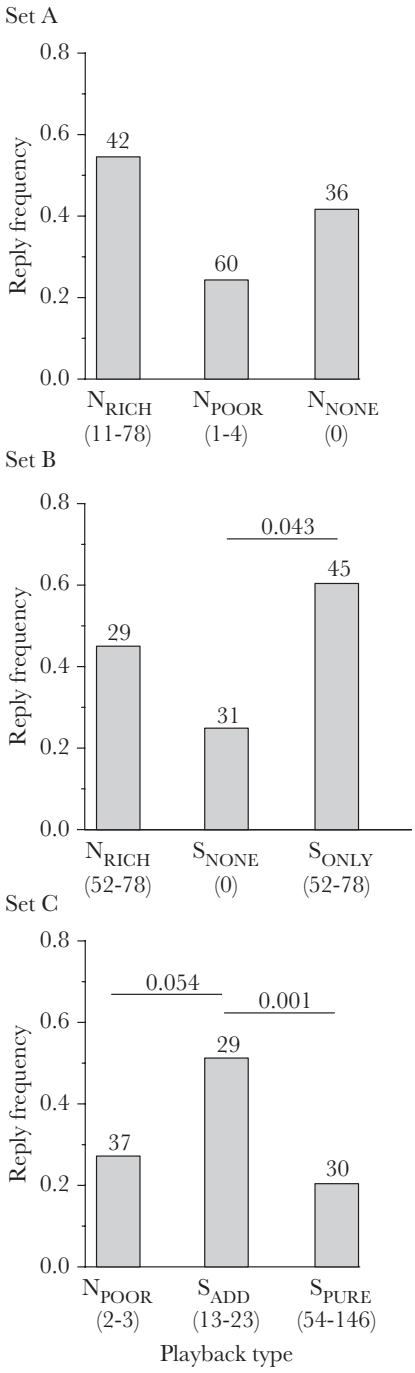

Figure 2
Reply rates by playback type in 3 sets of playback experiments. Set A: natural songs with differential number of snort vocal elements. N_{RICH}—natural song that contains 30–78 snorts, N_{POOR}—natural song that contains 1–4 snorts, and N_{NONE}—natural song that does not contain snort elements. Set B: artificial element omission. S_{ONLY}—manipulated song based on N_{RICH}, in which all elements but the 62–78 snorts were replaced with background noise, and S_{NONE}—manipulated song based on N_{RICH}, in which all 62–78 snort elements were replaced with chucks. Set C: artificial snort addition. S_{ADD}—manipulated song based on N_{POOR}, in which the number of snorts was artificially increased from 2–3 to 13–23, and S_{PURE}—manipulated song based on N_{POOR}, in which all elements were replaced with snorts (54–146 snorts). The number of snorts in each song playback type is denoted in brackets, and sample size is indicated above bars. Significant post hoc *P* values between playback types within each set are indicated.

In addition, hyraxes replied at a higher rate to playback experiments performed for this study than to natural conspecific singing (27% reply rate, $P = 0.005$) (Ilany et al. 2011). Reply rate to natural playbacks (set A) was not correlated with the number of times that each of the songs was played over the course of this study, suggesting that no signal habituation had occurred (Spearman correlation, $r_s = -0.11$, $P = 0.728$).

Playback type did not significantly affect reply rate to natural playbacks (Table 1, set A). Due to the possibility that hyraxes treated songs without snorts as a different category, we performed a separate analysis using only natural songs that contained snorts (N_{RICH} and N_{POOR}). Indeed, in this restricted analysis, the reply rate to snort-rich songs (54%) was significantly higher than to snort-poor songs (24%; Wald $\chi^2_1 = 5.07$, $P = 0.024$, Figure 2). To accommodate for the variation in duration of songs used in set A (i.e., natural songs), all set A songs were tested for the effect of number of snorts/song on the probability of reply. This analysis further confirmed that reply rate increases with the number of snort elements in a song (Wald $\chi^2_1 = 4.45$, $P = 0.035$, model $\beta \pm SE = 0.012 \pm 0.006$, Table 1). A similar positive association between number of snorts/song and probability of reply was detected when songs without snorts were excluded (Wald $\chi^2_1 = 6.98$, $P = 0.008$, model $\beta \pm SE = 0.017 \pm 0.006$; Figure 3). The number of snorts/song controlled for song duration also showed a positive significant effect on reply rate (Wald $\chi^2_1 = 8.12$, $P = 0.004$, model $\beta \pm SE = 0.019 \pm 0.007$).

