Fallow Bucks Attend to Vocal Cues of Motivation and Fatigue

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ABSTRACT

Vocalizations encode a range of information about the caller, and variation in calling behavior and vocal structure may provide listeners with information about the motivation and condition of the caller. Fallow bucks only vocalize during the breeding season and can produce more than 3000 groans per hour. Males modulate their calling rates, calling faster when other calling males and/or females are nearby. Groans also reveal caller fatigue, becoming shorter and higher pitched toward the end of the rut. Thus, fallow deer groans vary both over very short (minute to minute) and longer timescales (the rut). However, no studies have investigated how intraindividual acoustic variation in fallow deer groans is perceived and how the information is utilized. Using playback experiments, we examined if fallow bucks can extract information about callers from groans and how groaning rate and fatigue affect the perceived competition posed by a caller. Males became attentive sooner and remained attentive for longer during high-rate playbacks than low-rate playbacks. Furthermore, males were attentive for longer during playback of early rut groans that are indicative of males in better condition. Over short timescales, fallow bucks gain information about the motivation of callers through groaning rates. While over longer timescales, males can detect declines in call quality, corresponding to the loss of condition in callers. Thus, over the course of the rut, fallow bucks can extract honest information from dynamic vocalizations to continually assess the current state of conspecifics.

Introduction

Acoustic signals can encode and transmit a range of biologically salient information, including physical condition, competitive ability, motivational state, and fatigue, and these are key components of sexual selection. Vocalizations may provide information to both competitors and potential mates (Reby and McComb 2003a, 2003b; Bradbury and Vehrencamp 2011). Information can be encoded in a number of features of a vocalization, such as the calling rate and acoustic parameters, and these aspects may vary over both short and longer timescales, reflecting changes in the social, physical, and/or physiological states of the signaller (Gerhardt 1992).

Honest signals of an individual's quality must be costly to produce or maintain and be condition dependent, such that only individuals in good condition can afford the expenditure of their production (Zahavi 1975, 1977; Andersson 1986; Grafen 1990). Quality signals transmit information about the genetic and nongenetic characteristics of an individual (Andersson 1994) and thus reflect condition-dependent phenotypic traits (Bergeron et al. 2011). Information indicating the quality of an individual within vocalizations is typically a consequence of physical or physiological constraints that influence sound production (Fitch 2004). Thus, these signals broadcast competitive qualities, such as body size, weight, age, hormone levels, or dominance rank, to both rivals and potential mates (e.g., giant pandas, *Ailuropoda melanoleuca*: Charlton et al. 2011; baboons, *Papio cynocephalus ursinus*: Fischer et al. 2004; red deer, *Cervus elaphus*: Reby and McComb 2003a; and fallow deer, *Dama dama*: Vannoni and McElligott 2008, 2009).

Changes in the arousal or motivational state of an animal can be reflected in changes to the acoustic structure of vocalizations and may be related to social contexts such as the composition or reproductive state of the nearby conspecific population (Elowson and Snowdon 1994; Mitani and Brandt 1994; McElligott and Hayden 1999; Eckenweber and Knornschild 2013). Levels of arousal are likely to be encoded in parameters such as the calling rate, call duration, amplitude, and pitch (Ehret 2006; Briefer 2012). For instance, short-term variation in arousal may alter an individual's respiration rate and subsequently vocal production (Titze 1994; Scherer 2003). In red deer, approach or calling by a neighboring stag induces increased calling in a harem holder, and rates tend to increase as individuals get closer (Clutton-Brock and Albon 1979), potentially reflecting the increase in motivation or arousal of the calling individuals. Similar effects of neighboring individuals on vocal activity have been observed in a number of taxa, including birds (Liu 2004), pinnipeds (Fernandez-Juricic et al. 2001; Kunc and Wolf 2008), and bats (Eckenweber and Knornschild 2013).

How information is encoded in vocal signals is largely governed by the morphology of the vocal apparatus and the influence of physiological traits (Taylor and Reby 2010). The production of mammalian vocalizations can be described by the source-filter theory (Fant 1960; Taylor and Reby 2010). Vocalizations are generated by the vibration of the vocal folds (the source) and are then filtered by the supralaryngeal vocal tract (the filter). The vibration of the vocal folds determines the fundamental frequency of the vocalization, and the source is subsequently shaped by the vocal tract, resulting in spectral peaks (formants) formed by selectively dampened or enhanced frequencies (Fant 1960; Titze 1994). The fundamental frequency of a vocalization is influenced by factors including the length, longitudinal stresses, and the tissue density of the vocal folds (Titze 1994). Because the larynx is not constrained by the surrounding skeletal structure, and vocal folds are highly sensitive to testosterone, fundamental frequency is a poor indicator of body size but may provide cues about the physiological state of the caller (Fitch 1997; Fitch and Giedd 1999; Evans et al. 2006; Charlton et al. 2011). By contrast, the length of the vocal tract is largely restricted by surrounding skeletal structures and thus closely linked to body size. Consequently, formant frequencies are more reliable indicators of body size and less likely to vary due to changes in physiology (Fitch 1997; Fitch and Giedd 1999) but may still be influenced by factors such as stress (Briefer 2012). Playbacks of modified vocalizations have shown that both male and female red deer attend to changes in formants that simulate callers of different body sizes (Reby et al. 2005; Charlton et al. 2007a, 2007b). Similarly, dogs (*Canis familiaris*) played growls in which the formant dispersion was representative of either a small dog or a large dog, typically looked toward an appropriately size-matched model (Taylor et al. 2011).

