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DESCRIPTION OF VOCALIZATIONS IN EXOTIC EUROPEAN RED DEER STAGS (*CERVUS ELAPHUS*) DURING THE RUT IN NORTHWESTERN PATAGONIA (ARGENTINA)

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ABSTRACT

Polygynous deer are very vocal species, producing calls in various contexts. Male rutting calls in red deer (*Cervus elaphus*) have been most studied in captive and/or free-ranging European populations. The recent application of “source-filter theory” has identified the independent roles of fundamental frequency (F0) and formants in the production of deer calls and demonstrated the relation between formant spacing and anatomical characteristics such as body size. This paper describes and characterizes the acoustical properties of male rutting vocalizations for a free-ranging red deer population located in the ecotone of the eastern Andean cordillera within the Nahuel Huapi National Reserve (Neuquén, Argentina), the first acoustic study of free-ranging red deer stags outside their historic distribution. Recordings were made of 7 identified and several unidentified stags at the peak of the rut in 2007. Calculated F0 was found to be higher for these identified stags than for Scottish red deer on the island of Rhum. The analysis of formant spacing was used to calculate the length of the vocal tract (VTL) for the 7 males studied; values were comparable to those found in stags from Rhum. The longest calculated VTLs within these males corresponded to the 4 stags with the largest antler racks and the only stags holding harems. Previous studies have shown that VTL correlates with body size, age and reproductive success and that these deer have the ability to lower their larynx and extend their vocal tracts to a maximum, which is probably under sexual selection. Our data fit with this explanation. The higher F0s recorded in this population may result from the influence of wapiti genes, known to be present in these deer, as wapiti have a much higher frequency rutting call, the bugle. Alternatively, they may be related to the mating strategy, which varies substantially from the northern European populations.

Additional keywords: roars, formants, elk, pitch, mating behaviour.

INTRODUCTION

Communication plays a crucial role in social interactions in deer, as in other group-living mammals. Although not obvious to the casual observer, polygynous deer are very vocal species. Moreover, their vocalizations are notable for their diversity. Calls have been registered in both sexes and in different contexts: social contact, mother-young interactions, and male rutting calls, which function in both male-male competition and female choice (Taylor and Reby 2010; Reby *et al.* 2010; Reby *et al.* 2005; Reby and McComb 2003b). The vocalizations emitted during mating activities have received the most attention, particularly in red deer (*Cervus elaphus*), with captive and/or free-ranging populations having been studied in Scotland, France and Italy (Favaretto *et al.* 2006, McComb 1987, McComb 1991, Pepin *et al.* 2001, Reby and McComb 2003a, 2003b, and Reby *et al.* 2001, 2005, 2010).

The “source-filter theory” of mammalian sound production hypothesizes that the vocalizations produced result from two independent processes. First the sound is generated by the vocal folds of the glottis, which produce the fundamental frequency (F0). The sound then passes through the cavities of the superior vocal tract where it is filtered by the resonant frequencies of the cavities. Some frequencies are augmented (the formants) and others are dampened (Taylor and Reby 2010). The distribution of the formants or formant frequency dispersion, unlike F0, is related to the variation in the anatomical characteristics of the caller, such as body size, since it accurately reflects vocal tract length (Fitch 1997; Reby and McComb 2003a, 2003b). Using source-filter theory, the different contributions of the source, as F0, and the filter, as formant frequency dispersion, have clarified the form of production of many animal calls, how variations in F0 can reflect hormonal or motivational changes and how formant frequency dispersion is an accurate reflection of vocal tract length (VTL) and thus of body size (Taylor and Reby 2010). In red deer and fallow deer (*Dama dama*), the use of this theory led to the discovery that stags of these species can lower their larynxes during vocalization, thereby increasing their VTLs,

decreasing the formant frequency dispersion, and increasing their apparent size (Reby and McComb 2003a, McElligott *et al.* 2006). In red deer, formant frequency dispersion is used by stags to evaluate their opponents and by hinds to select a mate (Reby *et al.* 2005, Charlton *et al.* 2007).