The duration of songs had a differential effect on reply rate in different song types (Table 1). The reply rate to snort-rich (Wald $\chi^2_1 = 0.03$, $P = 0.865$) and snort-poor (Wald $\chi^2_1 = 0.43$, $P = 0.512$) songs was independent of song duration. However, the reply rate to songs without snorts significantly decreased with song duration (model $\beta \pm SE = -0.033 \pm 0.012$, Wald $\chi^2_1 = 7.45$, $P = 0.006$). These results support our notion that the receivers perceive songs without snorts as a distinct category, because singing for long without any snort elements resulted in a lower likelihood of reply.

For 72 out of 138 trials, we also acquired data on the residency status, social rank, and body weight of the receiver/responder, which enabled us to test the effect of these traits on playback reply rate. None of the receiver/responder traits we examined had any significant effect on the probability of reply (Table 1).

The findings from the manipulated playbacks showed that the overall omission of vocal elements (i.e., S_{NONE}, S_{ONLY}) from snort-rich songs did not affect the reply rate (set B, Table 1, Figure 2), but the post hoc comparison showed that the reply rate to S_{ONLY} (62%) was significantly higher than to S_{NONE} (26%; Bonferroni corrected, $P = 0.026$). The addition of snorts to natural snort-poor songs increased the reply rate (set C, Table 1, Figure 2). Snort-poor songs (N_{POOR}) that were augmented with 11–21 additional snorts (S_{ADD}) tended to elicit greater reply rates (52%) than unaltered songs (27%; Bonferroni corrected, $P = 0.054$; Figure 2), and significantly greater reply rates than S_{PURE} songs in which all elements were replaced by snorts (20%; Bonferroni corrected, $P = 0.001$). Furthermore, comparison between manipulated songs containing only snort elements, S_{ONLY} songs (snort-rich songs in which all other elements were removed), showed a greater response rate (62%) than snort-pure songs (20%) in which all elements were replaced with snorts (S_{PURE}; Wald $\chi^2_1 = 7.05$, $P = 0.008$), thus suggesting a possible role of element order within the signal.

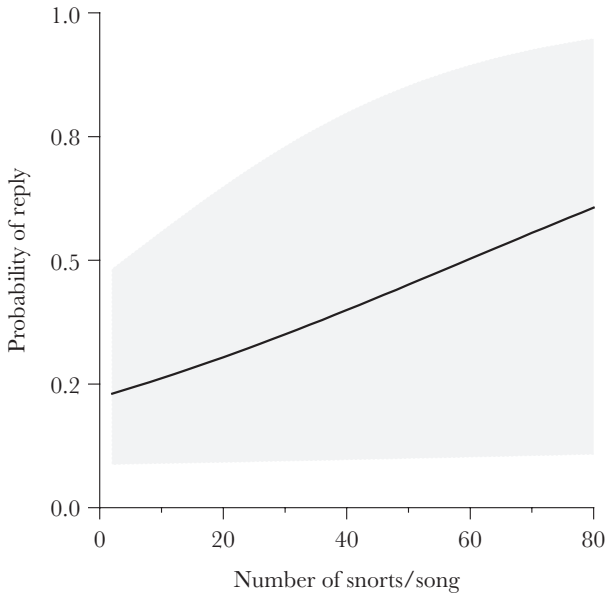

Figure 3
Probability of reply as a function of number of snorts per song. The logistic curve (±95% confidence interval as gray fill; Wald $\chi^2_1 = 5.39$, $P = 0.020$) was constructed for all songs that had snorts ($n = 102$). Songs without snorts were excluded from this analysis.

DISCUSSION

The effect of snort number and position

Our results support the initial hypothesis that snorts have an effect on receiver reply rate and that natural songs with fewer snorts have a lower reply rate than snort-rich ones (Figure 2, Table 1). However, our second prediction that individual traits of the receiver, such as residency, rank, and body weight, affect reply rate was not supported. Results from the differential snort content playbacks (set A) show that none of the tested traits affected the reply rate and all tested males demonstrated a similar response pattern. Following these findings, we revised our predictions and did not examine the effect of the various receiver traits in the later stages of the study (sets B and C).