Communication systems are vital to the mediation of interactions between individuals, such as intrasexual competition and agonistic encounters (Owings and Morton 1998; Bradbury and Vehrencamp 2011). Vocal communication systems evolve through a feedback loop linking vocal production mechanisms, the

acoustic structure of signals, and the perception and behavior of receivers (Taylor and Reby 2010). To understand the evolution of a vocal signal, it is vital to examine its variation at the level of vocal behavior, acoustic structure, and associated behavioral response from conspecifics (Vannoni and McElligott 2009; Taylor and Reby 2010). The sexually selected vocalizations of the fallow deer (*D. dama*) are an ideal system in which to examine the perception of motivation and condition-related cues in vocal displays. Fallow deer are a highly polygynous and size-dimorphic species (McElligott and Hayden 2000; McElligott et al. 2001). Males are silent for most of the year but produce a vocalization known as a "groan" during a short and discrete period around the breeding season or rut (late September to early November in the northern hemisphere). Common groans are short, low-pitched stereotyped calls that are characterized by a series of pulses (Reby et al. 1998; Vannoni and McElligott 2007) and are typically produced by mature males ($\geq$4 years old; McElligott et al. 1999). Groans contain 6 formants within the first 2.5 kHz. Males retract the larynx during vocalizations causing elongation of the vocal tract and hence decreases in formant frequency and dispersion along the groan (Fitch and Reby 2001; McElligott et al. 2006). The acoustic structure of fallow buck groans encodes information about the identity, size, age, and dominance of the caller (Reby et al. 1998; Vannoni and McElligott 2007, 2008, 2009; Briefer et al. 2010). However, because these traits are encoded within the same parameters, identity information is typically only stable within a breeding season, with changes to groan structure between seasons reflecting changes in age and rank (Briefer et al. 2010). Higher ranked males commence groaning several weeks before mating starts, and long-term investment in groaning throughout the rut is related to mating success (McElligott et al. 1999).

The rate at which fallow bucks groan varies in relation to the number of nearby competing males and estrous females because the presence and composition of surrounding conspecifics affect the arousal and motivation of calling individuals (McElligott and Hayden 1999, 2001; Naulty et al. 2013). Male groaning rate is lowest when no other individuals are in the immediate vicinity, but increases when other males are nearby, and again when estrous females are present. When both estrous females and other vocal males are present, bucks groan approximately 55 times per minute, peaking at approximately 70 times per minute immediately post-copulation (McElligott and Hayden 1999). McElligott and Hayden (1999) found that, in all contexts involving the presence of females, increases in groaning rate were associated with the presence of other vocal males, suggesting that the information conveyed by groaning rate was primarily a threat display directed at rival males.

During the rut, males largely cease feeding while increasing investment in mating-related behaviors, including vocal displays (Clutton-Brock et al. 1988). As a result, they undergo a dramatic decline in body condition during the rut, losing an average of 26% of their body weight (McElligott et al. 2003). During this time, changes to the acoustic structure of groans are also evident (Figure 1). The minimum fundamental frequency of groans is lowest around the middle of the rut when matings peak. Higher ranking fallow bucks produce groans with lower minimum fundamental frequency early in the rut, but the number of pulses and the duration of groans decrease toward the end of the rut (Vannoni and McElligott 2008, 2009). Vannoni and McElligott (2009) suggested that the production of low-pitched groans at high rates may require greater effort and control than higher pitched groans or lower rates. Thus, the groans of fallow bucks are potentially honest signals of a male's current quality and body condition, and any breakdown in the acoustic structure of calls is probably linked to physical exhaustion.

In this study, we used playback experiments to investigate the response of mature fallow bucks to changes in groaning rates and to fatigue-linked changes in the acoustic structure of groans. These parameters have been suggested to indicate changes in arousal and physical condition of callers. We first tested whether males responded differently to low and high groaning rates, indicative of low and high arousal rates in callers. Secondly, we examined the ability of males to detect and respond to the changes

in acoustic structure seen between early and late rut groans. If males can perceive short-term differences in groan rate, high groaning rates, which are hypothesized to indicate a more aroused/competitive caller, should be treated as a greater threat (Clutton-Brock and Albon 1979). Similarly, if bucks perceive changes in an individual's groans between the early and late rut, showing a decline in quality over time, late rut groans should represent a lower threat. By contrast, if bucks simply recognize individuals, or cannot detect the changes, no difference between early and late rut groans should be observed. Such perceptual abilities would allow fallow bucks to extract contemporary information about a caller's arousal and fatigue states and would experimentally demonstrate that fallow deer perceive groans as honest but yet highly variable sources of caller information.

