Effect of combined source (F0) and filter (formant) variation on red deer hind responses to male roars

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Studying female response to variation in single acoustic components has provided important insights into how sexual selection operates on male acoustic signals. However, since vocal signals are typically composed of independent components, it is important to account for possible interactions between the studied parameter and other relevant acoustic features of vocal signals. Here, two key components of the male red deer roar, the fundamental frequency and the formant frequencies (an acoustic cue to body size), are independently manipulated in order to examine female response to calls characterized by different combinations of these acoustic components. The results revealed that red deer hinds showed greater overall attention and had lower response latencies to playbacks of roars where lower formants simulated larger males. Furthermore, female response to male roars simulating different size callers was unaffected by the fundamental frequency of the male roar when it was varied within the natural range. Finally, the fundamental frequency of the male roar had no significant separate effect on any of the female behavioral response categories. Taken together these findings indicate that directional intersexual selection pressures have contributed to the evolution of the highly mobile and descended larynx of red deer stags and suggest that the fundamental frequency of the male roar does not affect female perception of size-related formant information. © 2008 Acoustical Society of America. [DOI: 10.1121/1.2896758]

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I. INTRODUCTION

Male courtship signals are often subject to sexual selection through female mating preferences (Searcy and Andersson, 1986; Ryan, 1998; Kokko et al., 2003). However, in order to appreciate how intersexual selection is generated it is necessary to understand how females perceive and react to signal variation. Since acoustic signals can be easily separated from other aspects of the male phenotype, they are ideally suited for studying female responses to variation in their properties (Gerhardt, 1991; Searcy, 1992). Indeed, many studies have shown how female preferences are affected by variation in single acoustic parameters (Andersson, 1994). However, as acoustic signals are typically composed of several components, possible interactions between them can mean that female responses to variation in single acoustic parameters may not predict how females respond to variation in different combinations of acoustic components (Ryan and Rand, 2003; Olvido and Wagner, 2004; Scheuber et al., 2004).

The generalization of the source-filter theory of voice production (Fant, 1960) to nonhuman mammals allows specific acoustic features of mammal calls to be linked to their production mechanisms. Furthermore, by doing so, predictions about which acoustic features of mammal calls have the potential to provide receivers with reliable information on the caller’s phenotype can be made. The source-filter theory states that mammal vocalizations result from a source signal, generated by vibrations of the vocal folds in the larynx, which is then filtered by the cavities of the vocal tract. The source signal determines the pitch, i.e., the fundamental frequency (F0), of the vocalization. When this signal passes through the vocal tract, which acts as a tube of air with natural resonances, some frequencies are selectively amplified: These frequencies are termed “formants.” Because source and filter components are independently produced, either or both have the potential to provide receivers with important information on the caller’s genetic quality and/or current physical condition.

The source-filter theory has been successfully applied to the study of mammal vocal communication, including male red deer roaring (Fitch and Reby, 2001; Reby and McComb, 2003a; Reby et al., 2005; Vannoni and McElligott, 2007). In particular, a number of studies have confirmed that formants provide accurate information to receivers on the caller’s body size (Fitch, 1997; Riede and Fitch, 1999; Reby and McComb, 2003a; Harris et al., 2006; Sanvito et al., 2007), due to a close relationship between the formant spacing, the caller’s vocal tract length (VTL), and overall body size (Fitch, 2000). This reliable information on body size may also allow receivers to gauge the caller’s maturity (Reby and McComb, 2003a), and even, in size dimorphic species, the caller’s sex (Rendall et al., 2004).

Both red and fallow deer males have a descended and highly mobile larynx that enables them to increase their VTL during vocalizations (Fitch and Reby, 2001; McElligott et al., 2006), thereby lowering their formant frequencies independently of F0. While size exaggeration as previously suggested as a possible mechanism for the evolution of this anatomical innovation (Fitch and Reby, 2001), the maximum extension of the vocal tract, achieved in most roars by red

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deer stags, is morphologically constrained by the sternum and hence minimum formant values are honest indicators of body size (Fitch and Reby, 2001; Reby and McComb, 2003a). Moreover, playback experiments using resynthesized roar stimuli have shown that both male and female red deer do actually attend to formants in the roars of simulated rivals (Reby et al., 2005) and potential mates, respectively (Charlton et al., 2007a, 2007b). Accordingly, we would only expect display characteristics that provide an honest advertisement of body size to be maintained by selection in these contexts (Grafen, 1990).