In line with our initial prediction, natural snort-rich (N_{RICH}) songs demonstrated a significantly higher reply probability in pairwise comparison to natural snort-poor (N_{POOR}) ones. However, zero-snort songs (N_{NONE}) do not follow this rule and are not replied to at a significantly lower rate than N_{RICH} songs. Moreover, we see that N_{NONE} songs actually show a higher probability of a reply than N_{POOR} ones (Figure 2). This contradicts our prediction of a positive linear correlation between snort content and reply rates, and our expectation that zero-snort songs would have the lowest reply rates among the 3 playback types. One possible explanation for the zero-snort (N_{NONE}) songs' high reply probability could be that they are performed mainly by young males (Koren and Geffen 2009). As such they can be easily evaluated as a low-quality signal and may provide an opportunity for a relatively large number of males to "win" an easy singing competition with an inept opponent, possibly as an opportunistic maximization of attractiveness (Jordao et al. 2012).

On the other hand, songs that we assigned to the snort-poor (N_{POOR}) category varied in the number of snorts (1–4). Such songs might require a more thorough evaluation by receivers and consequently have a lower reply rate than N_{NONE}. However, in order to reach a definite conclusion in this regard, further experimental work is required.

Since our previous results had indicated that snort elements correlated with the high quality and high social rank of adult males (Koren and Geffen 2011), a higher response rate to snort-rich playbacks (N_{RICH}) was an expected outcome. In the majority of male–male counter-singing systems, a more intense signal is followed by an increase in the response rate and strength (Clutton-Brock and Albon 1979; Behr et al. 2009; Kitchen et al. 2013), although several publications have shown opposite patterns of signaling behavior (Cramer and Price 2007; Garcia et al. 2014). According to the MS rules, and as previously reported in other species (Briefer 2012), harsh and low-frequency signals generally predict high levels of aggressiveness and willingness to fight (Morton 1977) and have been suggested to indicate actual fighting ability (Reby and McComb 2003). Our previous work has shown that the snort element is a harsh sound and that it highlights formants, which provide accurate information on hyrax social rank (Koren and Geffen 2009). Thus, it is possible that snort-rich songs emphasize the aggressiveness and rank information incorporated in the formant frequencies and consequently accentuate the fighting ability of the performing male. Such signals might be perceived as a high threat and the decision to reply might not be based solely on the receivers' ability to outperform the initiator but could also be a general attempt at announcing presence and perhaps deterring an aggressive intruder (Illes et al. 2006). Additionally, snort-rich hyrax songs may promote a reply in order to compete for female attention, similarly to red deer (*Cervus elaphus*), in which harsh sounds were found to recruit female interest in the signaler (Reby and Charlton 2012). Likewise, in our case, low snort content may indicate a lower quality male that is unable to impress its audience and is not considered a threatening competitor (Moseley et al. 2013).

In our examination of signal reduction effect on reply rate (set B, Appendix 1, Figure 1), both manipulated zero-snort (S_{NONE}; all snorts replaced by chucks) and manipulated snort-only (S_{ONLY}) songs received replies at a similar rate as the natural snort-rich control (N_{RICH}; Table 1). However, a significant post hoc test suggests that S_{ONLY} songs received higher reply rates than S_{NONE} (Figure 2). The similar reply rates to S_{ONLY} and N_{RICH} songs were unexpected as S_{ONLY} song contained only snort elements and lacked the syntactic structure created by the blend with other vocal elements (i.e., wail, chuck) (Kershenbaum et al. 2012). In contrast, the manipulated S_{PURE} songs (set C, Appendix 1), also containing only snort elements, failed to elicit a higher probability of reply from the listeners in comparison to S_{ONLY} songs (all but snort elements omitted). Both S_{ONLY} and S_{PURE} songs contained only snort elements; however, in S_{ONLY}, the snorts remained in their natural positions, while all other elements were replaced by background noise. In S_{PURE} in contrast, all vocal elements (wails and chucks) were replaced by snorts. This could have created a disharmony in the signal, impeding the receivers' ability to recognize S_{PURE} songs as part of the hyrax vocal repertoire or possibly their ability to efficiently extract and evaluate information, and thereby resulted in low reply rates.