Figure 1. Spectrograms (top) and oscillograms (bottom) of an early and a late rut groan recorded from the same individual.
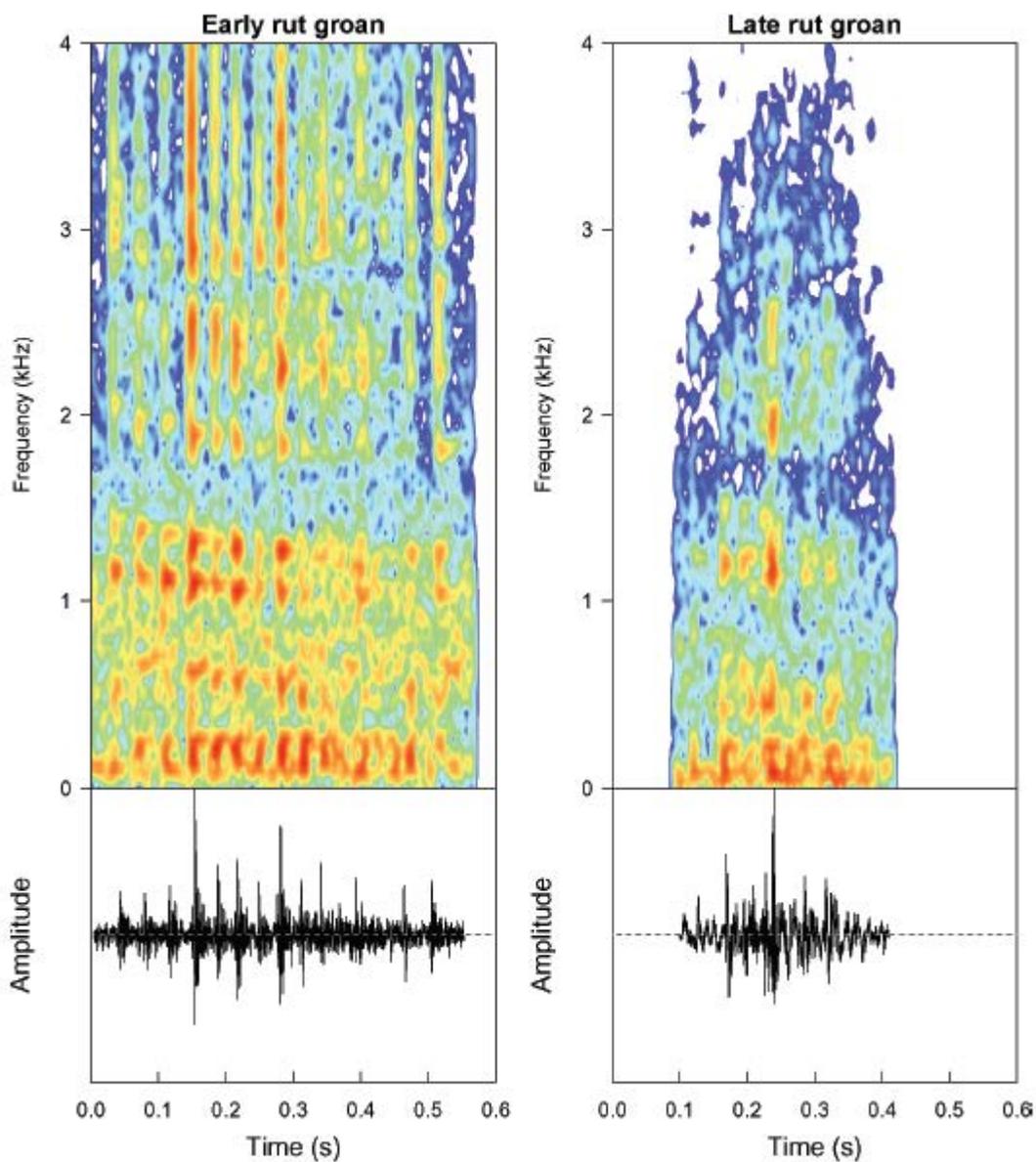
Methods

Study site and animals

We conducted this study in Petworth Park, West Sussex, United Kingdom (283 ha, 50°59′ 16″ N, 0°36 ′ 39″ W) during September and October 2011. The park has a population of approximately 700 fallow deer (Whitby D, personal communication). It is open to the public and the deer are therefore habituated to the presence of people. During the rut, some males in Petworth Park congregate on a traditional lek area (Clutton-Brock et al. 1988). Throughout the 2011 rut (October), at least 25 males were observed on the lek. The territorial behavior and habituation to people allow for approaches close enough to conduct playback experiments (Clutton-Brock et al. 1988).

We visually identified animals using a combination of pelage color type and antler morphology. Commencing in September, prior to the rut, we identified a subset of the adult males using a combination of photos, sketches, and notes of key features, such as obvious markings or antler formations. Only males later observed holding lek territories and vocalizing were used in the playback experiments (during October).

Vocalization recording site and recording procedure

The design of this study made it necessary to have recordings from both early and late in the rut. Because of this, we used recordings that had been previously collected, between 2002 and 2004, from fallow bucks in Phoenix Park (709 ha), Dublin, Ireland (53°21′ 36″ N, 6°19′ 32″ W). The population during this time was approximately 600 individuals (Vannoni et al. 2005). The recording procedure is described in Vannoni et al. (2005) and Vannoni and McElligott (2009). Comparison of the groans of individuals from these 2 populations showed that they are acoustically very similar and therefore suitable for use in this study (Stachowicz et al. 2014).

