



Original Article

Acoustic stability in hyrax snorts: vocal tightrope-walkers or wrathful verbal assailants?

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The source-filter theory proposes that information on caller properties is communicated through acoustic qualities, as physical state and performance ability are reflected in the voice. Vocal stability, manifested through harshness, is especially intriguing and has rarely been explored although harsh sounds are prevalent in nature. Male rock hyraxes (*Procavia capensis*) produce loud complex calls that we term songs. Only the calls of older, socially dominant males include a harsh sound termed snort. As snorts are the rarest element in songs, we hypothesized that high-quality snorts are difficult to produce, and that their quality consists in the ability to maintain smoothness throughout this low-pitched, harsh call. We quantified harshness by measuring periodicity deviations and expected to find a link between social parameters (residence, rank, and weight) and the ability to produce longer, smoother snorts. In addition, we presumed that if calls are used as vocal contests, conspecifics would avoid answering songs that exhibit a higher acoustic ability than their own songs. We found that in wild hyrax songs, snort harshness was associated with both weight and social rank, but in opposite directions. Heavier males produced smoother snorts and higher-ranked individuals produced harsher snorts, possibly indicating aggressiveness. Playback experiments showed that longer and harsher synthetic snorts, inserted into natural songs, reduced conspecific answer rates. Snorts may communicate complex information on hyrax weight and dominance by means of element length and harshness. Our present results provide a stimulating insight into the understanding of acoustics in mammalian vocal communication.

Key words: inner arousal theory, jitter, nonlinear vocalizations, source-filter theory, vocal communication.

INTRODUCTION

Sound waves, when lacking a constant period or amplitude, are termed nonlinear phenomena (NLP). As NLPs contain an unstable broadband of frequencies and amplitudes, they sound harsh to the human ear. Although rare in the vocalization of healthy human adults, NLPs are common in human infant cries, as well as the vocal repertoire of many animals (e.g., [Robb (2003), Blumstein et al. (2008), and Townsend and Manser (2011)] reviewed by Fitch et al. (2002)). Linear sound waves (i.e., containing a stable period and amplitude) may also contain differing levels of harshness when variability in amplitude or wavelength exists. As this variability grows,

the stability of the tone and amplitude is weakened, and harshness, as perceived by the human ear, is increased. This harshness can be quantified by measuring peak-to-peak and amplitude variation of the sound waveform, defined as *jitter* and *shimmer*, respectively (Equations 1 and 2 [Titze 2000]). In humans, both left–right and anterior–posterior asymmetries of the vocal folds contribute to NLP (Neubauer et al. 2001). As morphological symmetry is associated with elevated fitness (Mitton and Grant 1984), acoustic inspection of anatomical symmetry may serve as a factor in mate choice (Simmons and Richie 1996; Fitch et al. 2002). Thus, a lower proportion of NLPs or a lower level of harshness in calls may serve as an honest signal for higher vocal-fold symmetry, presumably perceived as more attractive to potential mates (Fitch et al. 2002).

Honest signaling can be categorized as handicap signals or as index signals. Under the handicap principle, signals must bear a

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cost that is otherwise disadvantageous for the signaler, thus boasting of its high quality. The cost prevents false signaling by individuals who are incapable of paying it. The cost must be directly connected to the information that is being transmitted and may be expressed via a physical burden, extra exposure to predation (Zahavi and Zahavi 1997), or intrasexual competition (Ligon and McGraw 2016). In contrast, index signals are constrained by physical properties (e.g., vocal tract length [Titze 2000]) or cognitive challenges (e.g., performing a complex signal [Janik and Slater 1997]) that do not impair the condition of the caller. We suggest that producing harsh sounds could serve as a handicap, in which animals can advertise their vocal abilities by maintaining a stable voice for a long duration, despite the vocal burden of an unstable sound.

Here we sought to investigate whether the stability in harsh sounds is used to encode individual quality in the rock hyrax (*Procapra capensis*). The rock hyrax is a social mammal that uses vocalization as its main means of communicating (Fourie 1977). Male hyraxes produce long complex calls termed songs (Koren and Geffen 2009), which increase before the annual mating season and decrease soon after (Koren and Geffen 2009). Since song acoustics and structural characteristics are associated with individual singer qualities (e.g., age and social rank [Koren and Geffen 2009; Demartsev, Bar-Ziv, et al. 2016]), we suspect that these vocalizations function as an advertisement of singer quality for the purposes of mate choice and intrasexual competition (Demartsev et al. 2014). This assumption is further strengthened by the responses that songs trigger from other males up to hundreds of meters away. Songs

can either be spontaneously performed without any evident stimulus or induced by an external event, such as a conspecific song, an alarm call, or an approaching predator. Song complexity is higher in induced songs in comparison to spontaneous songs (Demartsev et al. 2014), and it has been suggested that induced songs exploit a situation in which conspecifics are more alert and will pay more attention to a song (Ilany et al. 2011).