The results from our manipulated playbacks suggest that the snort component of male hyrax songs is independently informative and probably constitutes a major channel of information transfer in hyrax singing. In addition, our results point to the possibility that element order is important in keeping the overall signal comprehensive and meaningful. An example of the association between receiver response and call interelement interval or rhythm was

demonstrated in the dendrobatid frog *Allobates femoralis* (God et al. 2007; Velez et al. 2012).

Song as a multichannel signal

Our previous work has shown that the male hyrax song is a multimessage signal, meaning that different traits are transmitted independently through several acoustic and structural song attributes (Koren and Geffen 2009). We have also suggested that the singer's identity is communicated through parallel pathways of the song (Koren and Geffen 2011), making the song a multichannel signal in which the same information is doubled via different parameters, possibly as backup or as a mean to amplify and increase the accuracy and reliability of the transmitted message (Johnstone 1996). Most evidence on informational redundancy in vocal signals comes from songbird species and to a lesser extent from mammals. However, only a handful of studies have provided experimental data pertaining to vocal signals' informational robustness to reduction. In the long calls of the golden lion tamarin (*Saguinus oedipus*), the absence of a single harmonic did not affect the receivers' perception of the calls (Weiss and Hauser 2002), while in the chimpanzee (*Pan troglodytes*) pants, grunts, and hoots used for individual recognition were found to be resistant to acoustic modification by filtration (Kojima et al. 2003). Those studies have shown that the receivers are able to compensate for the distortion or partition of the vocal signal and interpret it correctly (Weiss and Hauser 2002; Kojima et al. 2003). However, the modified signals in those studies were presented to the receivers as a whole, whereas whether the modified parameter in the call can be independently informative (elicit a response similar to the intact signal) was not examined. In the present study, we have experimentally demonstrated that the high snort content of a male hyrax song elicits high reply rates by the receivers, possibly because the harsh nature of the snort elements highlights information about the performer's aggressive motivation and fighting ability. Similar information was accessible to the receivers in the degraded snort-only playback, leading to a similar response rate that demonstrated the signal robustness and high informativeness of its harsh component. The omission of snort elements did not affect reply rate, in comparison to natural (snort-rich) signals, possibly because the receivers could still extract the same information from the song's backup channels. This informational redundancy may be a way to compensate for potential signal distortion over distance in a noisy environment, in which reliable information delivery requires channels with different transmission properties (Bro-Jørgensen and Dabelsteen 2008).

Alternatively, as we have discussed earlier, zero-snort songs might promote high reply rates due to the performer's young age and lack of experience. If this is the case, natural zero-snort songs and snort-omitted playbacks might transmit different information to the receivers, eliciting similar behavior as to that to the natural song.

The results of our current study add to our previous body of work and demonstrate that male hyraxes have the ability to evaluate conspecific calls based on snort quantity in order to choose the appropriate reply tactics. The snort component is undoubtedly a significant and highly informative parameter that affects the dynamics of male hyrax counter-singing contests. However, there are probably other acoustical and/or structural parameters in the hyrax song that serve as a backup and transmit similar information to that of the snort-based channel. The discovery of these alternative channels together with a better understanding of the signals' syntax and temporal structure may provide us with a better insight into the principles of informational encoding and integration in complex vocal signaling.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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APPENDIX 1

List of tracks used for playbacks. Set A (differential snort content)—natural songs performed by different males, containing 0–78 snort elements; Set B (element omission)—a natural "control" and 2 manipulated variants with vocal elements omitted; Set C (snort addition)—a natural "control" and 2 manipulated variants with snort elements edited in.