Playback signal construction
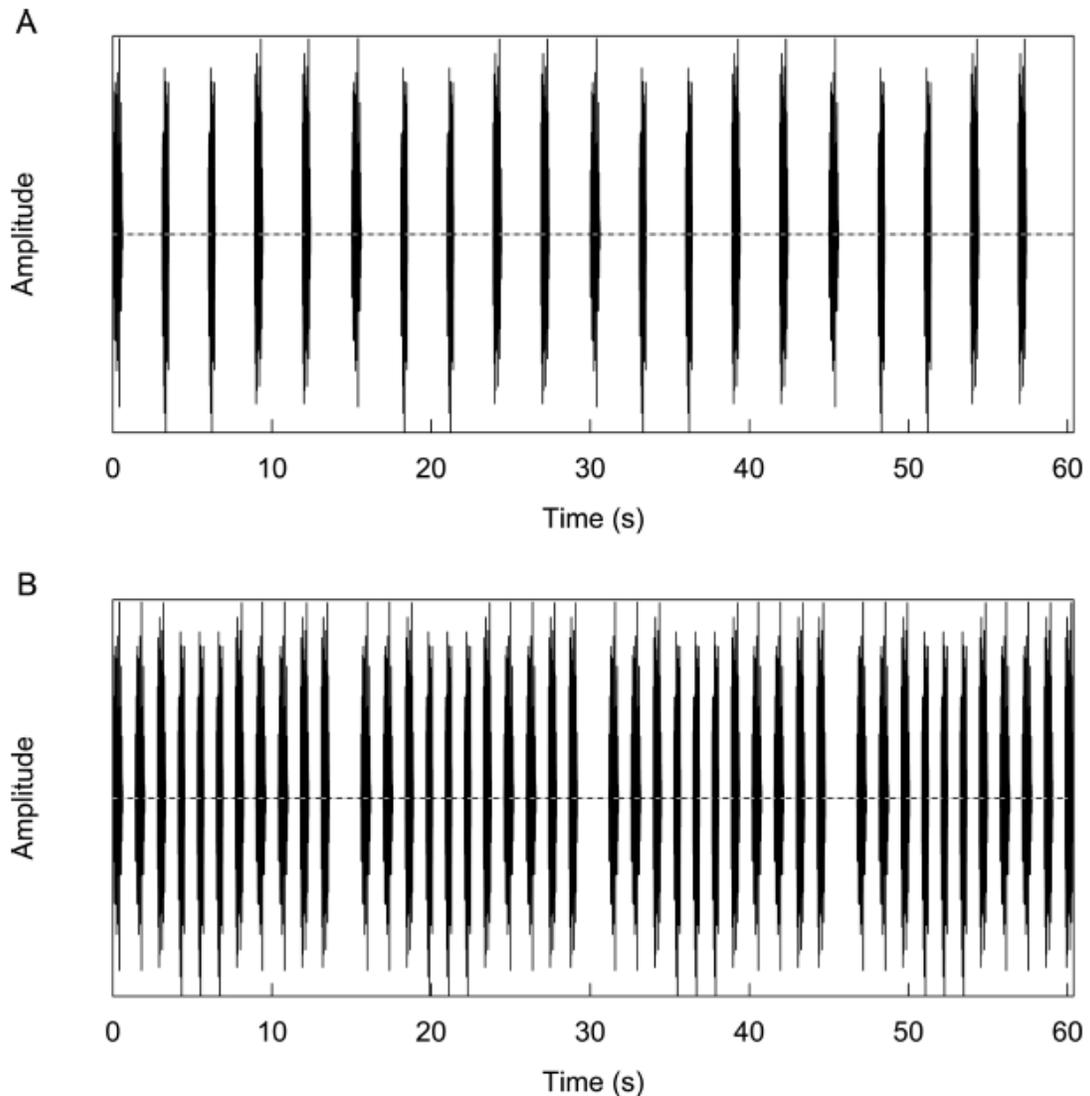
Low versus high groan rate
To create playback stimuli with varied groaning rates, pairs of 1-min sequences of groans were constructed with rates of on average 20 (low rate) and 50 (high rate) groans per minute (Figure 2; McElligott and Hayden 1999), corresponding to the hypothesized low and high motivation/arousal states. Sequences were constructed using 2‑3 groans, with high signal-to-noise ratios, recorded from the same individual but from different calling bouts. To control for the possible variation in the acoustic structure of groans in relation to rate (e.g., groan fundamental frequency and formant frequency increase in contexts with higher groaning rates; Charlton and Reby 2011), the same groans were used to construct both the low- and high-rate exemplars from each individual. Calls of different individuals were used to construct each pair of sequences. Groans were taken from recordings made during the "early rut" (Vannoni and McElligott 2009). Sequences were normalized to 95% and saved as 44.1 kHz, 16 bit.wav format sound files for playback using Adobe Audition 3 (Adobe Systems Incorporated, San Jose, CA).

Early versus late rut groans
Playback stimuli of early and late rut groans were constructed using groans recorded in the "early rut" and "late rut" periods (Figure 1; Vannoni and McElligott 2009). To control for differences in quality between bucks, pairs of early and late rut playbacks were constructed using groans from the same individual. Two to 3 groans of high signal-to-noise ratio from the same individual but different calling bouts were used from each period. Calls from different individuals were used for each pair of early and late rut groan playbacks. To ensure that the groans used in the playbacks were representative of the changes

observed by Vannoni and McElligott (2009) throughout the rut, we compared the number of pulses, the duration, and the mean fundamental frequency of the selected early and late rut groans using Praat (Boersma and Weenink 2012). As in Vannoni and McElligott (2009), the early rut groans used in this study had more pulses (early: mean $\pm$ standard deviation [SD] = 11.6 $\pm$ 1.5, late: mean $\pm$ SD = 8.9 $\pm$ 1.7, N = 16, paired t-test: $t15$ = 3.96, P = 0.001) and longer durations (early: mean $\pm$ SD = 0.49 $\pm$ 0.046 s, late: mean $\pm$ SD = 0.37 $\pm$ 0.070 s, N = 16, paired t-test: $t15$ = 4.24, P = 0.001) than late rut groans. Similarly early rut groans had lower minimum fundamental frequencies than late rut groans (early: mean $\pm$ SD = 16.48 $\pm$ 4.47 Hz, late: mean $\pm$ SD = 20.75 $\pm$ 4.10 Hz, N = 16, paired t-test: $t15$ = −2.34, P = 0.034), and as in Vannoni and McElligott (2009), they did not differ in the mean fundamental frequency (early: mean $\pm$ SD = 23.97 $\pm$ 2.73 Hz, late: mean $\pm$ SD = 24.11 $\pm$ 3.19 Hz, N = 16, paired t-test: $t15$ = −0.20, P = 0.846). Pairs of 40-s long sequences of early and late rut groans from the same individual with rates of approximately 40 groans per minute were constructed, normalized to 95%, and saved as 44.1 kHz, 16 bit.wav format sound files.