Here we present the first study of vocalizations of free-ranging red deer stags outside their historic distribution. Exotic red deer were first introduced to Argentina in the period 1902-10 by Pedro Luro to the La Pampa Province. The records from the company importing the red deer showed them all to be of Austrian/Hungarian stock from the mountains of the Alps and Karpaten (Wollenhaupt 1983). In the early 1920s, Robert Hohmann brought 20 individuals from Parque Luro to the 'estancia' Colluncó near San Martín de los Andes, from where they were liberated in 1922. In 1924, individuals from Colluncó were translocated to an enclosure on Peninsula Huemul in Nahuel Huapi National Park to be later released in 1926 (reviewed in Flueck and Smith-Flueck 1993 and Smith-Flueck 2003)

The population from which our males were sampled originated from the animals released at Peninsula Huemul. Today's distribution of free-ranging red deer includes a wide north-south stretch of the Andean-cordillera ecotone, including the lenga forest to the west and reaching out into the steppe to the east (Flueck *et al.* 1995, 2003), with numbers estimated at more than 100,000 individuals in Patagonia (Flueck *et al.* 2003). In the favourable ecotonal habitat, densities recently reached a high of 100 deer/km² (this study area) and 40–50 deer/km² in the steppe (Flueck *et al.* 2003), several fold higher than densities recorded for Scottish deer on the Island of Rhum (Clutton-Brock *et al.* 1982, p 268).

Besides an Austrian-Hungarian heritage, the red deer in this area have also been shown to contain genes identified specifically with N. American wapiti or elk (*Cervus elaphus canadensis*) which would have already been present in the first red deer imported from Europe one hundred years ago. The importation of American wapiti to Europe is well documented, with individuals brought to Austria, Poland and Hungary over 250 years ago to improve trophies for sport hunting. For one example, several hundred wapiti were said to have been introduced to Austria by the Emperor Franz Josef (1830-1916) where they hybridized with the native red deer (Whitehead 1993). Introductions of wapiti were primarily into deer parks from where subsequent introductions were made into wild populations (Perez-Espona *et al.* 2010). Wapiti, although currently classified as the same species as red deer (Nowak and Walker 1999), have a few phenotypic characteristics that make them easily discernible from their European relative: larger body size (several fold larger than Scottish red deer); an antler rack of greater size, weight and a different form; and easily distinguishable male rut calls. Whereas an elk is commonly known to *bugle* during the rut (Feighny *et al.* 2006), the red deer male *roars*. The bugle is a much higher frequency vocalization (F0 0.41 – 1.90 KHz) than the roar (F0 70-162 Hz).

The aim of this paper was to describe and characterize the acoustical properties of male vocalizations produced during the rutting period for a free-ranging red deer population located in the ecotone of the eastern Andean cordillera within the Nahuel Huapi National Reserve (Neuquén, Argentina). We also wanted to compare our results with those obtained from Scottish stags on Rhum (Reby and McComb 2003a) in order to determine whether red deer calls in this part of the world have different acoustical properties, which might be attributed to different environmental conditions or genetic origins.

MATERIALS AND METHODS

The study population inhabits the mountainous ecotone and steppe habitats of the eastern Andean cordillera in Patagonia where the dominant climate is temperate with main precipitation occurring between April and September, with an average of 1200 mm annual precipitation. The breeding season, occurring sometime between early March and late April, lasts 3 to 6 weeks, and peaks around the last 2 weeks of March. The study area was located on private land within the Nahuel Huapi National Reserve, (40°58"S; 71°12"W), Argentina at 950 m altitude, less than 20 km from the 1926 release site on Peninsula Huemul. The area over which the rut takes place is characterized by a mosaic of habitats, with the open mallins being the predominant habitat used by prime stags to set up their territories for retaining harems:

- (i) **forest patches:** represented by a variety of pure and mixed stands of *Nothofagus antarctica*, *Austrocedrus chilensis*, *Lomatia hirsuta*, *Maytenus boaria* and *Schinus patagonicus*.
- (ii) **brush patches:** represented predominately by *Berberis spp.*, *Colletia spinosissima*, and *Rosa mosqueta*.
- (iii) **mallins:** a type of wet grassland; common throughout the eastern cordillera of the Andes, which are defined as exhibiting running water or inundated soils all year round. Cyperaceae, Juncaceae and other wetland species dominate the wet central sections of the mallins. Of the graminoides, *Carex*

canescens and *Carex macloviana* (Cyperaceae) and *Juncus depauperatus* are the most prevalent species. The dryer outer edge of the mallin have more xeric graminoid and forb species, such as *Festuca pallescens*, *Hordeum chilense*, *Poa spp.*, and *Ranunculus peduncularis*.