The hyrax song is composed of 3 vocal elements sounded repetitively in succeeding outbursts (Koren and Geffen 2009). The least frequent element—the snort is a low, harsh sound (Figure 1) and the last element to appear in the vocal repertoire of younger singers (Demartsev, Bar-Ziv, et al. 2016). The relative occurrence of snorts in a song increases with age and with dominance independently (Koren and Geffen 2009; Demartsev, Bar-Ziv, et al. 2016), and artificial manipulation of snort quantity in playback experiments significantly affects the reply rate (Demartsev, Bar-Ziv, et al. 2016). These findings suggest that snorts carry important information on male quality, and that this quality increases with age and dominance.

Based on our previous knowledge of the structure and context of male hyrax songs, and of vocalization in other animals (Reby and McComb 2003; Demartsev, Bar-Ziv, et al. 2016), we hypothesized that snort stability is associated with physical and performance quality. Our hypothesis assumed that snorts are difficult to produce, as they are loud, rare, and have high entropy (Koren and Geffen 2009; Demartsev et al. 2014; Demartsev, Bar-Ziv, et al. 2016), and that the maintenance of uniform snorts over time is challenging.

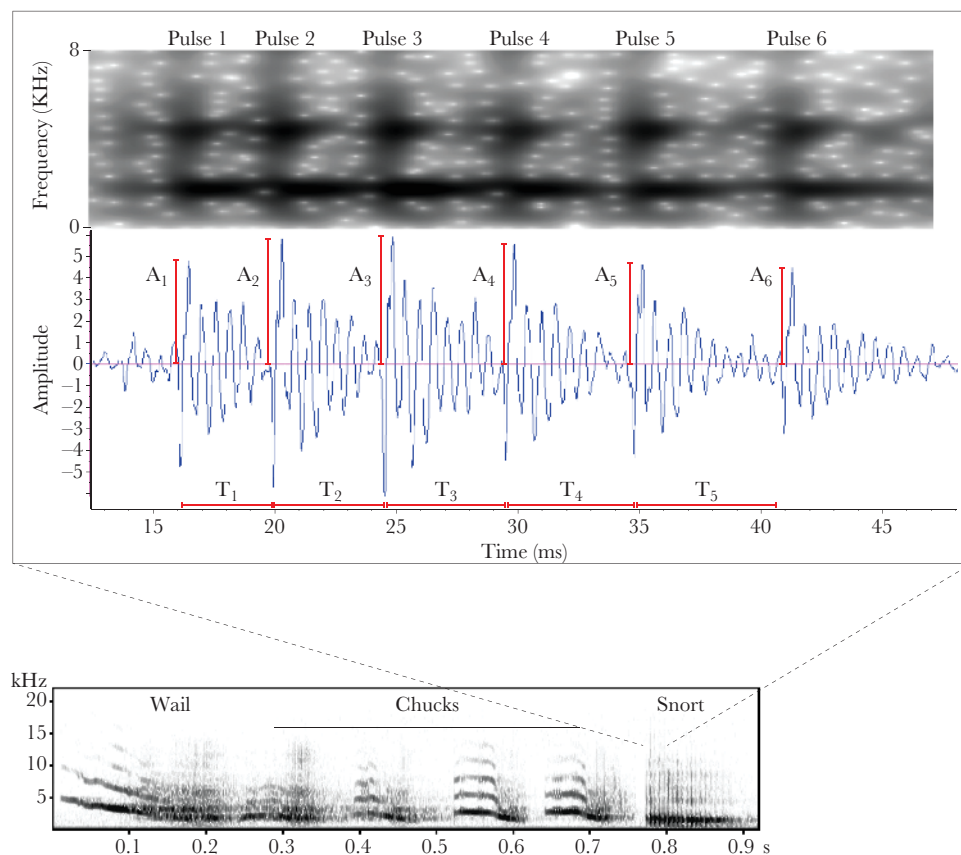


Figure 1

Wave form and sonogram of a typical snort element. The snort is 1 of 3 elements that construct songs and is shown in 1 bout on the bottom figure. Amplitude is presented schematically. T_i denotes the peak frequency and A_i the peak amplitude of the i pulse.

