

Bioacoustic cues and their relations to dominance rank in Père David's deer stags

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Abstract. The vocal display of male animals during the breeding season has received particular attention. To find out whether male acoustic signals could be a quality-assessment cue of callers, we conducted a study on Père David's deer (*Elaphurus davidianus*) characterised by a polygynous mating system and high male–male competition during the rutting season. We investigated the relationship between the stag's acoustic properties and the dominance rank as an indication of quality. Results showed that (1) there were two types of calls, the common roar and the chasing bark, (2) there was no significant difference between the call duration of the common roar and the chasing bark among different dominance ranks, (3) in the common roar, the value of the fundamental frequency, formant frequencies and formant spacing decreased significantly with the rise of dominance ranks and (4) vocal intensity of the common roar differed significantly among the three dominance ranks such as the harem master, the challengers and the bachelors. Our results suggested that some acoustic features, such as formant frequencies, formant spacing and vocal intensity of the common roar were closely related to the dominance rank and could be effective indicators of male competitive ability.

Additional keywords: acoustic properties, *Elaphurus davidianus*, rut strategy, social rank, vocal display.

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Introduction

Due to the energy consumption and the risk of predation, vocalisation is a costly and risky behaviour and may potentially encode some important information about the caller (McElligott and Hayden 1999; Doty and Welch 2001; Fischer *et al.* 2004). Vocalisation plays a unique role in reproduction among many species, with some taxa calling only during the breeding season (Clutton-Brock and Albon 1979; Cate *et al.* 2002; Ballentine *et al.* 2004). Male individuals advertise themselves to latent competitors and potential mates by projecting signals of genetic quality, motivational state and physical condition. Vocalisation is often performed under the pressure of predators (Reby and McComb 2003a, 2003b), thus making it difficult to cheat (Smith and Harper 1995).

The relationships between the quality or condition of male callers and their acoustic characteristics have received particular attention. The fundamental frequency and formant frequency are two parameters that have been comprehensively discussed in vertebrates displaying vocalisation (Hauser 1993; Reby *et al.* 2005; Charlton *et al.* 2008a, 2008b). According to the source-filter theory, the fundamental frequency is determined by the source signal, which is generated by the vibrations of the vocal folds in the larynx, whereas formant frequencies are frequencies

that are selectively amplified when the source signal passes through the vocal tract (Fant 1960). It has been confirmed that the formant frequency provides accurate information of the caller's body size in mammals (Fitch 1997; Reby and McComb 2003a; Harris *et al.* 2006).

Moreover, vocal intensity, also known as sound amplitude, was studied as an auditory distance cue (Nelson 2000; Murphy and Floyd 2005), or as the response to environmental noise in different species (Holt *et al.* 2008a, 2008b; Love and Bee 2010). Vocal intensity is difficult to measure in the wild, owing to the effect of attenuation and degradation (Wiley and Richards 1982), and few studies have discussed its function in intraspecific competition in wild mammals (Sanvito and Galimberti 2003; Wyman *et al.* 2008, 2012). Furthermore, some studies have investigated these acoustic features as indicators of body size and age, but fail to mention another quality-related characteristic, i.e. dominance rank, which is an important measurement of fitness in polygamous animals. Only studies of baboons (*Papio cynocephalus ursinus*) have revealed the correlations between acoustic features and male dominance rank (Fischer *et al.* 2002, 2004).

Deer are notable for vocalisation diversity during the rutting season, and the seasonality of loud calls links directly and

exclusively to reproductive activities (Reby and McComb 2003b). There has been an emphasis on studying vocal behaviour and the functional analyses of emitted sounds for a series of cervid species (Reby and McComb 2003a; Kidjo *et al.* 2008; Volodin *et al.* 2013). Père David's deer (*Elaphurus davidianus*) is characterised by a polygynous mating system, with high male–male competition and skewed reproductive success (Li *et al.* 2004, 2005; Jiang *et al.* 2006). The calling rate of this species can determine the outcome of vocal contests among stags of different ranks, since hinds prefer the dominant stags with a higher calling rate (Li *et al.* 2001). However, we still know little about the categories and function of calls in Père David's stags.

We assumed dominance rank as being indicative of male competitive ability and assessed whether vocal intensity could be an accurate acoustic indicator of male competitive ability. We investigated the relationship between vocalisation and dominance rank of Père David's deer stag, by examining the relationship between acoustic parameters (call duration, vocal intensity, fundamental frequency, formant frequency and formant spacing) and dominance ranks. We hypothesise that fundamental frequency and formant-related frequencies would be lower for stags with a higher rank, whereas the vocal intensity and call duration of dominant stags would distinguish them from those of subordinates.