(iv) **grass-dominated steppe:** represented by *Stipa speciosa* var. *major* and *Festuca pallescens* with variable occurrence of brush species like *Mulinum spinosum*, *Berberis spp.*, and *Colletia spinosissima*.

(v) **riparian:** a habitat with *Salix sp.* and *Nothofagus antarctica* the predominant species.

The recordings were conducted in 2007 during the peak of the rutting period (20-26 March), predominately during the height of daily activity (approximately sunrise to 1100 hours, and 1630 hours to sunset). For the 7 identified males recorded, behavioural records were taken as well as photographs: four of these were dominant breeders, each of which held a territory with 7 or more hinds present. Throughout the peak period of the rut, focal stags remained the entire day in their established territories in the open mallins, leaving only if disturbed. While these dominant stags often bedded down in the open in the heat of the day, the females, in contrast, often left to bed in the cover of the brush and forest patches on the nearby hillsides. Throughout the day, the males would continue to call, even while bedded, though sporadically and with less intensity. An occasional intruding male was cause for the bedded stags to rouse, concomitantly increasing the frequency of their calls. The roaring activity picked up again in the late afternoon, stimulated by hinds returning to the mallin, though timing varied daily according to the meteorological conditions. (Smith-Flueck and Flueck 2006).

The recordings of the vocalizations were made with a Sony TCD 5M portable recorder, type II cassettes and a unidirectional microphone (Audio-technica AT835b, frequency response=20 – 20.000 Hz) with a wind damper. The maximum recording distance was 100 meters. The tapes were then digitalized with Spectrogram 14 (sample rate: 11 kHz, 16 bit, FFT 512, freq. resolution 21.5) and acoustic characteristics (duration, low frequency and high frequency) analysed with Raven Pro. For formant and pitch analysis we selected 37 common roars from the 7 identified males and we extracted filter formant related acoustic features with Praat 5.1.37 DSP package (P. Boersma and D. Weenink, University of Amsterdam, The Netherlands). To characterize the filter, we measured the lowest frequency values for the first eight formants and the minimum spacing between them (Min Δ F), using the formant command in Praat (edit, formant, show formants). Formant analysis parameters were: maximum formant frequency = 2000 Hz, number of formants = 8, window length (s) = 0.1. In some cases the lowest frequency formants were not visible or the values obtained seemed too high. In these cases we compared the formant values from Praat with the formant means and ranges obtained by Reby and McComb (2003a) and then we decided whether this value was the first or second formant: eg. if the first formant indicated by Praat was 390 Hz, this value is closer to the second formant in Reby and McComb (2003a), and thus was interpreted as such. In these cases we did not put a value for the first formant and instead used only the higher formants. We determined the relationship between Δ F and VTL by the formula given by Reby and McComb (2003a) and Fitch (1997). We plotted the formant values as a graph of frequency (kHz) v. formant spacing (Δ F); then a linear regression line was fitted and the slope of the linear regression was used as the best estimate of Min Δ F. This graphic method was obtained from Reby (Reby and McComb, 2003a).

Because the F0s in many vocalizations were not visible, we measured the frequencies at the 5th harmonic using Spectrogram 14. In harmonic sounds, the harmonics are an integer multiple of F0 and spacing values between harmonics permitted us to estimate F0. Next we divided this value by five and then, we averaged these values to estimate F0 for each male to then make comparisons with red deer data from the Island of Rhum (Scotland). We obtained F0 for the 37 common roars analysed from the 7 identified stags.