Figure 2. Examples of (A) low groaning rate and (B) high groaning rate playback sequences.

Playback procedure and data analysis

Playbacks of low versus high groaning rate stimuli were conducted between 12 and 21 October in the lead up to and around the estimated peak of mating activity (20‑30 October; Clutton-Brock et al. 1988). Playbacks of early versus late rut stimuli were conducted between 22 and 27 October in the days following the peak of mating activity (Farrell et al. 2011). Playbacks were only presented to mature males that were observed to be holding territories on the lek and thus likely to be among the most successful individuals within the population (Clutton-Brock et al. 1988). Each experiment was conducted on 16 males, 9 of which were tested in both experiments. However, these individuals did not receive playbacks from the same callers, and experiments were separated by a minimum of 2 days.

Calls were broadcast at the mean peak amplitude of the natural calling bouts, measured using 3 individuals in Petworth Park, with a handheld Bruel & Kjar Type 2215 Precision Sound Level Meter Octave Analyzer (Bruel & Kjar Sound & Vibration Measurement A/S, Narum, Denmark), from approximately 15 m (mean $\pm$ SD = 51 $\pm$ 3 dBA). Playbacks were broadcast from a Skytronic TEC076 (AVSL Group, Manchester, United Kingdom) portable amplifier and speaker system connected to an Edirol R-09 (Roland Corporation, Los Angeles, CA) via a 40-m lead. The speaker was located 15‑20 m from the subject and was obscured from view using camouflage netting. The experimenter controlled the playback at a distance of 40 m from the speaker, and where possible, obscured from the subjects' view. The speaker was placed at the appropriate location a minimum of 5 min prior to the playback to allow animals to resume their normal behavior before the tests. All presentations were recorded using a Canon LEGRIA video camera for later analysis.

Playbacks of low versus high groan rates consisted of a 1-min silence control period to assess the baseline activity of the subject, followed by two 1-min periods of playback (e.g., high then low) separated by 1 min of silence. Early versus late rut groan playbacks consisted of a 40-s silence control, followed by two 40-s playback periods (e.g., early then late) separated by 40 s of silence. In both experiments, the order of presentation of the playback stimuli was quasi-randomized.

The response of subjects to the playbacks was measured from the videos of the tests by an observer who was blind to the presentation order. For each period, the observer measured the latency, from the beginning of the period until the subject became attentive, and the duration of attentive behavior during the period. An attentive subject was a subject looking toward the speaker, often also orientating its ears toward the speaker and changing its body orientation or posture. The latency to become attentive to the speaker and the duration of attention were measured in the same way during the control period to account for any changes in behavior due to the presence of a foreign object. If a subject did not become attentive during a period, the maximum duration of the period was used as the latency and the duration was zero. *t*-Tests were used to compare the acoustic parameters of early and late rut groans and Wilcoxon signed-ranks tests were used to compare the responses of subjects during playbacks. Statistical analyses were conducted using SPSS 16.0 for Windows (SPSS Inc., Chicago, IL).

Results

Low versus high groan rate

Fallow bucks displayed a significant increase in their attentiveness (i.e., looking and orienting toward the speaker) during the playback of the groans of another male, regardless of the rate, compared with the control period. This increase was observed in both the latency to become attentive (Figure 3A; control: mean $\pm$ SD = 46.31 $\pm$ 15.31 s; low rate: mean $\pm$ SD = 10.38 $\pm$ 14.36 s; high rate: mean $\pm$ SD = 6.06 $\pm$ 14.54 s; control‑low rate‑Wilcoxon signed-ranks test: Z = −3.41, N = 16, P = 0.001; control‑high rate‑

Wilcoxon signed-ranks test: $Z = -3.43$, $N = 16$, $P = 0.001$) and the duration of attentive behavior (Figure 3B; control: mean $\pm$ SD = 3.19 $\pm$ 3.90 s; low rate: mean $\pm$ SD = 26.75 $\pm$ 14.32 s; high rate: mean $\pm$ SD = 42.0 $\pm$ 19.93 s; control‑low rate‑Wilcoxon signed-ranks test: $Z = -3.42$, $N = 16$, $P = 0.001$; control‑high rate‑Wilcoxon signed-ranks test: $Z = -3.41$, $N = 16$, $P = 0.001$).

Males showed greater attentiveness to high-rate playbacks than they did to low-rate playbacks. They became attentive sooner during high-rate playbacks (Figure 3A; low rate‑high rate–Wilcoxon signed-ranks test: $Z = -2.33$, $N = 16$, $P = 0.020$) and remained attentive for longer compared with low-rate playbacks (Figure 3B; low rate‑high rate–Wilcoxon signed-ranks test: $Z = -2.23$, $N = 16$, $P = 0.026$). Thus, fallow bucks are sensitive to changes in groaning rates and perceive higher rates as more threatening than lower rates.