In contrast, mean fundamental frequency ($F_0$) is not correlated with aspects of male quality in red deer (Reby and McComb, 2003a) and has proven to be a poor predictor of body size within mammal species (Masataka, 1994; Rendall et al., 2005; but see Pfefferle and Fischer, 2006). In addition, red deer hinds show no preferences when presented with the choice between roars with low and high fundamental frequencies (McComb, 1991). Notwithstanding this, there are theoretical reasons for suspecting that $F_0$ may contribute to the perception of the formant frequencies in the male roar and consequently affect the attractiveness of the signal to females. When roars are delivered with a low fundamental frequency the density of harmonics sampling the formant envelope is increased, which may be expected to increase the salience of the formant structure (Rylls and Lieberman, 1982) and hence, affect the differential response of red deer hinds to size-related variation in formant spacing.

In the current study, we used resynthesis techniques to create roar stimuli in which we independently manipulated the formant frequencies and $F_0$, while leaving all other acoustic parameters (e.g., duration, amplitude, other timbral cues, etc.) unchanged. We then used these stimuli in playback experiments to examine the behavioral response of red deer hinds to male roars characterized by different combinations of these acoustic components. This allowed us to separately determine female responses to formant variation but also test whether the value of $F_0$ affects female response to size-related formant variation.

II. MATERIALS AND METHODS

A. Experimental site and animals

The playback experiments were conducted at Invermay Agricultural Centre and Tony Pearse’s Deer Farm in Mosgiel, New Zealand, during March and April 2006. A total of 96 adult red deer hinds from 20 different groups, all identified by numbered collars and ear tags, were used as subjects in the playback experiments. As our experiments were conducted early in the breeding season some of the hinds already had a resident stag placed (as a sire) in their enclosure. To minimize habituation, individuals within the same groups were presented with playbacks on separate days.

B. Selection of roars for resynthesis

To create the playback stimuli we selected two roaring bouts from each of four mature stags (aged 5–8 years). These roaring bouts, each comprising two roars, had been previously recorded at Redon Experimental Deer Farm, France, using a Telinga pro-III-S/(DAT) microphone and a DAT Sony TCD-D7 recorder (amplitude resolution: 16 bits, sampling rate: 48 kHz). This ensured that the current hinds were unfamiliar with these males that, ranging in weight from 210 to 230 kg, were representative of farmed stags. The original DAT recordings were transferred onto an Apple Macintosh G3 computer via a Digidesign Audiomedia III soundcard, saved in AIFF format as separate Sound-Edit 16 Version 2 sound files (16 bits amplitude resolution, 48 kHz sampling rate) and normalized to 100% peak amplitude.

C. Acoustic analyses

In order to determine the appropriate readjustment factors by which to resynthesize the roar stimuli, we initially measured the formant and fundamental frequency ($F_0$) values for each roar using the Praat 4.2.06 DSP package (Boersma and Weenink, 2005).

1. Formant frequency and spacing estimation

The frequency values of the first eight formants ($F_1, F_2, \ldots, F_8$) were extracted using Linear Predictive Coding via the “LPC: To Formants (Burg)” command in Praat. The analysis parameters were time step, 0.05 s; window analysis, 0.1 s; maximum formant values, 1700–1900 Hz; maximum number of formants, eight; pre-emphasis, 6000 Hz. The male roar is characterized by an initial drop in formant frequencies, which then plateau at minimum values before they rise again at the end of the roar. This is due to the mobile larynx of red deer stags that enables them to lengthen their vocal tract during vocalizations (Fitch and Reby, 2001), which in turn lowers the formant values and decreases the overall spacing of the formants across the roar (see Fig. 1). Therefore, in order to standardize formant measurement, the Praat output for each entire roar was examined and ten readings (at a time step of 0.05 s), from an area where the formants reach their minimum values, were selected and the values for each formant frequency averaged. These average minimum formant frequencies were used to estimate the minimum formant spacing achieved during each roar by finding the best fit for the equation

$$F_i = \frac{2i-1}{2} \Delta F.$$  \hspace{1cm} (1)

