



Articles

Fallow bucks get hoarse: vocal fatigue as a possible signal to conspecifics

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Many studies of sexually selected vocal communication assume that calls remain stable throughout the breeding season. However, during this period, physiological and social factors change and these can have strong effects on the structure of calls and calling rates. During the rut, fallow bucks, *Dama dama*, reduce their feeding and increase the time and energy spent on vocalizing and fighting to gain matings, and consequently their body condition declines greatly. The availability of matings and intensity of competition between males also change. Therefore, we predicted that male vocal signalling would vary over time in response to the changing intersexual and intrasexual selective environment. We measured the structure of fallow buck groans and the groaning rate throughout the rut. Fundamental frequency-related parameters were highest at the beginning and at the end of the rut, and lowest during the middle when most matings occur. The fundamental frequency perturbation along the groan (jitter) remained stable throughout the rut, whereas the number of pulses and duration of the groans decreased linearly. The minimum formant dispersion did not vary significantly over the rut. Groaning rate increased towards the middle of the rut and then rapidly decreased afterwards. We suggest that changes in the structure of groans and groaning rate are associated with the declining body condition of males and variation in the availability of mating opportunities. The breakdown in some aspects of call structure towards the end of the breeding season may represent an honest signal that could be widespread in other species.

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Recent research on mammal vocal communication has focused on determining the functions of calls by elucidating the information they convey to receivers (Fischer et al. 2002; Torriani et al. 2006; Pfefferle et al. 2007; Theis et al. 2007). The information transmitted through vocalizations can be encoded in different aspects of a call, such as the acoustic structure and calling rate (Clutton-Brock & Albon 1979; McComb 1991; McElligott & Hayden 1999; Fischer et al. 2004). These vocal features may be affected by both social and physiological factors and therefore vary over both short and longer timescales (Koren & Geffen 2009).

Social context-related changes in the acoustic structure of calls generally reflect changes in arousal or motivation of an animal (Elowson & Snowdon 1994; Mitani & Brandt 1994; McElligott & Hayden 1999; Rukstalis et al. 2003). Intensity of arousal might be communicated in vocal signals by altered patterns of calling in space and time and/or by changes in the acoustic parameters of calls (Fichtel & Hammerschmidt 2002; Fischer et al. 2002;

Bachorowski & Owren 2003). For example, adult male baboons, *Papio cynocephalus ursinus*, produce the 'wahoo' call at far greater rates during aggressive contests than comparatively low-arousal circumstances and the acoustic structure of these vocalizations changes following protracted calling (Fischer et al. 2002, 2004). Prolonged calling associated with high physical activity has been shown to alter both the frequencies of calls and the calling rate (Liénard & Di Benedetto 1999; Fischer et al. 2004).

Mechanisms at the basis of the different motivational states of the caller may contribute to the context-dependent acoustic modifications (Morton 1977, 1982). Short-term variation in the arousal state may alter respiration and therefore vocal production (Titze 1994; Scherer 2003). Moreover, fluctuations in hormone levels occurring during social interactions may influence both anatomical and neurophysiological structures involved in the production of vocal signals and therefore result in modified acoustic patterns (Rolf & Fischer 1990; Dabbs & Mallinger 1999; Semple & McComb 2000; Yamaguchi & Kelley 2002; Manteuffel et al. 2004).

To understand the evolution of any vocal signal, it is important to explore the source of its variation by investigating short-term changes in both the acoustic structure of calls and other aspects of vocal behaviour (e.g. calling rate), which might indicate different communicative functions. Modification of the acoustic structure of the call

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within individuals over time may have implications for individual recognition, whereas changes in the calling rate may provide information on the current motivation and condition of the caller (Jorgensen & French 1998; Rukstalis et al. 2003; Theis et al. 2007).

The sexually selected calls produced by fallow bucks provide an excellent model for investigating short-term vocal changes in mammals. When they become socially mature (>4 years old), males do not vocalize for most of the year, and then have an extremely intense period of vocal activity during the rut. At this time they produce a repetitive and stereotypic call known as a groan (Reby et al. 1998; Vannoni & McElligott 2007). Two types of groans can be identified: the common and the harsh groan. Harsh groans are generally only produced during intense chasing and herding behaviour, whereas common groans are given in all contexts (Vannoni & McElligott 2007). The acoustic structure of fallow buck groans is individually distinctive and contains information on male body size and dominance status (Reby et al. 1998; McElligott et al. 2006; Vannoni & McElligott 2007, 2008). Higher-ranked males start groaning several weeks before the first matings take place, and they maintain very high groaning rates over prolonged periods during the peak of the rut when most matings take place (McElligott & Hayden 1999; McElligott et al. 1999). Therefore several aspects of the vocal behaviour of fallow bucks represent honest signals of male quality potentially available to other males and females.