Early versus late rut groans

Both early and late rut groans elicited attention above the control period. Males became attentive sooner (Figure 4A; control: mean $\pm$ SD = 37.06 $\pm$ 9.42 s; early rut groans: mean $\pm$ SD = 8.44 $\pm$ 9.06 s; late rut groans: mean $\pm$ SD = 13.81 $\pm$ 12.31 s; control‑early rut groans‑Wilcoxon signed-ranks test: $Z = -3.26$, $N = 16$, $P = 0.001$; control‑late rut groans‑Wilcoxon signed-ranks test: $Z = -3.41$, $N = 16$, $P = 0.001$) and were attentive for longer (Figure 4B; control: mean $\pm$ SD = 0.62 $\pm$ 1.71 s; early rut groans: mean $\pm$ SD = 24.38 $\pm$ 11.44 s; late rut groans: mean $\pm$ SD = 12.44 $\pm$ 10.98 s; control‑early rut groans‑Wilcoxon signed-ranks test: $Z = -3.51$, $N = 16$, $P = 0.001$; control ‑ late rut groans ‑ Wilcoxon signed-ranks test: $Z = -3.41$, $N = 16$, $P = 0.001$) during the playback periods than the control periods.

Fallow bucks responded differently to early rut groans than to late rut groans. This difference was observed in the duration of the attentive response, but not in the latency to become attentive. Males spent more time attending to the playback of early rut groans than to late rut groans (Figure 4A; early rut groans‑late rut groans–Wilcoxon signed-ranks test: $Z = -3.39$, $N = 16$, $P = 0.001$) but showed no difference in the latency to become attentive to these playbacks (Figure 4B; early rut groans‑late rut groans–Wilcoxon signed-ranks test: $Z = -1.48$, $N = 16$, $P = 0.140$). This demonstrates that males can perceive fatigue-related changes in groans and react differently to early and late rut groans from the same individual, attending more to early rut groans that are indicative of males in better condition.

Discussion

We investigated if fallow bucks perceive potentially important information in the highly variable vocalizations of rival males. Our results show that they perceive changes in groaning rates, as well as changes linked to fatigue, within their natural ranges. Males were more attentive to groans presented at higher calling rates than to lower rates and attended more to early rut compared with late rut groans. Calling rate and the degradation of groan quality have previously been suggested to indicate changes in arousal and physical condition of callers. We suggest that fallow bucks are able to perceive variations in groans and groaning behavior, in order to extract contemporary information about a caller's arousal and fatigue states in groans. Dynamic cues to an individual's quality and motivation have the potential to provide honest information about short-term changes in the state of the individual, whereas static cues are more likely to provide information about long-term condition (Clutton-Brock and Albon 1979; Gerhardt 1991; Vehrencamp 2000; Ehret 2006; Schehka et al. 2007; Wyman et al. 2008). Competitors should therefore be able to take advantage of continuously changing dynamic cues to judge which rival is most vulnerable to be challenged and when to fight.

Figure 3. The response of males to playback of low- or high-rate groans or the control period. (A) The latency to become attentive and (B) the duration of attention.

A

B
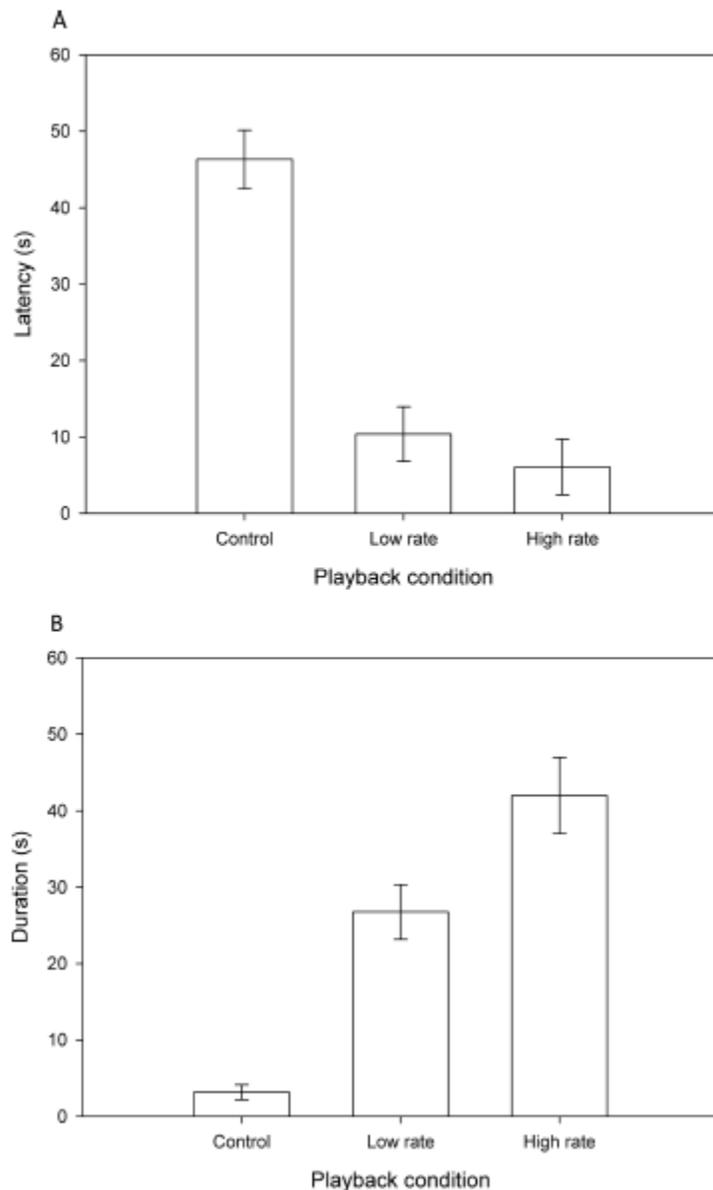
Variation in calling rates over shorter timescales may reflect the contemporary condition and motivation of the caller (McElligott and Hayden 1999, 2001; Reby and McComb 2003b). Fallow bucks appear to use groaning rates to perceive the motivation and subsequent level of threat posed by conspecifics. Bucks were attentive sooner during playback of high-rate groans and remained attentive for substantially longer compared with playback of low-rate groans. The high groaning rate presented in this study corresponds to the mean rate observed when callers are in the presence of vocal males and estrous females during the rut (McElligott and Hayden 1999). Conversely, the low groaning rate corresponds to the mean rate observed when nonvocal males are present without females (McElligott and Hayden 1999). McElligott and Hayden (1999) observed that, in all contexts involving the presence of females, increases in groaning rate were associated with the presence of other vocal males, suggesting that the information conveyed by