Playback Set	Treatment	Track ID	Number of snorts	Frequency of use	Number of receivers
Set A	N_{RICH}	1	78	11	8
		2	30	2	2
		3	78	9	8
		12	72	10	7
		13	62	10	7
	N_{POOR}	4	3	15	12
		5	1	3	2
		6	2	18	11
		7	2	14	14
		8	4	2	2
		14	2	8	7
	N_{NONE}	9	0	7	5
		10	0	12	11
		11	0	17	16
Set B	N_{RICH}	3	78	9	8
		12	72	10	7
		13	62	10	7
	S_{NONE}	3_{NONE}	0	12	10
		12_{NONE}	0	9	5
		13_{NONE}	0	10	6
	S_{ONLY}	3_{ONLY}	78	29	16
		12_{ONLY}	72	9	6
		13_{ONLY}	62	7	4
Set C	N_{POOR}	7	2	14	14
		14	2	8	7
		4	3	15	12
	S_{ADD}	7_{ADD}	13	13	7
		14_{ADD}	23	6	5
		4_{ADD}	20	10	7
	S_{PURE}	7_{PURE}	54	14	7
		14_{PURE}	111	7	5
		4_{PURE}	146	9	6

N_{RICH}—natural song with 11–78 snorts, N_{POOR}—natural song with 1–4 snorts, and N_{NONE}—natural song without snorts. S_{NONE}—synthetic song based on corresponding N_{RICH} track, in which all the snort elements were replaced with background noise, S_{ONLY}—synthetic song based on corresponding N_{RICH} track, in which all elements but the snorts were replaced with background noise. S_{PURE}—synthetic song based on corresponding N_{POOR} track, in which all elements were replaced with snorts, S_{ADD}—synthetic song based on corresponding N_{POOR} track, in which the number of snorts was artificially increased. Track ID defines each of the natural/manipulated songs used in the experiments. Frequency of use denotes number of times each track was used in the relevant experimental set.

REFERENCES

August PV, Anderson JGT. 1987. Mammal sounds and motivation-structural rules - a test of the hypothesis. J Mammal. 68:1–9.

Barocas A, Ilany A, Koren L, Kam M, Geffen E. 2011. Variance in centrality within rock hyrax social networks predicts adult longevity. Plos One. 6:e22375.

Behr O, Knornschild M, von Helversen O. 2009. Territorial counter-singing in male sac-winged bats (*Saccopteryx bilineata*): low-frequency songs trigger a stronger response. Behav Ecol Sociobiol. 63:433–442.

Blumstein DT, Recapet C. 2009. The sound of arousal: the addition of novel non-linearities increases responsiveness in marmot alarm calls. Ethology. 115:1074–1081.

Briefer EF. 2012. Vocal expression of emotions in mammals: mechanisms of production and evidence. J Zool. 288:1–20.

Bro-Jørgensen J. 2010. Dynamics of multiple signalling systems: animal communication in a world in flux. Trends Ecol Evol. 25:292–300.

Bro-Jørgensen J, Dabelsteen T. 2008. Knee-clicks and visual traits indicate fighting ability in eland antelopes: multiple messages and back-up signals. BMC Biol. 6:47.

Charlton BD, Wyman MT, Locatelli Y, Fitch WT, Reby D. 2014. Do red deer hinds prefer stags that produce harsh roars in mate choice contexts? J Zool. 293:57–62.

Clutton-Brock TH, Albon SD. 1979. Roaring of red deer and the evolution of honest advertisement. Behaviour. 69:145–170.

Cramer ERA, Price JJ. 2007. Red-winged blackbirds *Ageliaus phoeniceus* respond differently to song types with different performance levels. J Avian Biol. 38:122–127.

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. Behav Ecol. 25:1451–1458.

Fourie PB. 1977. Acoustic communication in the rock hyrax (*Procavia capensis*). Z Tierpsychologia. 44:194–219.

Gammell MP, De Vries H, Jennings DJ, Carlin CM, Hayden TJ. 2003. David's score: a more appropriate dominance ranking method than Clutton-Brock *et al.*'s index. Anim Behav. 66:601–605.

Garcia M, Wyman MT, Charlton BD, Fitch WT, Reby D. 2014. Response of red deer stags (*Cervus elaphus*) to playback of harsh versus common roars. Naturwissenschaften. 101:851–854.

God M, Franz A, Hodl W. 2007. The influence of internote-interval variation of the advertisement call on the phonotactic behaviour in male *Allobates femoralis* (*Dendrobatidae*). Amphibia-Reptilia. 28:227–234.