This equation describes the relationship between individual formant frequencies ($i=\text{formant number } 1, 2, 3, \ldots$) and the average overall formant spacing ($\Delta F$) in a vocal tract approximated as a straight uniform tube closed at one end (the glottis) and open at the other end (the mouth) (Titze, 1994). Finally the estimated apparent VTL, was directly deduced from formant spacing by using the equation

$$VTL = \frac{c}{2\Delta F},$$  \hspace{1cm} (2)

where $c=$ the approximate speed of sound in a mammal vocal tract (350 m/s) (Titze, 1994). Full details of this procedure are available in another paper (Reby and McComb, 2003a).
2. Fundamental frequency estimation

The mean fundamental frequency ($F_0$) values for each roar were extracted using a forward cross-correlation [to pitch (cc) command] algorithm in Praat. The time step in the analysis was 0.05 s and the specified range for the lower and upper limits of the expected range of $F_0$ were 30 and 250 Hz, respectively. A five point average smoothing filter removed any rapid variations in the $F_0$ contour before the mean value for $F_0$ across the entire roar was determined using the “get mean” command in Praat.

D. Resynthesis of roar stimuli

Previous data from a population of adult Scottish red deer males showed a variation of $\sim$5% around the mean for the largest and smallest adult apparent VTLs measured (Reby and McComb, 2003a). Therefore, in order to realistically simulate natural variation in male VTL between the largest and smallest adults representative of a population, we used values shifted $\pm$5% from the measured mean of our stag exemplars of 81.5 cm: Creating adult size variants with apparent VTLs of 85.7 and 77.5 cm, respectively. To simulate male callers with VTLs outside of the natural adult range, the formants of the roar stimuli were shifted $\pm$20% to represent abnormally large and small adult males with VTLs of 101.7 and 67.8 cm, respectively (see Fig. 2). This was done to test the hind’s responses to supernormal stimuli and to determine whether any innate directional preferences existed for males with abnormally long vocal tracts.

We conducted three levels of pitch manipulation for each of the four size variant conditions, corresponding to adult red deer males roaring at low (70 Hz), medium (100 Hz), and high (130 Hz) fundamental frequencies (see Fig. 2). Previous data taken from a population of 22 adult Scottish stags (in which the minimum, mean, and maximum
measured mean fundamental frequency values were 65.7, 111.7, and 168.3 Hz, respectively) indicate that these pitch variants fall within the natural range for adult male red deer (Reby and McComb, 2003a). The resynthesis factors for these mean fundamental frequency values were simply deduced by dividing the intended value by the original measured value for each roar.

A Praat script (originally written by C. J. Darwin) was used to batch process roar stimuli for the modification of formants and fundamental frequency (F0). Formant modification was achieved using a Pitch-Synchronous Overlap and Add (PSOLA) based algorithm that alters the apparent vocal tract lengths of the roar stimuli by shifting the formant frequencies by a factor (k1), while leaving all other acoustic parameters unchanged. This program works by initially multiplying F0 by k1 and duration by 1/k1 using PSOLA, before resampling at the original sampling frequency multiplied by k1 and finally playing the samples at the original sampling frequency. The fundamental frequency (F0) was adjusted at the same time by adding an additional line to this script, further raising or lowering the “pitch tier” (a Praat vector of F0 estimates) by the appropriate factor (k2).

E. Playback sequences

A total of 48 different playback sequences were created from the four stag exemplars and the 12 different combinations of size and pitch variation (four different adult size variants each with three levels of pitch manipulation, see Fig. 2). The playback sequences ranged between 9.6 and 10.6 s and consisted of two two-roar roaring bouts from the same stag exemplar separated by 0.5 s. In order to standardize the roaring rate for each stag exemplar, the roars within each bout were separated by 1 s of silence. This ensured that each of the four roars within a sequence was equally spaced across exemplars.

F. Playback experiments

Individual hinds with their head down grazing and at the periphery of a group were targeted for the playbacks. In this way we aimed to provide a standardized context for the playbacks and also to ensure that in each case the hind’s attention was not already directed toward the speaker position. The 48 different playback sequences (see above) were played back to 96 different hinds, making a total of 96 playback experiments. The playback sequences were presented to the hinds using an Anchor Audio Liberty 6000HIC speaker at sound pressure levels (SPLs) of 105 dB peak SPL at 1 m from the source (determined using a Radio Shack Sound Level Meter, set for C-weighted fast response). The loudspeaker was connected by a coaxial cable to an Apple Powerbook G4 with an external imic soundcard (Griffin technology) and a Sony digital camera (model DCR/TRV19E) used to capture behavioral responses on videotape for 2 min after each playback presentation.