RESULTS

Of the 731 vocalizations, we were able to analyse only 91, for the others were not clear enough, containing too much noise either from wind interference or overlapping vocalizations from nearby males. From the spectrograms, three principal types of vocalizations were identified. These were mainly distinguished by their structure and total duration in seconds (Fig. 1):

(i) *Common roar:* a harmonically structured sound with well-defined tones and formant frequencies. This vocalization had the greatest spectrographic variability, since some common roars had many harmonics and others had atonal parts (both at the beginning and at the end of the call); these vocalizations were emitted both in bouts and in isolation. N = 37, duration = 1.43 ± 0.19 (all means \pm s.e.) sec, low frequency = 183 ± 16 Hz, high frequency = 2828 ± 125 Hz. These values represent the frequency range of the calls.

(ii) *Harsh roar*: has a chaotic structure with some areas of greater intensity within its frequency range. This vocalization was produced both in bouts and in isolation. N= 31, duration = 0.65 ± 0.07 sec, low frequency = 89 ± 17 Hz, high frequency = 2706 ± 140 Hz.

(iii) *Bark*: the shortest vocalization, showed an atonal structure, and was produced either in a rapid series, or as single barks. N= 23, duration= 0.23 ± 0.01 sec, low frequency = 133 ± 26 Hz, high frequency = 2538 ± 249 Hz.

The most common vocalization was the common roar (47%), followed by the harsh roar (28%) and the least common was the bark (25%).

In addition to these parameters, for the 37 common roars sampled from the 7 identified males, we present the average values for mean fundamental frequency, Min ΔF and MaxVTL compared with values obtained by Reby and McComb (2003a) in Table 1. Although we do not know the ages of our recorded males, the calculations of ΔF and MaxVTL obtained allowed us to identify them as adult males by comparing them with values of Reby and McComb (2003a), in which the ages and weights of the Scottish stags were recorded. The four males with the highest VTL values (73.5 cm, 71.6 cm, 73.1 cm and 72.1 cm) were also the males with the largest antler racks, containing 11 to 14 points (M2, M4, M6, and M7) and had harems with hinds at the time of recording. The remaining 3 males had adult, but smaller, values of VTL (69.3, 70.4, and 71.3 cm), and lacked hinds at the time of recording.

Table 1. average of variables measured in our study for each male and comparison with values obtained for Reby and McComb (2003a)

Individual (n)	Fundamental frequency		Formant frequency		
	MeanF0 (Hz)	MinF0	MaxF0	Min ΔF (Hz)	MaxVTL (cm)
1 (7)	140.4			254.1	69.3
2 (6)	139.6			238.5	73.5
3 (4)	142.6			250.0	70.4
4 (5)	123.0			244.4	71.6
5 (3)	138.6			245.6	71.3
6 (3)	116.8			239.3	73.1
7 (9)	120.7			243.0	72.2
Mean	131.7			245.0	71.6
Reby and McComb 2003a	64.4	111.7	142.2	247	70.6

DISCUSSION

From our recordings of the vocalizations produced by red deer stags (*Cervus elaphus*) in the study area of Nahuel Huapi, the reproductive calls were found to be similar to their native European counterparts in that we could identify the same 3 main vocalizations as described for the deer of the Island of Rhum in Scotland (Reby and McComb 2003a, 2003b). Although some red deer from Nahuel Huapi have a genetic component from wapiti (*Cervus elaphus canadiensis*) with the superoxide dismutase allele typical for wapiti found to occur in 11% of animals in this study population (Flueck and Smith-Flueck 2011), these deer have roars typical of red deer. The bugle, which is the rut vocalization characteristic of wapiti (Feighny *et al.* 2006), was never distinguished in any of the vocalizations recorded. Instead, during our study period, which fell during the rut peak (Smith-Flueck, unpublished data), the common roar was the most frequently produced vocalization. Harsh roars during this time period were mainly observed in agonistic interactions between stags and alternated with common roars.

Reby and McComb (2003b) described two types of barks distinguished by their behavioural context: the isolated bark, or single bark, which is directed to a stationary female and the serial bark, which corresponds to the chase bark and is emitted by stags when chasing a female or a competitor. In addition, in the Nahuel Huapi population, the single bark has been observed in males in cases such as (i) when trying to get a stationary female in his harem to move, and (ii) when suddenly faced with an

unknown disturbance. The chase bark is frequently used by a territorial male chasing a juvenile male out of his territory (Smith-Flueck, unpublished data).