We predicted that lower harshness in snorts would be associated with increased physical quality or with higher acoustic performance abilities that may increase with experience. Thus, we predicted that both higher weight and higher dominance would be associated with a lower snort harshness and longer snorts. Furthermore, as hyraxes seem to perform better (i.e., higher song duration and complexity) in induced songs (Demartsev et al. 2014), we predicted that induced songs would contain higher quality snorts (i.e., longer and more stable) than spontaneous songs. Finally, assuming that songs are used as vocal contests (i.e., males that can exceed the performance heard in a song are more likely to reply to it [Davies and Halliday 1978; Albon and Clutton-Brock 1979]), we predicted that song reply rate would decrease as snort length and stability increase.

MATERIALS AND METHODS

Field methodology

Hyraxes live in groups composed of an adult resident male and a number of adult females (Rubsamen et al. 1982). Group members share sleeping setts and often browse together (Olds and Shoshani 1982). Adult males that are not stably associated with social groups are defined as bachelors (Barocas et al. 2011). We have been monitoring wild rock hyrax populations in 2 gorges in the Ein Gedi oasis (31°27' N, 35°23' E) in the Judean Desert in Israel as part of an ongoing project since 1999. Each year we observe hyraxes for 5 months, between March (start of parturition) and August (end of the mating season). In the current study, we used data collected between 2002 and 2012. Field-work, observation, and vocalization recording procedures have been previously described in detail (Koren and Geffen 2009; Barocas et al. 2011; Ilany et al. 2011; Demartsev et al. 2014).

Acoustic analysis

We used the same song library already used by Demartsev et al. (2014). All snorts in these songs had been manually identified and marked using Avisoft SAS Lab Pro software (version 5.2.07; Avisoft Bioacoustics, Berlin, Germany). We selected 53 high-quality songs performed by 21 different males and analyzed on average 7.2 ± 7.5 snorts from each song, a total of 379 snorts. Out of the 21 males, we analyzed songs from 8 that were bachelors, 11 that were residents, and 2 males that sang both as bachelors and as residents over the course of time. Out of the 53 songs, 15 were sung by bachelors and 38 by residents. Twenty-one of the songs were induced and 32 were spontaneous. Snorts for analysis were selected from throughout the song in order to account for changes in snort structure along songs as they progress (Demartsev et al. 2017). Each snort is composed of a series of consecutive pulses, each pulse starting with a maximal amplitude which decays over time (Figure 1). Pulse length averaged 10.6 ± 5.1 ms. Pulses were identified manually or, when possible, using Avisoft's Pulse Train Analysis tool. Amplitude (standardized within each snort) and time of each pulse were noted. Within each snort, we measured the variation between pulses in time and in amplitude using jitter and shimmer (Farrús and Hernando 2009), respectively (Equations 1 and 2, Figure 1),

$$Jitter = \frac{1}{N-1} \sum_{i=1}^{N-1} |T_i - T_{i+1}|, \quad (1)$$

$$Shimmer = \frac{1}{N-1} \sum_{i=1}^{N-1} |20 \log(\frac{A_i}{A_{i+1}})|, \quad (2)$$

where T is the peak frequency at pulse i , A is the peak amplitude at pulse i , and N is the total number of pulses in the snort (Figure 1). Both jitter and shimmer measure the harshness of the snort element: low values imply greater evenness in frequency and amplitude (i.e., smoothness) and high values reflect greater disorder in frequency and amplitude within the snort (i.e., harshness). Both jitter and shimmer were calculated using MATLAB (version R2015a Natick, Massachusetts: The MathWorks Inc., 2010).

Playback experiments

Playback experiments were performed using a remotely activated FoxPro Wildfire speaker with a TX9 wireless remote control (FOXPRO Inc., Lewistown, PA), following our previously published protocols (Ilany et al. 2011; Demartsev et al. 2014; Demartsev, Bar-Ziv, et al. 2016). The speaker was placed near 1 of 17 different locations inhabited by hyraxes, facing the focal male. Playback was activated when at least 4 individuals were identified in the vicinity of the speaker, indicating a high probability of a male presence, or when a male hyrax was identified. Reply was noted if a song was detected within 2.5 min after the playback (Demartsev et al. 2014). To confirm that the reaction was a response to our playback, we waited at least 5 min after positioning the speaker or after any other hyrax song or warning trill was heard in the vicinity before the experiments. If any disturbance occurred during playback or response period, the experiment was terminated. To avoid habituation to playbacks, each group received a maximum of 2 experimental treatments per day, with a gap of at least 30 min between experiments.