G. Behavioral analysis

The videotapes were analyzed frame by frame (frame =0.04 s) using Gamebreaker 5.1 digital video analysis system for Mac OS 10. In order to quantify the strength of the hind’s response to each playback condition, the duration of the first look given by the hind while stationary toward the speaker position and the total time that each hind spent stationary with their head up looking around during the 2 min period after each playback presentation were measured. Looking was defined as having begun the frame before that in which the hind raised her head to look around or, in the case of the first look duration, turned her head to face the speaker, having previously faced away. This behavior ended the frame before that in which the head began to move back down to a grazing position or in which the hind ceased to be stationary. The time between the onset of the playback and the first behavioral response (latency to first response) and the number of looks given during the 2 min period after each playback presentation were also quantified.

H. Statistical analysis

Log (10) transformations were used to normalize the data distribution for parametric statistics. Additionally, in order to normalize the data distribution for latency to first response without removal of data, subjects responding more than 10 s after playback onset were given maximum values of 10. A principal components analysis was made using first look duration, total look duration, and number of looks to reduce these highly correlated variables to one “looking response component” explaining 70%) of the variance (subjects with greater first look duration, total look duration, and number of looks had the highest scores).

Separate univariate analyses of covariance (ANCOVA) were computed for looking response component and latency to respond to compare the response of hinds to both the size and pitch variant conditions, in which the presence or not of a resident stag was the single covariate (a resident stag was present for 66 out of 96 playback experiments). A preliminary analysis indicated that the presence of a resident stag was negatively correlated to total look duration (F1,96 =4.473, P=0.037) and bordering on significance for number of looks given (F1,96=3.885, P=0.052). Pair-wise comparisons were also used to compare the behavioral responses to the different size and pitch variant conditions. Finally, Levine’s tests were used to determine whether the variance of hind response to size-related formant information was reduced by lower fundamental frequencies, as might be expected if lower fundamental frequencies significantly improved the ability of hinds to perceive the formant structure in the male roar. Alpha levels were set at 0.05 and two-tailed probability values quoted.

III. RESULTS

A. Looking response component

The univariate ANCOVA revealed that the looking response component was significantly affected by the size variant condition [F(3,96)=6.694, p<0.001] but not the pitch variant played back [F(2,96)=0.863, p=0.426] [see Figs. 3(a) and 3(b)]. Moreover, no interaction between the size and pitch variant played back was detected [F(6,96)=0.423, P =0.862], indicating that the pitch of the male roar had no

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effect on the looking response of hinds to the different size variants. The pair-wise comparisons showed that looking response was significantly greater for hinds presented with male roars simulating abnormally large adults (VTL = 101.7 cm) than those simulating both small (VTL = 77.5 cm) (p = 0.001) and abnormally small adult size variants (VTL = 67.8 cm) (p < 0.001). In addition, looking response was significantly greater when hinds were presented with male roars simulating a large adult (VTL = 85.7 cm) than those simulating both small (VTL = 77.5 cm) (p = 0.022) and abnormally small adults (VTL = 67.8 cm) (p = 0.013). Last, no significant differences were detected in looking response between the small and abnormally small adult size variants (p = 0.842) or between the large and abnormally large adult size variants (p = 0.228). In addition, no differences in the variance of hind response to the pitch variants [Levene’s test: F(2, 93) = 0.895, p = 0.412] or the different combinations of size and pitch variant were detected [Levene’s test: F(11, 84) = 1.181, p = 0.312].