groaning rate was primarily a threat display directed at rival males. Short-term increases in rate are likely to reflect higher arousal in callers (McElligott and Hayden 1999; Charlton and Reby 2011). Although linked to the presence of other vocal males, because the highest rates of groaning are observed in contexts where estrous females are present, it is possible that the increased attention paid to high-rate calls reflects males using groan rate as a cue to locate estrous females within the population. However, the differences in attentiveness to early and late rut groans played at the same high rate suggests that males are gaining information about the caller and not simply looking for the presence of potential mates. Further, irrespective of short-term changes in groaning context, groaning rates show a curvilinear pattern through the rut, increasing toward the peak of the rut when the majority of mating occurs and decreasing to the late rut (Vannoni and McElligott 2009). The rapid decrease in groaning rate toward the end of the rut may in part be related to declining body condition of males (Clutton-Brock and Albon 1979; Vannoni and McElligott 2009). Our finding that high-rate groaning is linked with increased attention supports the hypothesis that groaning rate is indicative of the potential threat level and representative of the motivational or arousal state and condition of the caller.

Figure 4. The response of males to playback of early or late rut groans or the control period. (A) The latency to become attentive and (B) the duration of attention.
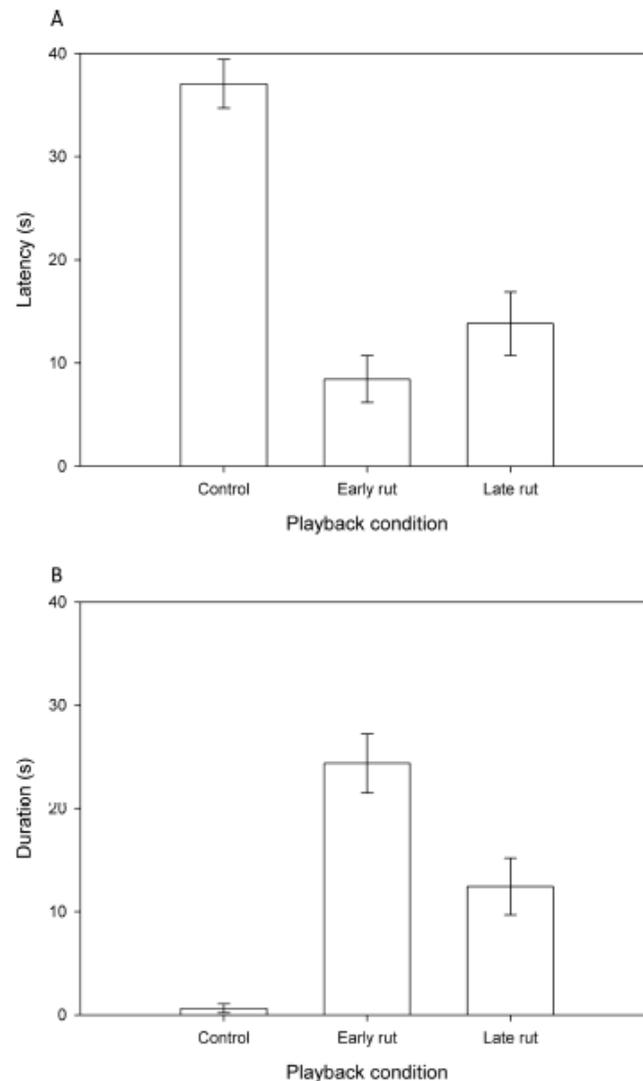
Like fallow deer, red deer vocalize at higher rates in situations where they are likely to be challenged, and winners of fights typically call at higher rates than their competitors (Clutton-Brock and Albon 1979). Male South American sea lions (*Otaria flavescens*) increase their calling rates in the presence of non-neighbor males and when monopolizing greater numbers of potential mates (Fernandez-Juricic et al. 2001). Similarly, male Australian sea lions (*Neophoca cinerea*) respond more rapidly and more aggressively to playbacks of higher barking rates (Charrier et al. 2011). Increased calling rate is likely to be a good indicator of increases in the arousal of an individual and may be linked to associated changes in physiology, such as respiration rates (Titze 1994; Scherer 2003; Ehret 2006; Vannoni and McElligott 2009).