We chose 4 natural songs from 4 different males and replaced all the snorts in each song with a single snort, obtained from that specific song, while leaving all other elements in place (hereafter template songs). We chose songs that were relatively rich in snorts (6–14 snorts per song), to ensure the manipulations would be noticeable. The snort that we selected was one of the longer snorts in the song, to enable shortening. We then constructed 4 types of synthetic snorts: long and harsh, long and smooth, short and harsh, and short and smooth (Table 1). The longer snorts were constructed by doubling the duration of the natural snort template and the short snort was constructed by halving the duration of the natural snort template (Table 1). Harsh snorts were set as 2.5-fold greater in jitter and shimmer than in the natural snort template for the harsh and long snort class, and 3-fold greater for the harsh and short snort class (Table 1). Smooth snorts were set as a third (i.e., 0.3) of the jitter and shimmer of the natural snort template for the smooth and long snort class, and as a fifth (i.e., 0.2) for the smooth and short snort class (Table 1). We selected these synthetic levels of change in harshness because they represented the extreme values that we had observed in nature and were easily distinguishable by ear. The shorter snorts needed more extreme deviation in order to be detected by ear as harsher sound. All pulses used to create each of the manipulated snorts were extracted from the original snort template of each song. For the treatment songs, we replaced all the snorts in each of the template songs with 1 of 4 synthetic snort types. At the end of this process, our playback set was composed of 16 songs of which each 4 were of a specific synthetic type. In addition, we used 2 control songs, the natural unaltered (control 1) 4 songs, and the template songs (control 2). All the synthetic songs were constructed using MATLAB (version R2015a Natick: The MathWorks Inc., 2010), and the editing tools in Avisoft SASLab Pro software (version 5.2.07, Avisoft Bioacoustics).

Table 1
Acoustic manipulations and control tracks used for the playback experiments

Playback type	Control 1	Control 2	Long Harsh	Long Smooth	Short Harsh	Short Smooth
<i>Snort Identity</i>	natural variation	single snort	single snort	single snort	single snort	single snort
<i>Snort Character</i>	natural	natural	manipulated	manipulated	manipulated	manipulated
<i>Snort Length</i>	natural variation	1T	2T	2T	0.5T	0.5T
<i>Snort Harshness (jitter)</i>	natural variation	1J	2.5J	0.3J	3J	0.2J
<i>Snort Harshness (shimmer)</i>	natural variation	1S	2.5S	0.3S	3S	0.2S

Snort Identity—snorts were either natural or manipulated by using a single snort from the natural song to replace all other snorts. *Snort Character*—snorts were either left in their natural state or manipulated acoustically to be of differing length and harshness. *Snort Length*—T is the natural length of the chosen snort from each song. 2T are twice as long, and 0.5 are short snorts. *Snort Harshness (jitter)*—J is the natural jitter of the chosen snort from each song. *Snort Harshness (shimmer)*—S is the natural shimmer of the chosen snort from each song. 2.5 J/S are harsher songs and 0.3 J/S are smoother.

Altogether, we had 6 tracks for each of the 4 hyrax songs. Each of these 24 tracks was played 4–5 times in 101 successful playback experiments. To avoid individual recognition of singers, we used 4 hyrax songs that were recorded in distant locations and at least 4 years prior to the experiments. To avoid bias, all playback tracks were randomized and played in a blind order, without knowing the nature of the manipulation during the experiment.

Statistical analysis

We evaluated the effect of residency status (resident or bachelor), song type (spontaneous or induced), singer weight, and singer social rank (David's score (Gammell et al. 2003)) on the acoustic properties of the snort element (i.e., jitter, shimmer, and length) using linear mixed models. Although correlated, it has been shown that male hyrax body weight cannot be accurately used to predict social rank in this population, as many heavy males were low-ranking (Demartsev, Ilany, et al. 2016), and therefore, we tested these factors as separate predictors. We specified male ID as a random effect in all these analyses. Linear mixed model fitting was done in JMP (Version 12. SAS Institute Inc., Cary, NC). We assessed variable importance using the Independent Resampled Inputs approach, which works by random sampling of the observed values for each main effect in the model (Saltelli 2002). This procedure is implemented in the program JMP.

To evaluate the effect of snort length and harshness on reply rate to the playback trials, we used a logistic regression under the framework of the generalized estimating equations (GEE). GEE are an extension of generalized linear models (GLM) for mixed models, designed precisely for repeated measures within the same subjects (Overall and Tonidandel 2004). Group ID was specified as a random effect in the GEE analysis. The significance of each effect was tested using the Wald χ^2 . GEE analysis was conducted in SPSS (Version 22, IBM Inc., Armonk, NY).

Ethical statement

This study was conducted with permits from the Israeli Nature and Parks Authority for capturing, handling, and vocal experimentation on the hyraxes at the Ein Gedi Nature Reserve (2002/14674, 2003/14674, 2004/17687, 2005/17687, 2007/27210, 2008/31138, 2009/32871, 2010/37520, 2011/38061, 2012/38400, 2013/38803, 2016/41174). All procedures performed in this study were in accordance with the ethical standards of the Israeli Nature and Parks Authority. No observable long-term stress or other interference effects were detected for individual animals or for the entire study population. Both general population numbers and the integrity of the specific social groups in the research area remained stable for the duration of this study.