Materials and methods

Study site and population

The study was conducted in Beijing Milu Park (39°7'N, 116°03'E), Beijing, China. In this park, annual average temperature is 13.1°C, with a mean temperature of –3.4°C in January and 26.4°C in July. Average annual precipitation is ~600 mm. More than 100 individuals were bred in a 60 ha enclosure. This population included 56 stags and subadult stags, 62 hinds and several 1-year-old fawns. All individuals were distinguished by ear tags. Antler shape and facial characteristics were used to identify individuals when the ear tags were unavailable.

In the present study, we adhered to the 'Guidelines for the treatment of animals in behavioural research and teaching', as published by Animal Behaviour (2006), and also adhered to the Wild Animals Protection Law of the People's Republic of China. All animals in the study were cared under animal research protocol IOZ-2006 approved by the Animal Care Committee of Institute of Zoology, Chinese Academy of Sciences, and cared for in accordance with the principles and permissions approved by Beijing Milu Park.

Observation and recording

We carried out behavioural observation during the daytime (0600 hours to 0700 hours) from June to August (the rutting season) in 2012. We monitored the change of dominance rank, and vocal and other behaviour within the group. On the basis of the previous studies by Jiang *et al.* (2004) and Li *et al.* (2004), the dominance status of Père David's deer stags are distinguishable during the rutting season as the following three distinct groups: (1) the 'harem master', (2) the 'challengers' and (3) the 'bachelors'. The 'harem master' is the most dominant stag that controls the harem and drives out intruders. The 'challenger' challenges the

harem master for control of the harem. Last, the 'bachelors' are the subordinate stags that form a bachelor group and remain separated from the harems during the rutting season. To avoid the lack of independence in data, we ceased recording the call of a particular stag once it changed its rank, and chose another stag that corresponded with its previous social status, to replace it. Studies have found the existence of age-related variance in acoustic structure of vocalisation (Reby *et al.* 1999; Fischer *et al.* 2002; Reby and McComb 2003a). Thus, we chose only stags ~6–10 years old to minimise this age effect on acoustic parameters.

In total, 292 incidents of vocalisation were recorded from 34 adults during field observation. We recorded the vocalisations from dawn to dusk every 4 days, using a normal directional microphone connected to a digital recorder (VASO VM-398N, Shenzhen Vaso Digital Technology Development Co., Ltd., Shenzhen, China). At the same time, we used a laser rangefinder (Yardage Pro 400, Bushnell Performance Optics, Lenexa, KS, USA) to measure the distance from the observer to vocalising animals. The sounds were transferred to digital storage by using Adobe Audition 3.0 software (Adobe Systems, San Jose, CA, USA) at a sampling rate of 44.1 kHz and 16-bit resolution in WAV format. In all recording procedures, we recorded the call with the directional microphone facing towards the target animals.

Additionally, we performed a playback experiment to investigate the relationship between vocal intensity and observation. By recording a playback of a recorded call from a Père David's deer stag from varying distances in a playground when the noise level was low, we calculated the coefficient between vocal intensity and distance. The same microphone and digital recorder equipped in the field were used to record stag vocalisations at the distances of 24 m, 39 m, 54 m and 72 m, facing towards the source signal. We recorded the playback at each distance three times.

Acoustic analyses

After reviewing all recordings, we discarded low-quality vocalisations recorded from remote distance beyond 80 m or with high-level background noises. Eventually, we chose 103 high-quality recordings of 24 individuals, which were used to perform the acoustic analysis. All acoustic analysis relied on the PRAAT DSP package version 5.3.34 (Boersma and Weenink 2012). We calculated the mean duration of all recordings for each stag. The narrow-band spectrograms (Fig. 1a: window length = 0.04 s, time steps = 0.002 s, maximum frequency = 4000 Hz, Gaussian window shape) of roars (the common roar and the chasing bark) were generated by the 'to spectrogram' command. Mean fundamental frequency was extracted using the 'to pitch' command (time step = 0.01 s, pitch floor = 75 Hz, pitch ceiling = 300 Hz). We used the 'pitchier' command to determine whether there were any abnormal values present, which were then adjusted. The uncertain value was identified by the spectrum (slice) analysis. We then obtained the mean fundamental frequency for each individual by averaging the frequency data of all recordings.