B. Latency to respond

The univariate ANCOVA revealed that latency to respond was significantly affected by the size variant \(F(3, 96) = 2.726, p = 0.049\) but not the pitch variants played back \(F(2, 96) = 0.061, p = 0.941\) [see Figs. 3(c) and 3(d)]. Moreover, no interaction between the size and pitch variant played back was detected \(F(6, 96) = 0.471, p = 0.828\), indicating that the pitch of the male roar had no effect on the response latency of hinds to the different size variants. The pair-wise comparisons showed that latency to respond was lower for playbacks simulating abnormally large adults (VTL = 101.7 cm) than those simulating small adult size variants (VTL = 77.5 cm) (bordering on significance: \(p = 0.064\)). Additionally, hinds responded significantly faster to male roars simulating large adults (VTL = 85.7 cm) than those simulating small adult size variants (VTL = 77.5 cm) (\(p = 0.006\)). Lastly, no significant differences for latency to respond were detected between the abnormally large versus

FIG. 3. Female [(A), (B)] looking responses and [(C), (D)] latency to respond to resynthesized male roars simulating the different size and pitch variants. Estimated marginal means ±S.E are taken from pair-wise comparisons; those sharing the same letter are not significantly different.
large ($p=0.356$), abnormally large versus abnormally small ($p=0.713$), large versus abnormally small ($p=0.199$), and small versus abnormally small ($p=0.136$) size variant conditions. In addition, no differences in the variance of hind response to the pitch variants [Levene’s test: $F(2,93)=0.207$, $p=0.814$] or the 12 different combinations of size and pitch variant were detected [Levene’s test: $F(11,84)=0.308$, $p=0.982$], indicating the fundamental frequency did not significantly affect the variability of hind response.

### IV. DISCUSSION

There are three main results from this study. The first is that red deer hinds showed greater overall attention, judged on the number and duration of looks, and had lower response latencies to playbacks simulating adult males with VTLs (and hence body sizes) greater than the natural population mean. The second is that the value of the fundamental frequency in the playback stimuli had no effect on the response of the hinds. The final result is that there was no interaction between the value of the fundamental frequency and the value of the formant spacing affecting the observed response of the hinds; suggesting that the value of the fundamental frequency in roars does not affect how receivers perceive size-related variation in formant frequency spacing.

### A. Formants and female response

We know from previous work that red deer hinds move preferentially toward male roars in which the formants indicate larger callers when they are in peak oestrus (Charlton et al., 2007b). Our findings here suggest that males producing roars with lower formant values, indicative of longer vocal tracts and larger bodies, would also elicit greater attention from peri-oestrous females during the breeding season. Accordingly, roars with lower formants may serve as an initial attractor for females just prior to oestrus, making them more likely to join the harems of larger males. Such a preference would be adaptive for females because they would then be better positioned to mate with larger males when they came into oestrus and hence, gain the indirect genetic benefits of larger more competitive offspring. It also seems likely that by joining the harems of larger males during the breeding season, discriminating females could get direct fitness benefits such as increased protection from male harassment (Clutton-Brock et al., 1982; Reale et al., 1996).

Interestingly, although female response increased most steeply across the natural range of male size variants, our results showed that hinds gave their greatest responses to roars simulating abnormally large males with VTLs outside of the normal population range. This is consistent with previous work demonstrating that, when given a relative choice between roars simulating large and small male callers, oestrous red deer hinds moved preferentially toward the larger size variant (Charlton et al., 2007b). Moreover, these findings lend support to the hypothesis that directional intersexual selection pressures have contributed to the evolution of the mobile larynx of red deer stags and other cervids (Fitch and Reby, 2001; McElligott et al., 2006), enabling them to lengthen their vocal tract and lower their formants during vocalizations. Future studies would be needed to determine whether this female sensory bias was pre-existing (Ryan et al., 1990) or evolved to select for roars with the very lowest formant values, in order to maximize the chances of mating with the largest available male (Enquist and Arak, 1998).

### B. Fundamental frequency and female response

The fundamental frequency manipulation had no significant separate effect on any of the female response parameters. This is consistent with another study in which red deer hinds showed no preference when presented with the choice between roars with high and low fundamental frequencies (McComb, 1991). Nevertheless, male roars with the lowest fundamental frequencies of 70 Hz appeared to induce the greatest average response from hinds across formant frequency variants (although this was not statistically significant), particularly when large and small adult size variants within the normal range were played back. Indeed, although no known correlations between mean fundamental frequency and aspects of male quality have previously been detected in red deer, the fundamental frequency (mean and max) is significantly higher in the roars of subadult than adult stags (Reby and McComb, 2003a) and therefore has the potential to act as an additional cue to the maturity of the caller alongside the formants.