RESULTS

Natural songs

We examined the effect of residency (resident or bachelor), song type (spontaneous or induced), body weight, social rank, and their 2-way interactions on snort jitter, shimmer, and length. None of the independent variables significantly explained the variation in snort shimmer (Table 2). However, song type and body weight were the most important predictors for explaining the variation in snort jitter (variable importance total effect was 0.671 and 0.616, respectively). Social rank and residency showed minor effect on jitter (variable importance total effect ≤ 0.2). Song type was also a very important predictor of snort length (variable importance total effect = 0.915), whereas all the other 3 predictors had little effect (variable importance total effect ≤ 0.25).

We detected several interesting interactions with song jitter. Although in residents, mean jitter was higher in induced songs than in spontaneous songs (Table 2, Figure 2), in bachelors there were no significant differences between the song types. In the model presented in Table 2 (all effects and 2-way interactions; $AIC_C = 489.5$), this interaction showed only a marginal effect ($P = 0.077$). However, in an almost equally supported model (all effects, 2-way interactions, and Residency*Social rank*Songs type interaction; $AIC_C = 492.1$), the interaction between residency and song type showed a significant effect on jitter ($F_{1,98} = 4.5$, $P = 0.037$). These results suggest that residency has an effect on jitter, but the magnitude of this effect is small. Moreover, our model showed a significant interaction between song type and social rank (Figure 3a) and between song type and body weight (Figure 3b). Although in induced songs jitter was fairly constant across social rank or body weight, in spontaneous songs jitter increased with higher social rank and decreased with body weight. In other words, jitter can serve as a significant predictor of body weight or social rank in spontaneous songs, but not in induced songs, where it is consistently high (Table 2, Figure 3).

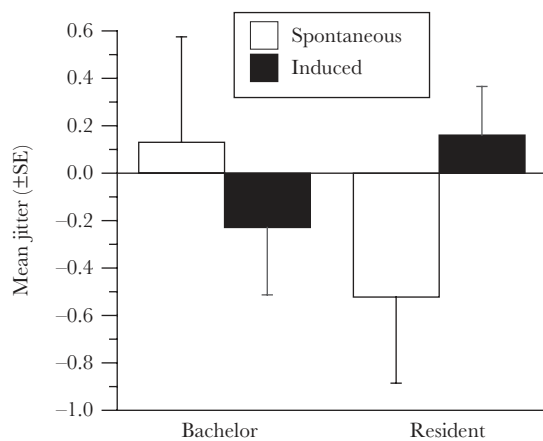
Last, mean snort length was shorter in spontaneous than in induced songs (Table 2). Additionally, longer snorts had lower values of shimmer ($\beta = -0.159$, model $r^2 = 0.14$, $F_{1,315} = 8.4$, $P = 0.004$) and jitter ($\beta = -0.14$, model $r^2 = 0.42$, $F_{1,349} = 6.5$, $P = 0.011$). However, the effect of snort length, when included in the greater model presented in Table 2, on shimmer ($F_{1,192} = 1.7$, $P = 0.192$) and jitter ($F_{1,196} = 0.5$, $P = 0.467$) was insignificant. All other significant effects for jitter and shimmer in these extended models remained unchanged. Therefore, we did not include snort length as a covariate in our models but only examined how it was affected by morphological and social predictors (Table 2). Finally,

Table 2

The mix-model estimate (β), $F_{(1,df)}$, and the probability value of the effect of residency (resident or bachelor), song type (induced or spontaneous), body weight, social rank, and their interactions on the jitter, shimmer, and the length of snorts in hyrax male songs

Effects	Jitter				Shimmer				Snort length			
	β	df	F	P	β	df	F	P	β	df	F	P
Residency (RS)	0.13	10	0.3	0.609	0.21	14	0.80	0.385	-0.13	13	0.3	0.591
Song type (ST)	0.10	93	0.7	0.413	-0.06	81	0.17	0.685	0.37	84	8.9	0.004
Body weight (BW)	-2.67	21	7.0	0.015	0.35	31	0.11	0.742	0.05	27	0.0	0.962
Social rank (SR)	0.39	17	3.0	0.103	0.23	18	0.99	0.334	0.03	19	0.0	0.909
RS * ST	-0.26	151	3.2	0.077	0.06	172	0.10	0.749	-0.21	167	1.9	0.174
RS * BW	-0.34	8	0.3	0.622	0.30	8	0.24	0.636	0.12	9	0.0	0.859
RS * SR	0.07	8	0.2	0.708	0.15	8	0.75	0.411	-0.10	9	0.3	0.606
ST * BW	2.93	161	16.7	<0.001	-0.35	174	0.18	0.675	0.26	170	0.1	0.728
ST * SR	-0.47	141	9.3	0.003	-0.04	115	0.04	0.835	-0.06	128	0.1	0.726

Male identity was designated as a random effect. Significant effects are indicated in bold.