Changes in the acoustic properties or intensity of sexually selected vocalizations over the course of a breeding season are likely to honestly reflect the changing condition of the caller and thereby provide important information to listeners (Vehrencamp 2000). We found that fallow bucks remained attentive for almost twice as long during playback of early rut groans than playback of the same individual's late rut groans. In fallow deer, acoustic parameters provide information about caller dominance, with higher ranked males typically producing groans with lower pitch and formant frequencies than other individuals (Vannoni and McElligott 2008; Briefer et al. 2010). Vannoni and McElligott (2009) found that fallow buck groans degrade throughout the rut. Toward the end of the rut, groans become higher pitched and have shorter durations. The authors suggest that this change is related to the large decline in body condition during the rut (males lose on average 26% of their body weight; McElligott et al. 2003; Vannoni and McElligott 2009) and that groans are likely to be honest signals of a male's contemporary quality. The decreased response to late rut groans compared with early rut groans of the same individual seen in our study indicates that fallow bucks can perceive these changes in the acoustic quality of groans and can treat fatigued, late rut, groans as less dangerous. Fallow bucks are likely to be able to take advantage of these dynamic cues of quality to judge when rivals are declining in condition and when to fight (McElligott et al. 1998).

The involvement of fatigue in the short-term variation of sexually selected vocal displays has received very little attention but has been documented in North American bison (*Bison bison*; Wyman et al. 2008), oyster toadfish (*Opsanus tau*; Mitchell et al. 2008), and Italian tree frog (*Hyla intermedia*; Castellano and Gamba 2011). However, these studies have focused on the changes in displays rather than the ability of other individuals to perceive changes. Study of bird song has shown that song consistency is a good indicator of male quality and reproductive success (Sakata and Vehrencamp 2012). Bird song has been shown to have relatively low metabolic costs compared with other activities (Oberweger and Goller 2001; Ward et al. 2004), and changes in song amplitude within natural ranges do not affect metabolic energy consumption beyond background variation (Zollinger et al. 2011). Despite this, producing consistent songs requires the generation of nervous control of the vocal motor system, coordination of the vocal tract and respiratory muscles, and resistance to fatigue (Lambrechts and Dhondt 1988; Suthers and Zollinger 2008; Sakata and Vehrencamp 2012). Similarly, extensive loud singing does not increase energy expenditure in rock hyrax (*Procavia capensis*; Ilany et al. 2013). Although the handicap principle (Zahavi 1977) assumes that costs accrue more rapidly for lower quality individuals, in signalling contests, winners often show higher metabolic rates and thus greater depletion of energy resources than losers. Although winners use energy at a higher rate, losers face a greater impact if they are poor quality individuals with lower reserves (Hack 1997; Briffa and Sneddon 2007). In fallow bucks, production of groans only occurs in the lead up to and during the rut (McElligott et al. 1999). Although the exact metabolic cost of increased vocal activity has not been quantified, feeding is greatly reduced during this time (Newman et al. 1998) and males lose approximately 26% of their body weight (McElligott et al. 2003). The breakdown in the acoustic quality of calls is likely to reflect fatigue and subsequent loss of coordination in the vocal

production system. Hence, fallow buck groans potentially provide unavoidable honest information about the current body condition of callers to conspecifics.

Signals that provide information about changeable traits have been described as "current-state signals" (Bergman and Sheehan 2013). Among primates, current-state signals have been suggested at short timescales to signal intent, such as aggression or submission, and at longer timescales to signal states such as fertility (Bergman and Sheehan 2013). Receivers can potentially integrate current-state signals with social knowledge to mediate interactions with conspecifics. In addition to providing contemporary information about the motivation and condition of callers, fallow buck groans are individually stereotyped within a breeding season (Reby et al. 1998; Vannoni and McElligott 2007; Briefer et al. 2010). Because identity and quality information are encoded in the same acoustic components of groans, there is a trade-off in stability over time between these traits (Briefer et al. 2010). However, groans potentially provide sufficiently consistent information for individual recognition within a given year (Briefer et al. 2010). Individual recognition between males could allow bucks to reduce the frequency and intensity of aggressive interactions by making judgments about other individuals based on previous experience (Isvaran and St. Mary 2003). The inclusion of "current-state" quality information in vocalizations would further allow listeners to know when a particular male is declining in condition and is likely to be challenged by formerly subordinate males. Typically, highly successful males, which start vocalizing earlier in the year than others, begin to display hoarse, lower quality groans toward the end of the rut and are then challenged and displaced by lower ranking individuals (McElligott et al. 1998, 1999; Vannoni and McElligott 2009). Similarly, in North American bison, high ranking males tend to mate early in the breeding season, losing body condition, and ceasing mating earlier than lower ranking males (Wolf 1998; Wyman et al. 2012). Changes in the amplitude and bellow rate of bison may allow bulls to assess the changing competitive ability of competitors (Wyman et al. 2008). It is likely that in a number of species, vocalizations contribute, beyond the initial establishment of a social structure, to the ongoing assessment of individuals. The breakdown of call structure could thus provide important information about the changing condition of callers (Vannoni and McElligott 2009). Future research into the degradation of acoustic signals and their role as cues to quality should examine the interaction between an individual's quality and the rate of degradation of its signal.

Fallow bucks are more attentive to playback of high-rate groans, suggesting that they perceive these groans as more threatening than low-rate groans. Males also perceive changes in groan structure, responding less to fatigued, late rut groans than to early rut groans. Fallow bucks thus extract honest information from groans about the contemporary quality of the caller, simultaneously gaining information about caller motivation and fatigue. This study demonstrates that variable, sexually selected vocalizations can dynamically encode information about the quality and motivation of an individual over both long and short timescales and highlights the need for researchers to examine variation in the vocal signals of other taxa, both between and within individuals.

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