Formant frequency was estimated by linear predictive coding (LPC) analysis. The first three formant frequencies were evident

and visible on the spectrogram (Fig. 1a). First, we used the 'to formants (burg)' command (time step = 0.00625 s, maximum number of formants = 4, maximum formant = 2000 Hz, window length = 0.025 s, pre-emphasis from = 50 Hz) to obtain the mean frequency of three formants for each recording. To ensure the accuracy of data and avoid the wrong outcome of the machine, we conducted another analysis using 'to LPC (autocorrelation).' First, we used the command of 'sound: convert-resample' to sample the sound to a sampling rate of 11 000 Hz. We then ran the 'to LPC (autocorrelation)' command (prediction order = 10/11/16, window length = 0.025 s, time step = 0.005 s, pre-emphasis frequency = 50 Hz). Finally, we calculated the values of F1, F2 and F3 by the 'to spectrum (slice)' command along the recording. We then obtained the mean frequency of F1, F2 and F3 for each individual by averaging these values. These values were helpful in evaluating the results from automatic formant analysis. Afterwards, we calculated the overall formant spacing of each recording using the equation: $\Delta F = (F3 - F1)/2$ (adjusted from Reby and McComb 2003a).

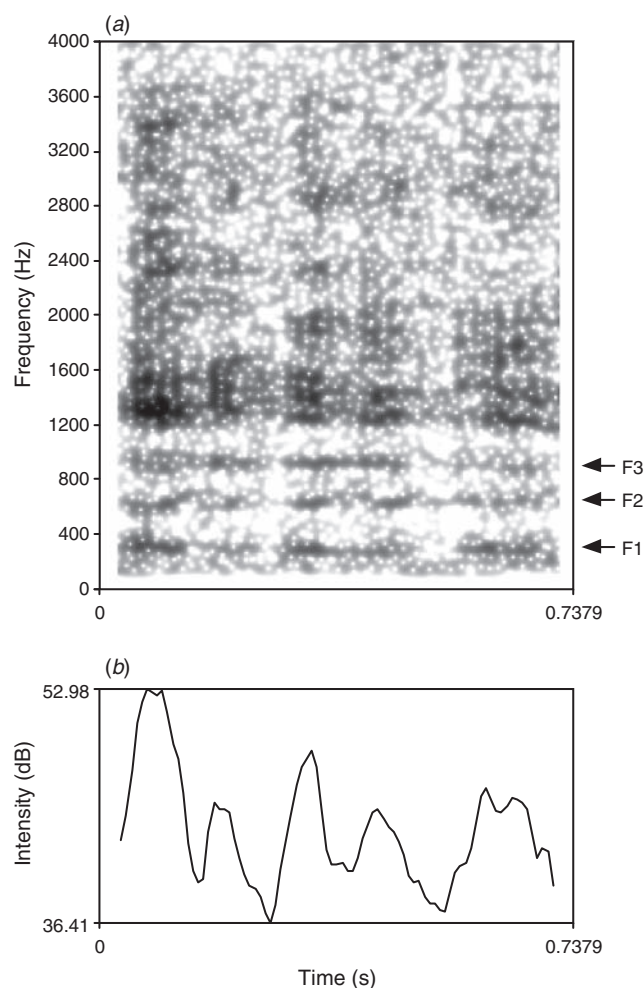


Fig. 1. The narrow-band spectrogram and intensity contour of a common roar extracted by PRAAT. (a) The spectrogram, window length = 0.03 s, time steps = 0.002 s, maximum frequency = 4000, Gaussian window shape. (b) The intensity contour, minimum pitch = 100 Hz, time step = 0.008 s. The F1, F2 and F3 represent the first, second and third formant, respectively.

We obtained the mean vocal intensity through the 'to intensity' command (minimum pitch = 100 Hz, time step = 0.008 s). We then used the 'down to intensitytier' command to view and check the analysis results (Fig. 1b). The vocal intensity of each stag was the average value of all recordings.

Statistical analyses

All stags (24 individuals, 103 calls) involved in the analysis of dominance rank were independent, except for one stag that occupied two dominance ranks (harem master and challenger) in different times, and vocalisations in the rank of challenger were discarded in the analysis for this individual. All statistical analyses were conducted by SPSS 13.0 (SPSS, Chicago, IL, USA). First, the Kolmogorov–Smirnov test was used to examine the distribution of all acoustic parameters and the results showed that the distribution of all parameters followed a normal distribution ($P > 0.05$).

We then used linear regression to calculate the coefficient of vocal intensity (mean value of three measurements in a certain distance extracted by PRAAT) and distance (24, 39, 54 and 72 m). The regression results showed that the perceived intensity would decrease by 0.2 dB with the increase of 1 m in distance ($F = 23.99$, d.f. = 1, $P < 0.05$; Fig. 2). This coefficient was further used to calculate the vocal intensity of sound produced by stags, with the intensity value obtained by recorder and observation distance. The purpose of this calculation was to ensure that the sound we recorded in the field was from the same distance.

Last, we used the univariate general linear model (GLM) to test the difference of acoustic parameters among and within different dominance ranks. For all statistical tests, $P < 0.05$ was taken as significantly different.