**Figure 2**

The effect of song type on snort harshness. Mean jitter (\pm SE) in spontaneous and induced songs produced by resident and bachelor males. Values of jitter are Johnson SU transformed.

singer residency did not show a significant effect on snort length ($F_{1,10} = 3.0$, $P = 0.113$).

Playback trials

In our playback experiments, both snort harshness and length significantly affected reply rate. Songs with shorter snorts were replied to at a significantly higher rate (64%) than songs with long snorts (38%; logistic mix model, Wald $\chi^2_1 = 5.2$, $P = 0.022$; Figure 4a). Songs with smoother snorts were replied to at a significantly higher rate (61%) than songs with harsher snorts (41%, Wald $\chi^2_1 = 8.8$, $P = 0.003$; Figure 4b). The interaction between snort length and harshness was insignificant (Wald $\chi^2_1 = 0.9$, $P = 0.355$). Natural, unaltered songs (i.e., control 1) were replied to at a similar rate (59%, $n = 17$) as songs with long snorts (sequential Bonferroni multiple comparison, $P = 0.258$), short snorts ($P = 0.790$), harsh snorts ($P = 0.199$), and smooth snorts ($P = 0.999$). Songs with a single similar snort (i.e., control 2) were replied to at a lower rate of 41% ($n = 17$), which is similar to songs with long snorts ($P = 0.935$) and significantly lower than the reply rate to songs with short snorts ($P = 0.009$). Control 2 songs were replied to at a rate similar to songs with harsh snorts ($P = 0.670$) and at a significantly lower rate than to songs with smoother snorts ($P = 0.043$).

DISCUSSION

Snorts may communicate complex information on hyrax weight (a proxy for age) and social rank by means of element length and harshness. Although weight and social status may be associated in some social systems, in rock hyraxes they are not. Intriguingly, hyrax snort harshness was related to weight and social status in opposite directions. We found that elements of the signal were context-dependent and influenced the response of conspecifics. Thus, we argue that snorts cannot be exclusively categorized either as handicap or index signals, as conflicting lines of evidence can be explained by a different male life history strategy.

Our findings show that the context in which snorts were used influenced the signal that was transmitted. Snorts in spontaneous songs were shorter, and their harshness varied with male weight and rank so that heavier individuals produced smoother snorts. This supports our hypothesis that stable snorts with uniformly distributed and shaped pulses may be a sign of quality. In our study population, hyrax weight has been shown to be a reliable predictor for age (Koren et al. 2008). It is reasonable to assume that with age (i.e., weight) and experience, hyraxes may improve their vocal ability. It may seem maladaptive to boast vocal stability by performing an unstable sound, but we suggest that the snort, precisely because of its harshness, may provide a handicap that improves signal resolution, advertising vocal ability by maintaining a stable voice in an unstable acoustic platform. This is analogous to a tightrope-walker boasting superb stability in an unstable environment. The handicap of walking on a thin tightrope, swinging high up in the air, highlights the abilities of the walker to keep very stable, allowing the audience to judge skills at a fine resolution, in contrast to testing the walker's stability on a wide sidewalk. Hyraxes can thus let conspecifics assess their quality at a higher resolution in performing smooth snorts rather than a smooth sound. Thus, differences in harshness in hyraxes using this call can serve as a handicap signal. A similar phenomenon was observed in chimpanzees' (*Pan troglodytes*) "pant hoot" (Riede et al. 2007). These were found to be vocalized at the edge of an individual's vocal linear calling range, while keeping NLPs at a minimum. Thus, NLPs can be used for advertising purely by minimizing them, while nonetheless carrying the burden of a vocal handicap. In spontaneous songs, we also found that snort harshness increased with social rank. This seems surprising, as we also found that harsher snorts indicated a smaller, less experienced individual and therefore, a lower quality vocalization.