In addition, studies on humans suggest that speakers with lower F0’s have higher testosterone levels (Evans et al., 2006) and female listeners rate male speakers with lower pitched voices as more attractive (Feinberg et al., 2005). Interestingly, human females find male speakers with low formants and fundamental frequency particularly attractive when they are ovulating (Feinberg et al., 2006). Accordingly, although we found no evidence of female preferences based on fundamental frequency in the current study, future work on oestrous red deer hinds may show that this acoustic component is relevant in a mate choice context, possibly as a cue to the caller’s maturity or hormonal quality.

### C. The effect of fundamental frequency on female perception of size-related formant variation

Our analysis revealed no interactions between the size and pitch variants played back for any of the response categories, indicating that the overall response pattern observed across the size variant conditions was similar for all the pitch variations (70, 100, and 130 Hz). This suggests that the ability of females to perceive size-related formant information in the roars of stags is unaffected by the fundamental frequency of the call when it is varied within the natural range.

Given that denser spectral sampling provided by lower fundamental frequencies improves human perception of formants (Ryalls and Lieberman, 1982), we may have predicted that lower fundamental frequencies would increase the salience of the formant structure, in turn increasing the magnitude of the differential responses to the size variants and/or lowering the variance of the hinds’ response. The fact that neither of these were observed suggests that lower fundamental frequencies do not significantly enhance the percep-
tion of the formant structure within the male roar nor alter the behavioral response of red deer hinds to the signal. One possible reason for this result is that the mean fundamental frequency values that we used (70–130 Hz) were lower than the minimum formant frequency spacing of our four size variant conditions (ranging from 172 to 258 Hz), therefore providing a sufficiently dense spectral source for revealing the vocal tract resonances. Accordingly, as the perception of size-related formant information by red deer hinds does not appear to be affected when the spectral envelope is sampled at a lower rate than that known to significantly impair human vowel discrimination (Ryalls and Lieberman, 1982), we suggest that using formants to estimate a caller’s size is less likely to rely on the precise judgment of individual formants (as it is for vowel perception) than an estimate of overall formant spacing.

Further studies comparing the effect of a wider range of fundamental frequencies on the perception of size-related formant information in red deer are warranted. As the peak fundamental frequencies on the perception of size-related formant information when the harmonic spacing is wide appear to be affected when the spectral envelope is sampled at a lower rate than that known to significantly impair human vowel discrimination (Ryalls and Lieberman, 1982), we suggest that using formants to estimate a caller’s size is less likely to rely on the precise judgment of individual formants (as it is for vowel perception) than an estimate of overall formant spacing.

In conclusion, the use of multicomponent signals for female mate choice in animals has received recent theoretical (Johnstone, 1995; Candolin, 2003) and empirical attention (Patricelli et al., 2003; Scheuber et al., 2004; Poole and Murphy, 2007). In this study we examined the combined effect of variation in two separate components of a male mammal’s sexual call on female response. Our results reinforce the idea that formants, being a long-term indicator of male body size and hence genetic quality, are important to red deer hinds as acoustic cues for mate assessment during the breeding season. Moreover, as the fundamental frequency does not appear to influence the perception of the formant structure in the male red deer roar, we suggest that the extremely low-pitched male rutting calls of Corsican (Cervus elaphus corsicanus) and fallow deer (Dama dama) (Reby and McComb, 2003b) are unlikely to represent an adaptation to facilitate the transmission of size-related formant information.

However, fundamental frequency variation may be functionally significant to oestrous red deer and other female mammals during their time of peak conception. Fundamental frequency is often highly modulated within the roars of red deer stags and both the range and mean values are variable between and within individuals (Reby and McComb, 2003a).

In addition, minimum $F_0$ is positively correlated to reproductive success in red deer (Reby and McComb, 2003a). In fact, because higher fundamental frequencies require greater stiffness and tension of the vocal folds, and probably higher subglottal pressures to produce, the fundamental frequency may dynamically reflect a callers’ short-term condition (Gerhardt, 1991) of direct importance to receptive females. We suggest that future work should adopt the same resynthesis techniques and playback approach to present male sexual calls with different combinations of fundamental frequency and formants not only to oestrous red deer hinds but also to other female mammals, to explore these possibilities.

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