Results

Description of reproductive call

On the basis of behavioural observations, we divided the calls of stags into two types, including (1) the common roar (85 calls; Fig. 3a), and (2) the chasing bark (18 calls; Fig. 3b). The common roar was highly variable and consisted of two basic elements,

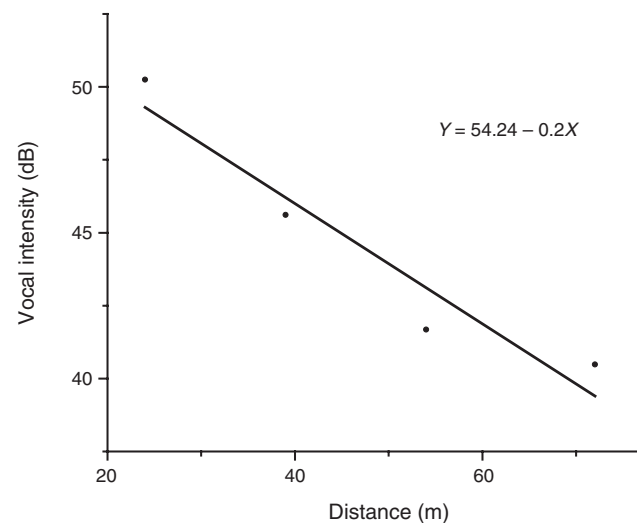


Fig. 2. The linear regression of vocal intensity and observation distance.

namely a brief roar and a longer rumbling roar. Sometimes stags produced a series of brief roars (2–8) over a short period, which collectively formed a long continuous note, which was often repeated two or three times in a call. Their calls took several possible forms, including (1) a simple single-element call consisting of a brief roar, (2) a long note or (3) a longer rumbling roar. Alternatively, a call could be a random combination of any of the three above-mentioned categories. There was always only one longer rumbling roar at the end of a common roar. Roaring contests between stags were often observed during the rutting season.

The chasing bark was observed when the master was driving challengers and herding hinds, or when challengers were chasing and herding those hinds that temporarily fled the harem. Most of chasing barks included 5–20 monotone short barks, sometimes with a longer rumbling roar as the last note. The largest number of barks in a chasing bark we recorded was 28 from a master,

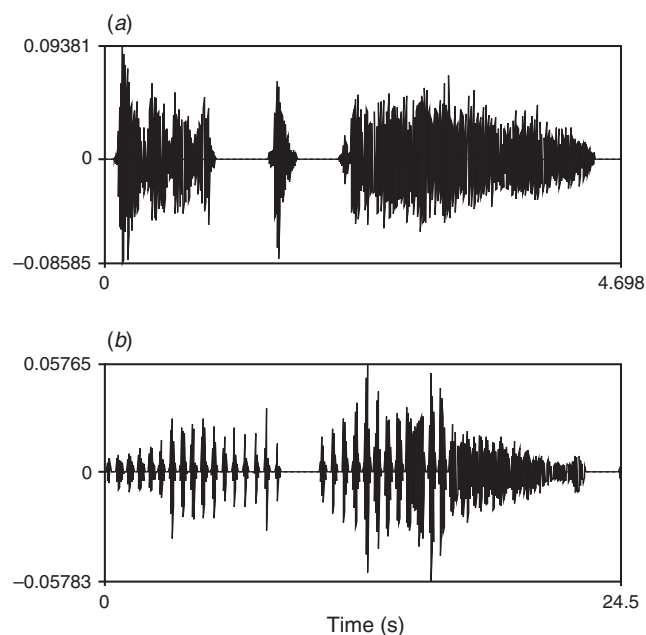


Fig. 3. The waveform of two call types and a narrow-band spectrogram with frequency modulation. (a) The waveform of common roar. (b) The waveform of chasing bark.

which consisted of 26 short barks, one long note made up of two brief roars, and a longer rumbling roar after the master drove a challenger out of harem, and, subsequently, ran back towards the hinds. The common roar was observed in all dominance ranks, whereas the chasing bark was rarely detected among bachelors.

Variance of the common roar among different dominance ranks

According to the results of the GLM analysis, the call duration of the common roar was shorter for more dominant ranks, but the relationship was not significant ($P > 0.05$; Table 1). The fundamental frequency of the common roar was also insignificantly different among the three dominance ranks ($P > 0.05$; Table 1).

The formant frequencies (F1, F2, F3) of the common roar of the master were significantly lower than those of the challengers and bachelors ($P < 0.01$; Table 1).

The vocal intensity of the common roar showed significant differences among different dominance ranks of Père David's deer stag ($P < 0.01$; Table 1).

Variance of chasing bark among different dominance ranks

The call duration of the chasing bark tended to increase along with the rise of dominance rank, but the difference was not significant ($P > 0.05$; Table 2). The fundamental frequency of the chasing bark was also insignificantly different among the three dominance ranks ($P > 0.05$; Table 2).