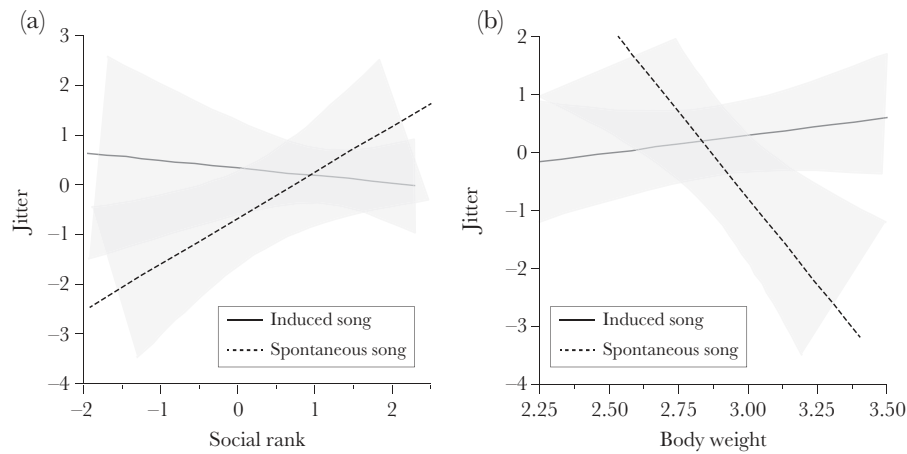


Figure 3

The interaction in jitter between song type and social rank (David's score; a), and between song type and body weight (kg; b). Gray areas denote 95% confidence intervals. Values of jitter are Johnson SU transformed.

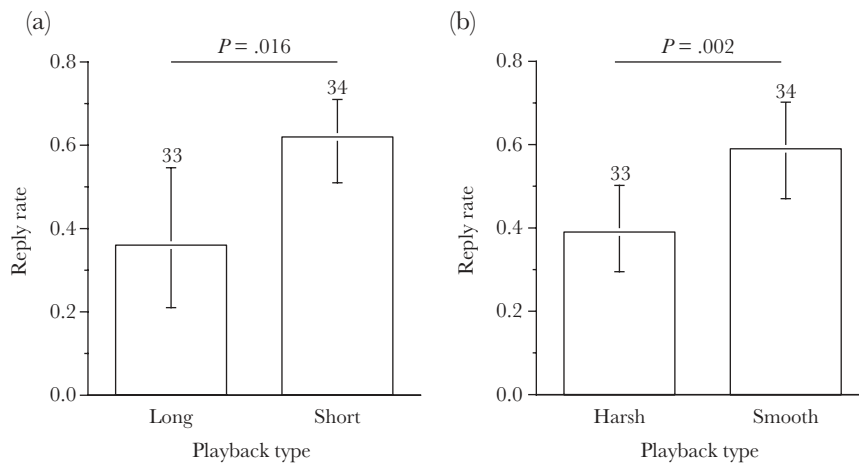


Figure 4

The predicted reply rate (\pm 95% CI) to playbacks with long and short snorts (a), and to playbacks with harsh and smooth snorts (b). P values are indicated above bars.

Induced songs, which have been shown to include higher quality acoustics (Demartsev et al. 2014), included harsher snorts, independently of singer weight or rank. We expected that induced songs would include smoother snorts (i.e., higher-quality) that would enhance quality differences between males. In contrast to our predictions, playback trials with harsher snorts received significantly fewer replies than those with smoother snorts. All of these findings support the notion that snorts are an honest index signal for inner arousal, via the polyvagal theory (Porges 2001) that suggests that the acoustic qualities of calls include reliable information on the physiological and emotional states of the caller as the neural mechanisms involved in vocalizations are linked to the autonomic nervous system. Multiple recent studies suggest that NLPs generally occur in circumstances of high inner arousal (Owren and Rendall 2001; Blumstein et al. 2008), and that in linear calls harshness increases with the level of arousal. For example, in meerkats (*Suricata suricatta*), more urgent alarm calls include a higher proportion of NLPs (Manser 2001). Jitter is a good predictor for classification of arousal levels in the calls of rhesus macaques (*Macaca*

mulatta) and African elephants (*Loxodonta africana*) (Soltis et al. 2005; Li et al. 2007). Furthermore, both anger and elation in the human voice are associated with increased jitter and shimmer (Whiteside 1998), and jitter is a reliable indicator of a stressor-provoked anxiety (Fuller et al. 1992). All of these examples show that arousal, whether reflecting fear, anger, anxiety, or happiness, reduces vocal control.