Variation in the number of nearby competing males and oestrous females during the rut determines short-term changes in arousal and motivation of the males and these affect their vocal behaviour (McElligott & Hayden 1999). Furthermore, the dramatic decline in body condition that males undergo at this time (McElligott et al. 2003) may also affect both physiology and behaviour, including vocal display. Male vocal activity is generally reduced over the last days of the rut and males often appear fatigued (E. Vannoni & A.G. McElligott, personal observation). Moreover, groans given at the end of the rut usually sound noisier and higher in pitch (fundamental frequency, F_0) than those given at the beginning (Reby et al. 1998; E. Vannoni & A.G. McElligott, personal observation). Changes in vocal behaviour during the rut may therefore be used as a potential source of information for competing males that may be monitoring the motivation and condition of their opponents. Fights between males differing widely in terms of dominance rank are infrequent early in the rut, but become more frequent towards the end (McElligott et al. 1998). This supports the suggestion that changes in the condition of dominant males are detectable to conspecifics. It additionally or alternatively supports the hypothesis that the threshold criteria used in the cost-benefit assessment of challenging a more dominant individual varies during the rut in response to changing availability of oestrous females. Similarly, both long-term investment in male vocal display and short-term indicators of male current condition may be used by females to evaluate prospective mates (Komers et al. 1999; McElligott et al. 1999; Farrell 2001). There is already good evidence to show that male and female deer are able to perceive relatively small changes in call structure and use them for intrasexual assessment or mate choice, respectively (Reby et al. 2005; Charlton et al. 2007a, b).

In this study, we investigated changes in the acoustic structure of common groans and groaning rate throughout the rut for the same individuals. We first measured the acoustic parameters of groans recorded at multiple time points, and then examined whether they had changed. We were therefore able to assess whether the various components of male vocal signalling would vary in response to the known changes in body condition, and the changes in the availability of oestrous females and therefore intensity of sexual selection, that occur during the rut.

METHODS

Study Site and Population

The study was carried out on a herd of European fallow deer in Phoenix Park (53°22'N, 6°21'W), Dublin, Ireland. The ages and identities of the males used in this study were known because they had been tagged as fawns, as part of routine management of the herd by the park authorities.

Recording and Selection of Groans

Recordings were made between dawn and sunset using a Sennheiser MKH70 directional microphone connected to a Sony digital audio tape recorder, DAT-TCO D100. Groans were recorded at a distance of 10–50 m from the vocalizing animals. We only considered common groans with low levels of background noise for analysis.

Vocalizations were imported into a computer using Avisoft-SAS-Lab Pro 4.38 (Avisoft Bioacoustics, Berlin, Germany) at a sampling rate of 22.05 kHz and saved in WAV format, and at 16-bit amplitude resolution (Vannoni et al. 2005; Vannoni & McElligott 2007). Recordings were then down-sampled to 16 kHz for a better frequency resolution. Narrow-band spectrograms of groans (FFT method, window length = 0.03 s, time step = 1000, frequency step = 250, frequency resolution = 20 Hz, Gaussian window shape, dynamic range = 35 dB) were edited using Praat 4.5.01 (P. Boersma & D. Weenink, University of Amsterdam, The Netherlands).

Recordings were carried out during three consecutive breeding seasons (2002, 2003 and 2004) between 8 October and 31 October. This period includes some days before the first matings occur (mid-October; McElligott et al. 1999), and we refer to it as the rut. We included in our analysis only males for which we had good recordings over a period of at least 6 days throughout the rut. These males were between 5 and 8 years old because this is the age range that contains the most highly vocal individuals (McElligott et al. 1999). Moreover, they had reached their asymptotic size and were not undergoing large changes associated with senescence (McElligott et al. 2002).

Sound Analysis and Phase of the Rut

Groans are low-pitched vocalizations and are generally characterized by a pulse train structure (Fig. 1). The pulses represent the vibrations of the vocal folds, and the number of pulses divided by duration determines the fundamental frequency (F_0) of the call. Although closely interrelated, we included the number of pulses, F_0 and duration of calls in our detailed analyses because any or all of these variables could be perceived by conspecifics. F_0 can also be defined as the inverse of the interpulse interval and this can be measured as the distance between consecutive pulse onsets. Distances between pulses were measured automatically from the envelope (amplitude versus time) of the signal by using pulse train analysis in Avisoft-SASLab Pro 4.38 (Vannoni & McElligott 2007). We calculated the values of the F_0 along the groan and then averaged these values to obtain the mean F_0 ($F_{0\text{mean}}$). Because the fundamental frequency varies over the duration of the groan, the minimum and the maximum F_0 ($F_{0\text{min}}$ and $F_{0\text{max}}$) were also included in the analysis. From the envelope of the signal, we also calculated the number of pulses (Pulses) and the duration of the groan (Duration) as the distance between the onset of the first pulse and the end of the last one. Finally, we quantified the variation in F_0 along the call using a measure of F_0 perturbation, known as Jitter (Titze 1994). Jitter has been used as a measure of vocal quality in mammals (Rendall 2003) and it has been shown to vary

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