The formant frequencies (F1, F2, F3) and the formant spacing of the chasing bark showed no significant difference among different dominance ranks ($P > 0.05$; Table 2).

Between two dominance ranks, the difference of vocal intensity of the chasing bark was also not significant ($P > 0.05$; Table 2).

Discussion

In polygynous animals, male competition is intense during the rutting season. Apart from fights among themselves, males also invest energy in ritualised competition. For instance, parallel walk and vocal contest are usually found in red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and Père David's deer (McComb 1991;

Table 1. Statistical results of common roar in Père David's deer stags

The parameters are call duration (Duration), fundamental frequency (F0), first-formant frequency (F1), second-formant frequency (F2), third-formant frequency (F3) and overall formant spacing (ΔF). Each parameter value represents the mean \pm s.e. of rank group. Univariate test of general linear model.

* $P < 0.05$; n.s., not significant

Parameter	Dominance rank			F-value	d.f.	Significance (2-tailed)
	Harem master	Challenger	Bachelors			
Duration (s)	5.40 \pm 1.51	5.46 \pm 1.54	5.90 \pm 1.70	0.13	2	n.s.
Intensity (dB)	60.92 \pm 3.04	57.96 \pm 2.37	55.08 \pm 3.72	5.98	2	*
F0 (Hz)	117.55 \pm 2.86	118.10 \pm 3.36	118.36 \pm 4.09	0.12	2	n.s.
F1 (Hz)	332.45 \pm 27.53	433.82 \pm 38.44	444.37 \pm 91.68	17.96	2	*
F2 (Hz)	909.73 \pm 112.15	1019.12 \pm 62.27	1232.74 \pm 215.14	9.49	2	*
F3 (Hz)	1419.69 \pm 93.51	1583.13 \pm 50.64	1717.18 \pm 239.72	12.42	2	*
ΔF (Hz)	539.51 \pm 43.88	568.17 \pm 30.13	641.16 \pm 76.19	6.63	2	*

Table 2. Statistical results of chasing bark in Père David's deer stags

The parameters are call duration (Duration), fundamental frequency (F0), first-formant frequency (F1), second-formant frequency (F2), third-formant frequency (F3) and formant spacing (ΔF). Each parameter value represents the mean \pm s.e. of rank group. Univariate test of general linear model. n.s., not significant

Parameter	Dominance rank		F-value	d.f.	Significance (2-tailed)
	Harem master	Challenger			
Duration (s)	8.87 \pm 3.94	4.96 \pm 4.29	1.35	1	n.s.
Intensity (dB)	60.78 \pm 3.48	57.32 \pm 1.34	1.71	1	n.s.
F0 (Hz)	113.56 \pm 3.00	116.42 \pm 5.01	0.95	1	n.s.
F1 (Hz)	353.6 \pm 61.54	424.24 \pm 76.61	2.35	1	n.s.
F2 (Hz)	943.19 \pm 68.58	950.67 \pm 57.46	0.13	1	n.s.
F3 (Hz)	1455.47 \pm 49.21	1577.28 \pm 41.79	6.23	1	n.s.
ΔF (Hz)	541.07 \pm 28.69	542.9 \pm 5.22	0.01	1	n.s.

Li *et al.* 2001; Reby and McComb 2003b; Bartoš *et al.* 2007). We distinguished that Père David's deer vocalised using two types of calls, namely, (1) the common roar and (2) the chasing bark during the rutting season. Although we sampled a limited number of chasing barks in our study, we seldom noticed this call type from the bachelor group. Previous studies have similarly revealed that the bellowing rate of the bachelors was the lowest among the three dominance ranks in Père David's deer (Li *et al.* 2001). We presumed that the chasing bark was more costly than the common roar, because it exclusively occurred when the stag was running, and usually lasted for a longer time, which might explain why the chasing bark was rarely observed among the bachelors.

In previous studies, the duration of vocalisation has been considered an indicator of gene quality, with longer duration indicating superior genetic quality, consequently leading to improved mating success (McComb 1991; Welch *et al.* 1998; Doty and Welch 2001). Studies of various mammals demonstrated that call duration is positively related to the dominance rank or the factors that vary with dominance rank (Gouzoules *et al.* 1984; Kitchen *et al.* 2003). However, in the present study, there were no significant differences of call duration of the common roar and the chasing bark among the different dominance ranks within Père David's deer stag. Other studies of Père David's deer and red deer have suggested that the calling rate of the dominant stag is apparently higher than that of stags of lower rank (Clutton-Brock and Albon 1979; Li *et al.* 2001; Bolt 2013). Thus, in the present study, we determined that male Père David's deer expressed their capability of competition by the calling rate rather than by the call duration.