Common roars are the vocalization most used in previous acoustical and statistical analyses (McComb 1987, Reby *et al.* 2001, Reby and McComb 2003a, Charlton *et al.* 2007, Charlton *et al.* 2008, Reby *et al.* 2010). Bouts of common roars permit individual identification (Reby *et al.* 2006). The application of source-filter theory to red deer common roars showed that minimal formant frequency dispersion in general is negatively correlated with body size and thus an honest indicator of fighting ability (Reby and McComb 2003a; Reby *et al.* 2005). In red deer, minimal formant frequency dispersion is also a good indicator of age (decreasing with age) and is positively correlated with reproductive success (Reby and McComb 2003a). During the emission of the common roar, the stag raises its head and stretches its neck, inducing a descent of the larynx, which decreases the spacing between the formants (ΔF), the minimal formant frequencies, and increases the VTL.

We found that the 4 males with the lowest ΔF and the longest calculated VTLs were the only identified males holding harems, which is in agreement with the findings of Charlton *et al.* (2007). Using playbacks of common roars re-synthesized to indicate longer VTLs and thus larger body size, those authors determined that hinds prefer males whose roars have formants with lower minimum frequency dispersion and ΔF . Another study of male behaviour during the rut on this same Nahuel Huapi population showed only males of larger body mass and antlers with a greater number of points defending and holding territories and females who chose to remain in those territories (Smith-Flueck and Flueck 2006).

In our data, the male with the lowest F0 is not the male with the highest value of VTL (and therefore largest body size), because F0 is not a good indicator of body size (Reby and McComb 2003a). Although mean F0 and male quality are not correlated, F0 is higher in the roars of subadults than adult stags (Reby and McComb 2003a) and thus potentially can act as an additional cue to the maturity of the stags (Charlton *et al.* 2008). Recent studies have also found that estrous red deer hinds prefer stags with higher F0s, so that sexual selection could be acting to raise the F0 (Reby *et al.* 2010). The mean values of F0 for our population (Table 1) are higher than the values obtained previously for adult males (7-13 years old) and closer to the values for subadult red deer (5-6 years old, Reby and McComb 2003a).

These results show that an exotic European red deer population separated from Europe for over a century has vocalization patterns almost indistinguishable from native red deer. The fact that the F0s observed in the Patagonian red deer are somewhat higher than those observed in the red deer from Rhum (Reby and McComb 2003a) may indicate a genetic influence of wapiti on the roars, given that Patagonian red deer do have some wapiti genetic markers (Flueck and Smith-Flueck 2011). Wapiti, however, have much higher F0s (0.41-1.9 kHz) (Feighny *et al.* 2006). Although wapiti have also been introduced in the past two centuries to Great Britain (Whitehead 1982), deer from the Scottish highlands were shown to have little introgression of haplotypes from wapiti when analysing a paternally inherited genetic marker on the Y chromosome (Pérez-Espona *et al.* 2010), indicating that exotic wapiti there seem to have had little impact on the genetic make-up of the Scottish Highland red deer. In contrast, we might explain the notably stronger wapiti influence on the genetic make-up of the Nahuel Huapi population by the fact that the founder population started with 20 individuals that likely had a high genetic make-up of wapitoid species, reflecting the history of numerous wapiti introductions to Austria. Also with few founders in Patagonia, substantial dilution over the past century would not be expected.

Another explanation for the higher F0s in the calls of the Patagonian red deer might be related to the different mating strategies utilized, which in turn could be influenced by environmental factors (Carranza *et al.* 1995). The dominant males of this study population display territoriality (Smith-Flueck and Flueck 2006) in contrast to prime males in Scotland defending mobile harems (Clutton-Brock *et al.* 1982). Factors that alone or in combination could affect mating strategies include habitat quality, population density, sex and age composition, and genetic make-up of the population.

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Figure 1. Spectrogram of calls [(a) bout of common roars, (b) bout of harsh roars (c) bout of chase barks] recorded during the rut in Patagonian red deer.
Spectrogram from RavenPro