In our study, social rank is calculated via David's score (Gammell et al. 2003), which tabulates the outcome of agonistic interactions. Therefore, more aggressive individuals are often more dominant. Harsher snorts may be a reliable index signal for dominant, aggressive males. Morton's motivational-structural rules state that vocalizations in aggressive circumstances tend to be low-pitched and harsh (Morton 1977), supporting our suggestion that hyrax snorts reflect aggression (Koren and Geffen 2009). Although prior research has not associated vocal harshness with caller dominance (Briefer et al. 2010), vocal harshness of female African elephants was higher when associating with dominant males (Soltis et al. 2005). It is interesting to note that during agonistic interactions, the

aggression of the higher-ranked animal, and the excitement or fear of the lower ranked individual, may both induce a similar acoustic outcome. If harsher snorts are perceived as more aggressive, they may deter conspecifics from escalating conflict (Owren and Rendall 2001; Zimmermann et al. 2013), explaining why harsher snorts received significantly fewer replies than smoother snorts in playback experiments. Also, possibly, in induced songs, snorts are at the maximal harshness potential, due to high excitation or aggression levels. Our findings of higher snort harshness in socially dominant males may reject our hypothesis that smoother snorts reflect high quality. An increased harshness may actually be a desirable acoustic quality, signaling higher levels of dominance and aggression.

Another advantage of NLPs is that they elevate attention levels (Belin et al. 2008; Blumstein and Récapet 2009; Townsend and Manser 2011) due to the disharmony in the frequencies produced, resulting in signal unpredictability (Karp et al. 2014), or an association with neural desynchronization (Shapira Lots and Stone 2008). Furthermore, NLPs are generally predicted to be less prone to habituation due to their strong link with fear and arousal (Karp et al. 2014). Male hyraxes take advantage of attention-grabbing events to advertise themselves (Ilany et al. 2011) and perform their best during such events (Demartsev et al. 2014). We also know that hyrax males reply more frequently to snort-rich songs (Demartsev, Bar-Ziv, et al. 2016). Thus, snort harshness may be designed to arouse the alertness of nearby listeners. In this case, the smoother snorts used by larger or older hyraxes can be viewed purely as an index signal, whether it is physically related to size or to experience. Being an honest predictor of size and an honest predictor of social rank, snorts may be used as both a reliable index signal and an attention-grabbing call.

How could snort harshness be both negatively related to individual weight and positively related to social rank via aggressiveness in the context of attention-grabbing without masking the signal? As hyrax songs carry multiple signals for body weight (Koren and Geffen 2009), listeners may evaluate the harshness that they hear in snorts and compare it with the expected harshness derived from other cues. Songs containing multiple cues for a large individual that include harsher than expected snorts indicate that the singer is both large and aggressive. Most individuals, however, do not use both contrasting functions at the same time because the majority of males are low-ranked. These males use smooth stable snorts to indicate high weight, thus age and experience, whereas unstable snorts are indicative of a lack of control, at the other end of the skill continuum. As males mature, they improve their songs and snort element production. Thus, heavier (i.e., older) males produce more stable snorts. The minority of the males that attain a higher social rank due to aggressiveness or personality, may invest more in advertising their aggressiveness and attracting attention from conspecifics than in advertising their size via stable snorts, as information on size may be transmitted to listeners via alternative cues (Koren and Geffen 2009). Thus, our conflicting result may be explained by 2 different life strategies.

As we expected, snorts in induced songs were longer than those in spontaneous songs. These results support our previous findings that singers increase call complexity and quality in induced songs, where an audience is present (Demartsev et al. 2014). Presently, it is not clear why this effect was not found in bachelors, albeit possibly due to limited statistical power. Results from the playback trials showed that longer snorts were answered less, as we expected, possibly because they signaled a higher performance level, which

is harder to match or exceed. Longer snorts may also imply a more experienced individual or a larger hyrax that is more likely to win a physical confrontation. Replying to calls of a larger individual may constitute risk-taking, as it may increase the likelihood of an agonistic interaction (Demartsev et al. 2014; Garcia et al. 2014). Our controls supported the trends that we had observed in the treatment trials. Reply rate to the control 1 playbacks (natural unaltered songs) did not differ from that of any of the treatments and was similar to those found in previous experiments with snort-rich songs (Demartsev, Bar-Ziv, et al. 2016). This suggests that snorts in natural songs are more variable in length and harshness than in our manipulated songs and thus generated more variable responses. In contrast, the control 2 playbacks, which contained a relatively long snort that replaced all other snorts, received similar responses as the long and harsh snort treatments. The fact that songs with elongated snorts did not receive more replies than the control song may indicate that natural snort variation was already at the maximal level, and that a super stimulus did not exist in this case. Overall, our playback trials demonstrate that snort length and harshness can each dramatically change the way that conspecifics experience and respond to the information transmitted in songs.

In conclusion, we found that the harshness and length of a single vocal element, the snort, encode information about singer quality and state of aggression. Snorts may be used as both a handicap signal and an index signal in our study population. We also showed that the social context in which songs were performed had a profound effect on snort characteristics. Our results provide a novel insight into the micro-coding of key individual singer parameters within snorts and offer a deeper understanding of the function of harsh vocal elements and the role of vocal structure in the hyrax communication system.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Weissman et al. (2018).

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