Our data indicated that formant-related frequency was closely related to the dominance rank of Père David's deer. Previous studies have confirmed that stags produce groans with higher mean fundamental frequency when other vocal males and females are present, which suggests that fundamental frequency might encode predominantly dynamic and motivation-related information (Charlton and Reby 2011). Other studies have suggested that the formant frequencies are more indicative of the inherent and static properties (Reby *et al.* 1999; Reby and McComb 2003b; Charlton *et al.* 2008b). Therefore, the inherent variance played a more important role than did motivational variance in the male competition of Père David's deer. In addition, the findings of studies of some other polygynous animals have demonstrated opposite results. For example,

lower fundamental frequency and formant spacing is indicative of higher rank in fallow deer stags (Vannoni and McElligott 2008). In primates, high-ranking baboon males vocalise with higher fundamental frequency (Fischer *et al.* 2004). That is to say, there is a species-dependent variability of fundamental frequency and/or formant frequency. The study of sexual selection by females using male vocalisation has demonstrated the existence of female preference of frequencies (Reby *et al.* 2001, 2010; Charlton *et al.* 2008a), which could be a plausible explanation for the variability among different species.

We found that vocal intensity of the common roar was positively related to the dominance rank of Père David's deer stag, whereas the difference of intensity of the chasing bark was not significant between the master and the challenger. Liu (2014) found that the duration of the chasing bark was significantly higher than the duration of the common roar in the master, whereas the duration of the chasing bark was significantly lower than the duration of the common roar in the challenger. Moreover, the vocal intensity of the common roar was higher than the vocal intensity of the chasing bark in both the master and the challenger. That is to say, stags invested more energy in the common roar than in the chasing bark. Thus, we inferred that males competed against each other through vocal intensity, mostly by using the common roar. The vocal intensity of the common roar is a true indication of the caller's physical prowess. Similar results have been found for the American bison (*Bison bison*) as well as human beings (Henrich *et al.* 2005; Murphy and Floyd 2005; Wyman *et al.* 2008, 2012). In playback experiments, researchers have found that males increase call amplitude in response to playbacks of environmental noise (Love and Bee 2010). Such results imply the importance of vocal intensity in social contact, and support the notion that males may use vocal intensity to assess rival males during male competition.

Previous studies on mating success have shown that higher-ranking males always have higher mating success (Li *et al.* 2005; Deaton 2008; Wroblewski *et al.* 2009), which implies that the dominance rank might represent female preference towards male quality. The acoustic parameters could be regarded as indirect indicators of mating opportunity, considering they are closely related to dominance rank. Evidently, the competition increases the chance of competitive males occupying a higher status, thus leading to the divergence of mating strategies. In conclusion, acoustic features of male calls were closely related to the dominance rank and could be an effective indication of

competitive ability of Père David's deer stag. Considering the structural complexity of the common roar with a different combination of components found in Père David's deer, we assumed that some information might also be encoded by the variable combinations, which requires further research by conducting re-synthesis and playback experiments.