Gouzoules H, Gouzoules S. 1989. Design features and developmental modification of pigtail macaque, *Macaca nemestrina*, agonistic screams. Anim Behav. 37:383–401.

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. Anim Behav. 85:995–1001.

Ilany A, Barocas A, Koren L, Kam M, Geffen E. 2011. Do singing rock hyraxes exploit conspecific calls to gain attention? Plos One. 6:e28612.

Illes AE, Hall ML, Vehrencamp SL. 2006. Vocal performance influences male receiver response in the banded wren. Proc Biol Sci. 273:1907–1912.

Johnstone RA. 1996. Multiple displays in animal communication: 'Backup signals' and 'multiple messages'. Philos Trans R Soc Lond B Biol Sci. 351:329–338.

Jordao JM, Fonseca PJ, Amorim MCP. 2012. Chorusing behaviour in the Lusitanian toadfish: should I match my neighbours' calling rate? Ethology. 118:885–895.

Kershenbaum A, Ilany A, Blaustein L, Geffen E. 2012. Syntactic structure and geographical dialects in the songs of male rock hyraxes. Proc Biol Sci. 279:2974–2981.

Kitchen DM, Cheney DL, Engh AL, Fischer J, Moscovice LR, Seyfarth RM. 2013. Male baboon responses to experimental manipulations of loud "wahoo calls": testing an honest signal of fighting ability. Behav Ecol Sociobiol. 67:1825–1835.

Kojima S, Izumi A, Ceugniet M. 2003. Identification of vocalizers by pant hoots, pant grunts and screams in a chimpanzee. Primates. 44:225–230.

Koren L, Geffen E. 2009. Complex call in male rock hyrax (*Procavia capensis*): a multi-information distributing channel. Behav Ecol Sociobiol. 63:581–590.

Koren L, Geffen E. 2011. Individual identity is communicated through multiple pathways in male rock hyrax (*Procavia capensis*) songs. Behav Ecol Sociobiol. 65:675–684.

Koren L, Mokady O, Geffen E. 2008. Social status and cortisol levels in singing rock hyraxes. Horm Behav. 54:212–216.

Morton ES. 1977. Occurrence and significance of motivation structural rules in some bird and mammal sounds. Am Nat. 111:855–869.

Moseley DL, Lahti DC, Podos J. 2013. Responses to song playback vary with the vocal performance of both signal senders and receivers. Proc Biol Sci. 280:20131401.

Overall JE, Tonidandel S. 2004. Robustness of generalized estimating equation (GEE) tests of significance against misspecification of the error structure model. Biometrical J. 46:203–213.

Ramachandran VS. 1996. Short note: on the unpleasantness of certain harsh sounds. Med Hypotheses. 46:487.

Reby D, Charlton BD. 2012. Attention grabbing in red deer sexual calls. Anim Cogn. 15:265–270.

Reby D, McComb K. 2003. Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. Anim Behav. 65:519–530.

Seyfarth RM, Cheney DL. 2003. Signalers and receivers in animal communication. Annu Rev Psychol. 54:145–173.

Slaughter EI, Berlin ER, Bower JT, Blumstein DT. 2013. A test of the nonlinearity hypothesis in great-tailed grackles (*Quiscalus mexicanus*). Ethology. 119:309–315.

Taylor AM, Reby D. 2010. The contribution of source-filter theory to mammal vocal communication research. J Zool. 280:221–236.

Townsend SW, Manser MB. 2011. The function of nonlinear phenomena in meerkat alarm calls. Biol Lett. 7:47–49.

Vannoni E, McElligott AG. 2008. Low frequency groans indicate larger and more dominant fallow deer (*Dama dama*) males. Plos One. 3:e3113.

Vehrencamp SL, Hall ML, Bohman ER, Depeine CD, Dalziell AH. 2007. Song matching, overlapping, and switching in the banded wren: the sender's perspective. Behav Ecol. 18:849–859.

Velez A, Hodl W, Amezquita A. 2012. Sound or silence: call recognition in the temporal domain by the frog *Allobates femoralis*. Ethology. 118:377–386.

Weiss DJ, Hauser MD. 2002. Perception of harmonics in the combination long call of cottontop tamarins, *Saguinus oedipus*. Anim Behav. 64:415–426.