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References

- Animal Behaviour (2006) Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour* **71**, 245–253.
- Ballentine B, Hyman J, Nowicki S (2004) Vocal performance influences female responses to male bird song: an experimental test. *Behavioral Ecology* **15**, 163–168. doi:10.1093/beheco/arg090
- Bartoš L, Fričová B, Bartošová-Vichová J, Panamá J, Šustr P, Šmidová E (2007) Estimation of the probability of fighting in fallow deer (*Dama dama*) during the rut. *Aggressive Behavior* **33**, 7–13. doi:10.1002/ab.20162
- Boersma P, Weenink D (2012) 'Praat: doing phonetics by computer (Computer program). Version 5.3.34.' Available at <http://www.praat.org/> [Verified 1 June 2015]
- Bolt LM (2013) Squealing rate indicates dominance rank in the male ring-tailed lemur (*Lemur catta*). *American Journal of Primatology* **75**, 1174–1184.
- Cate CT, Slabbekoorn H, Ballintijn MR (2002) Birdsong and male-male competition: causes and consequences of vocal variability in the collared cove (*Streptopelia decaocto*). *Advances in the Study of Behavior* **31**, 31–75. doi:10.1016/S0065-3454(02)80005-5
- Charlton BD, Reby D (2011) Context-related acoustic variation in male fallow deer (*Dama dama*) groans. *PLoS One* **6**(6), e21066. doi:10.1371/journal.pone.0021066
- Charlton BD, McComb K, Reby D (2008a) Free-ranging red deer hinds show greater attentiveness to roars with formant frequencies typical of young males. *Ethology* **114**, 1023–1031. doi:10.1111/j.1439-0310.2008.01539.x
- Charlton BD, Reby D, McComb K (2008b) Effect of combined source (F0) and filter (formant) variation on red deer hind responses to male roars. *The Journal of the Acoustical Society of America* **123**(5), 2936–2943. doi:10.1121/1.2896758
- Clutton-Brock TH, Albon SD (1979) The roaring of red deer and the evolution of honest advertising. *Behaviour* **69**, 145–170. doi:10.1163/156853979X00449
- Deaton R (2008) Use of microsatellite paternity analysis to determine male mating success in the western mosquitofish, *Gambusia affinis*. *Behaviour* **145**, 795–814. doi:10.1163/156853908783929151
- Doty GV, Welch AM (2001) Advertisement call duration indicates good genes for offspring feeding rate in gray tree frogs (*Hyla versicolor*). *Behavioral Ecology and Sociobiology* **49**, 150–156. doi:10.1007/s002650000291
- Fant G (1960) 'Acoustic theory of speech production.' (Mouton: The Hague, The Netherlands.)
- Fischer J, Hammerschmidt K, Cheney DL, Seyfarth RM (2002) Acoustic features of male baboon loud calls: influences of context, age, and individuality. *The Journal of the Acoustical Society of America* **111**, 1465–1474. doi:10.1121/1.1433807
- Fischer J, Kitchen DM, Seyfarth RM, Cheney DL (2004) Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology* **56**, 140–148. doi:10.1007/s00265-003-0739-4
- Fitch WT (1997) Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *The Journal of the Acoustical Society of America* **102**, 1213–1222. doi:10.1121/1.421048
- Gouzoules S, Gouzoules H, Marler P (1984) Rhesus monkey (*Macaca mulatta*) screams: representational signaling in the recruitment of agonistic aid. *Animal Behaviour* **32**(1), 182–184. doi:10.1016/S0003-3472(84)80336-X
- Harris TR, Fitch WT, Goldstein LM, Fashing PJ (2006) Black and white colobus monkey (*Colobus guereza*) roars as a source of both honest and exaggerated information about body mass. *Ethology* **112**, 911–920. doi:10.1111/j.1439-0310.2006.01247.x
- Hauser MD (1993) The evolution of nonhuman primate vocalizations: effects of phylogeny, body weight and social context. *American Naturalist* **142**, 528–542. doi:10.1086/285553
- Henrich N, d'Alessandro C, Doval B, Castellengo M (2005) Glottal open quotient in singing: measurements and correlation with laryngeal mechanisms, vocal intensity, and fundamental frequency. *The Journal of the Acoustical Society of America* **117**(3), 1417–1430. doi:10.1121/1.1850031
- Holt MM, Noren DP, Veirs V, Emmons CK, Veirs S (2008a) Speaking up: Killer whales (*Orcinus orca*) increase their call amplitude in response to vessel noise. *The Journal of the Acoustical Society of America* **125**(1), 27–32.
- Holt MM, Veirs VAL, Veirs S (2008b) Noise effects on the call amplitude of southern resident killer whales (*Orcinus orca*). *Bioacoustics* **17**(1–3), 164–166. doi:10.1080/09524622.2008.9753802
- Jiang Z, Li C, Zeng Y, Windemo F (2004) 'Harem defending' or 'challenging': alternative individual mating tactics in Père David's deer under different time constraint. *Current Zoology* **50**, 706–713. [formerly Acta Zoologica Sinica]
- Jiang Z, Li C, Zeng Y (2006) Mating system, mating tactics and effective population in Père David's deer (*Elaphurus davidianus*). *Acta Ecologica Sinica* **26**(7), 2225–2260.
- Kidjo N, Cargnelutti B, Charlton BD, Wilson C, Reby D (2008) Vocal behaviour in the endangered corsican deer: description and phylogenetic implications. *Bioacoustics* **18**(2), 159–181. doi:10.1080/09524622.2008.9753598
- Kitchen DM, Seyfarth RM, Fischer J, Cheney DL (2003) Loud calls as indicators of dominance in male baboons (*Papio cynocephalus ursinus*). *Behavioral Ecology and Sociobiology* **53**, 374–384.
- Li C, Jiang Z, Zeng Y (2001) Bellowing, rank-class and mating success in Père David's deer stags. *Zoological Research* **22**(6), 449–453.
- Li C, Jiang Z, Zeng Y (2004) Relationship between serum testosterone, dominance and mating success in Père David's deer stags. *Ethology* **110**, 681–691. doi:10.1111/j.1439-0310.2004.01003.x
- Li C, Jiang Z, Zeng Y (2005) Rutting tactics in Père David's deer stags under different population densities and during different rut periods. *Biodiversity Science* **13**, 424–431. doi:10.1360/biodiv.050062
- Liu N (2014) Behavioral mechanism and mating success of reproductive strategies in Père David's deer stag. MSc Thesis, Sichuan Agriculture University, Ya'an, China.
- Love EK, Bee MA (2010) An experimental test of noise-dependent voice amplitude regulation in Cope's grey treefrog, *Hyla chrysoscelis*. *Animal Behaviour* **80**, 509–515. doi:10.1016/j.anbehav.2010.05.031
- McComb KE (1991) Female choice for high roaring rates in red deer, *Cervus elaphus*. *Animal Behaviour* **41**(1), 79–88. doi:10.1016/S0003-3472(05)80504-4
- McElligott AG, Hayden TJ (1999) Context-related vocalization rates of fallow bucks, *Dama dama*. *Animal Behaviour* **58**, 1095–1104. doi:10.1006/anbe.1999.1237

- Murphy CG, Floyd SB (2005) The effect of call amplitude on male spacing in choruses of barking treefrogs, *Hyla gratiosa*. *Animal Behaviour* **69**, 419–426. doi:10.1016/j.anbehav.2004.03.016
- Nelson BS (2000) Avian dependence on sound pressure level as an auditory distance cue. *Animal Behaviour* **59**, 57–67. doi:10.1006/anbe.1999.1278
- Reby D, McComb K (2003a) Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal Behaviour* **65**(3), 519–530. doi:10.1006/anbe.2003.2078
- Reby D, McComb K (2003b) Vocal communication and reproduction in deer. *Advances in the Study of Behavior* **33**, 231–264. doi:10.1016/S0065-3454(03)33005-0
- Reby D, Cargnelutti B, Joachim J, Aulagnier S (1999) Spectral acoustic structure of barking in roe deer (*Capreolus capreolus*). Sex-, age- and individual-related variations. *Comptes Rendus de l'Académie des Sciences, Series III* **322**(4), 271–279.
- Reby D, Hewison M, Izquierdo M, Pépin D (2001) Red deer (*Cervus elaphus*) hinds discriminate between the roars of their current harem-holder stag and those of neighbouring stags. *Ethology* **107**, 951–959. doi:10.1046/j.1439-0310.2001.00732.x
- Reby D, McComb K, Cargnelutti B, Darwin C, Fitch WT, Clutton-Brock T (2005) Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proceedings. Biological Sciences* **272**, 941–947. doi:10.1098/rspb.2004.2954
- Reby D, Charlton BD, Locatelli Y, McComb K (2010) Oestrous red deer hinds prefer male roars with higher fundamental frequency. *Proceedings. Biological Sciences* **277**, 2747–2753. doi:10.1098/rspb.2010.0467
- Sanvito S, Galimberti F (2003) Source level of male vocalizations in the genus *Mirounga*: repeatability and correlates. *Bioacoustics* **14**, 47–59. doi:10.1080/09524622.2003.9753512
- Smith MJ, Harper DGC (1995) Animal signals: models and terminology. *Journal of Theoretical Biology* **177**, 305–311. doi:10.1006/jtbi.1995.0248
- Vannoni E, McElligott AG (2008) Low frequency groans indicate larger and more dominant fallow deer (*Dama dama*) males. *PLoS One* **3**(9), e3113. doi:10.1371/journal.pone.0003113
- Volodin I, Volodina E, Frey R, Carranza J, Torres-Porras J (2013) Spectrographic analysis points to source-filter coupling in rutting roars of Iberian red deer. *Acta Ethologica* **16**(1), 57–63. doi:10.1007/s10211-012-0133-1
- Welch AM, Semlitsch RD, Gerhardt H (1998) Call duration as an indicator of genetic quality in male gray tree frogs. *Science* **280**, 1928–1930. doi:10.1126/science.280.5371.1928
- Wiley RH, Richards DG (1982) 'Adaptations for acoustic communication in birds: sound transmission and signal detection.' (Academic Press: New York)
- Wroblewski EE, Murray CM, Keele BF, Schumacher-Stankey JC, Hahn BH, Pusey AE (2009) Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour* **77**(4), 873–885. doi:10.1016/j.anbehav.2008.12.014
- Wyman MT, Mooring MS, McCowan B, Penedo MCT, Hart LA (2008) Amplitude of bison bellows reflects male quality, physical condition and motivation. *Animal Behaviour* **76**, 1625–1639. doi:10.1016/j.anbehav.2008.05.032
- Wyman MT, Mooring MS, McCowan B, Penedo MCT, Reby D, Hart LA (2012) Acoustic cues to size and quality in the vocalizations of male North American bison, *Bison bison*. *Animal Behaviour* **84**, 1381–1391. doi:10.1016/j.anbehav.2012.08.037